

DISSERTATION

DENSITY, DEMOGRAPHY, AND SEASONAL MOVEMENTS OF SNOWSHOE  
HARES IN CENTRAL COLORADO

Submitted by

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## ABSTRACT

### DENSITY, DEMOGRAPHY, AND SEASONAL MOVEMENT OF SNOWSHOE HARES IN CENTRAL COLORADO

Snowshoe hares (*Lepus americanus*), their famous 10-year population cycle, and close association with Canada lynx (*Lynx canadensis*) have been well-studied in boreal Canada for decades. Snowshoe hare range, however, extends south into the Sierra Nevada, Southern Rockies, upper Lake States, and Appalachian Mountains. Ecology of snowshoe hares in these more southerly regions is not as well understood, though hare research in the U.S. Rocky Mountains has accelerated over the past decade. Through this recent work, biologists have identified stands of young, densely-stocked conifers and those of mature, uneven-aged conifers as primary hare habitat in the region. Both stand types are characterized by dense understory vegetation that provides both browse and protection from elements and predators.

From 1999 to 2006, Canada lynx were reintroduced into Colorado in an effort to restore a viable population to the southern portion of their former range. Snow tracking of released individuals and their progeny indicated that the majority of lynx winter diet in Colorado was comprised of snowshoe hares. Thus, long-term success of the lynx reintroduction effort hinges, at least partly, on maintaining adequate and widespread populations of snowshoe hares in the state.

To improve our understanding of snowshoe hare ecology in the southern portion of their range, and enhance the ability of agency personnel to manage subalpine landscapes for snowshoe hares and lynx in Colorado, I conducted an observational study to evaluate purported primary hare habitat in the state. Specifically, I estimated snowshoe hare density, survival, recruitment, and movement indices in mature, uneven-aged spruce/fir (*Picea engelmannii*/*Abies lasiocarpa*) and 2 classes of young, even-aged lodgepole pine: 1) “small” lodgepole pine (*Pinus contorta*) stands, which were clear cut 20–25 years prior to this study and had regenerated into densely stocked stands with trees 2.54–12.69 cm in diameter, and 2) “medium” lodgepole pine stands (tree diameter = 12.70–22.85 cm) which were clear cut 40–60 years prior to this study and pre-commercially thinned ~20 years prior. I used a combination of mark-recapture and radio telemetry to estimate parameters. I sampled during both summer and winter to cover the range of annual variation in parameters.

Animal density is one of the most common and fundamental parameters in wildlife ecology and was the first metric I used to evaluate the stand types. However, density can be difficult to estimate from mark-recapture data because animals move on and off of a trapping grid during a sampling session (i.e., lack of geographic closure). In Chapter 1, I developed a density estimator that uses ancillary radio telemetry locations, in addition to mark-recapture information, to account for lack of geographic closure resulting in relatively unbiased estimates of density. I derived the variance for this estimator, showed how individual covariates can be used to improve its performance, and provided an example using a subset of my snowshoe hare data.

In Chapter 2, I completed a series of simulations to test the performance of this “telemetry” estimator over a range of sampling parameters (i.e., capture probabilities, sampling occasions, densities, and home range configurations) likely to be encountered in the field. I also compared the percent relative bias of the telemetry estimator to two other commonly used, contemporary estimators: spatially explicit capture-recapture (SECR), and mean maximum distance moved (MMDM). The telemetry estimator performed best over most combinations of sampling parameters tested, but was inferior to SECR at low capture probabilities. The telemetry estimator was unaffected by home range configuration, whereas performance of SECR and MMDM was dependent on home range shape.

Density is an important metric of habitat quality, but it can be misleading as some habitats with high animal density may function as population sinks. A complete assessment of habitat quality requires estimation of habitat-specific demographic rates in addition to density. In Chapter 3, I used the telemetry estimator to estimate snowshoe hare densities in each stand type during summer and winter, 2006–2009. I then combined mark-recapture and telemetry data to estimate survival via the Barker robust design model as implemented in Program MARK. Finally, I used age- and habitat-specific density and survival estimates to estimate recruitment in each stand type. During summer, hare densities were highest in small lodgepole ( $0.20 \pm 0.01$  (SE) to  $0.66 \pm 0.07$  hares/ha), lowest in medium lodgepole pine ( $0.01 \pm 0.04$  to  $0.03 \pm 0.03$  hares/ha), and intermediate in spruce/fir ( $0.01 \pm 0.002$  to  $0.26 \pm 0.08$  hares/ha). During winter, densities became more similar among the 3 stand types. Annual survival was highest in spruce/fir ( $0.14 \pm 0.05$  (SE) to  $0.20 \pm 0.07$ ) and similar among the 2 lodgepole stands types ( $0.10 \pm$

0.03 to  $0.16 \pm 0.06$ ). Across stands, summer-winter survival was nearly twice as high as winter-summer survival. Recruitment of juvenile hares occurred during all 3 summers in small lodgepole stands, 2 of 3 summers in spruce/fir stands, and in only 1 of 3 summers in medium lodgepole. Stand attributes indicative of dense cover were positively correlated with density estimates and explain relatively more process variance in hare densities than other attributes. These same attributes were not positively correlated with hare survival.

In addition to density and demography, movement is an informative aspect of animal ecology. Timing, extent, and frequency of movements can reflect predation pressure, food scarcity/abundance, availability of mates, or seasonal changes in any of these parameters. In Chapter 4, I used telemetry data to assess movement patterns of snowshoe hares at 2 scales (within-season, between-season) in all 3 stand types. Within-season movements of hares were larger during winter than during summer and tended to be larger in small lodgepole stands. Within-season movements of males tended to be larger than females during summer, possibly as a means of maximizing mating opportunities. Movements were similar between the sexes during winter. Hares in both small and medium lodgepole stands tended to make larger movements between seasons than hares in spruce/fir stands, possibly reflecting the variable value of these stands as mediated by snow depth.

In summary, snowshoe hare density, survival, and recruitment were relatively low in thinned, medium lodgepole stands compared to spruce/fir or small lodgepole. Thus, while hares occur in these stands, they do not appear to be capable of supporting self-sustaining hare populations, and this stand type is probably less important than mature

spruce/fir and small lodgepole stand types. Management for snowshoe hares (and lynx) in central Colorado should focus on maintaining the latter. Given the more persistent nature of spruce/fir compared to small lodgepole, and the fact that such stands cover considerably more area, mature spruce/fir may be the most valuable stand type for snowshoe hares in the state.

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## CHAPTER 1

### USING TELEMETRY TO CORRECT FOR BIAS: AN APPROACH TO ESTIMATING DENSITY FROM TRAPPING GRIDS

**Abstract.** I formalize a method for estimating density from trapping grids using radio telemetry to correct for bias induced by lack of geographic closure. To implement the method, animals are captured and radio-tagged during a traditional live-trapping session. Immediately following the session, traps and bait are removed from the site and the investigator uses telemetry to estimate the proportion of locations within the former grid for each animal. I use a traditional Huggins (1989, 1991) estimator to model capture probability for each individual ( $p_i^*$ ) as a function of time, behavior, heterogeneity, and/or pertinent individual covariates. I define a second parameter ( $\tilde{p}_i$ ) as the estimated proportion of locations on the trapping grid for each individual based on telemetry. The summation of  $1/p_i^*$  across all captured individuals gives an estimate of the super population of animals that could have used the grid during the sampling session (i.e., abundance estimate without geographic closure). Replacing the numerator in the summation with estimates of  $\tilde{p}_i$  corrects the abundance estimate to reflect only the estimated “whole” and “partial” animals residing on the sampling grid. This quantity can then be divided by the area of the sampling grid to obtain an unbiased estimate of density, accounting for lack of geographic closure. I present variations of the estimator to accommodate cases when only a subset of captured animals can be radio-tagged.

Contrary to other traditional and contemporary approaches, this method is free from assumptions concerning home range stationarity, or immigration into the grid induced by baited traps.

**Key Words.** *density; closure; geographic closure; trapping grid; telemetry; temporary immigration.*

## **1.1 INTRODUCTION**

Estimation of animal density is fundamental to wildlife ecology. It is used to evaluate system responses to environmental perturbations and treatments (Converse et al. 2006b, Manning and Edge 2008), it can function as a benchmark for listed species recovery (U. S. Fish and Wildlife Service 1998), it can be useful for understanding system dynamics (Soule et al. 2003), or assessing habitat suitability for dependent species (Zahratka and Shenk 2008), and it is routinely used in population monitoring and modeling (Thompson et al. 1998). Ecologists often pursue density estimates using grids of detectors to sample animals. However, under such a sampling framework reliable estimates can be difficult to obtain due to two fundamental challenges inherent in sampling wildlife.

First, abundance can rarely be measured directly due to imperfect detection of animals. Fortunately, mark-recapture methods have advanced considerably over the past several decades and a well-developed literature now exists for estimating abundance using a variety of “closed-capture” models that account for imperfect detection (Otis et al. 1978, White et al. 1982, Huggins 1989, 1991, Williams et al. 2002). These models do, however, assume the population of interest is closed both demographically (i.e., no births, deaths, immigration, emigration) and geographically (i.e., no movement on or off the

sampling unit) during the sampling session (Otis et al. 1978, Williams et al. 2002). Short sampling sessions appropriately timed with the natural history of the species of interest can ensure achievement of demographic closure. Outside of a few exceptions (e.g., sampling small islands, ponds), geographic closure is unlikely in most applications (White et al. 1982).

Lack of geographic closure is the second fundamental challenge associated with density estimation using grids. Animals that reside near the edge of a grid can move off and on during the sampling session, and animals naturally residing outside the grid may make temporary forays to take advantage of baited traps (White et al. 1982, Williams et al. 2002, Royle and Dorazio 2008 p. 225, 242). As a result, abundance estimates obtained from closed capture models rarely reflect the number of animals on a grid, but rather the “super population” of animals that could have used that grid at any time over the course of the sampling period (Schwarz and Arnason 1996, Kendall et al. 1997). Intuitively, this super population occupies the grid plus some area of unknown size around the grid (Williams et al. 2002). Because the “effective area” over which the animals were sampled is unknown, it is not clear how to convert abundance to density.

Ecologists have struggled with geographic closure since its recognition decades ago (Dice 1938). Initial efforts to address the issue focused on estimating the effective area sampled, (i.e., the area containing the super population), and a variety of techniques were used to estimate the distance by which the grid should be buffered ( $w$ ) in order to encompass the area used by animals available for capture on the grid. Some techniques assigned  $w$  based on estimated home range size or maximum movements obtained from trapping data (e.g., Dice 1938, Wilson and Anderson 1985b). Others estimated  $w$  by



exploiting relationships between capture rates or abundance estimates obtained from inner traps vs. those obtained from outer traps of the grid (e.g., MacLulich 1951, Hansson 1969, Otis et al. 1978). Still others employed “assessment lines” where, post-sampling, extra trap lines radiating outward from the grid were sampled, and the ratio of marked to unmarked animals captured along these lines was used to delineate the reach of the initial trapping effort (e.g., Smith et al. 1971, Van Horne 1982). Most of the myriad of approaches encompassed in these broad categories have fallen out of favor due to logistical problems with implementation, unrealistic data requirements, or ad hoc rather than theoretical foundations (Tanaka 1980, Anderson et al. 1983, Thompson et al. 1998 p. 308, Williams et al. 2002 p. 314, Efford 2004). A notable exception is the method based on mean maximum distance moved between trapping events (Otis et al. 1978, Wilson and Anderson 1985b), which has received criticism as an ad hoc approach (Williams et al. 2002, Royle and Dorazio 2008), but is still popular (Karanth and Nichols 1998, Trolle and Kery 2003, Converse et al. 2006a, Zahratka and Shenk 2008).

Spatially explicit capture-recapture (SECR) and trapping webs are two contemporary density estimation approaches that circumvent the difficulties of estimating the effective area trapped by estimating density directly. The population parameter of interest for SECR is density of home range centers rather than abundance, and detection is represented by a sub-model (rather than single parameter) as a declining function of the distance from the home range center of an individual to each trap in the grid (Efford 2004, Borchers and Efford 2008, Royle and Dorazio 2008). Trapping webs consist of an array of traps equally spaced along “spokes” radiating out from a “hub” such that traps form concentric circles with outer rings of traps occurring at a lower density than inner

traps. With this design, the principles of point-transect distance sampling or geometric analysis can be employed to estimate animal density (Anderson et al. 1983, Link and Barker 1994).

Trapping webs have been tested via simulation and field trials and have performed well (Wilson and Anderson 1985a, Parmenter et al. 1989, Parmenter et al. 2003). SECR has not received the same level of testing, but seems promising. Both approaches suffer from drawbacks that may preclude their use in some situations. First, both require that home ranges are stationary during the sampling session; individuals are not allowed to make “unnatural” forays from their home range into the grid (but note that a geometric analysis of trapping web data does not suffer this disadvantage). This may be an unreasonable assumption if bait is used in the sampling process. Trapping webs generally require a large number of traps, and cover a relatively larger area than conventional trapping grids, which can be logistically challenging. SECR assumes animals are distributed in Poisson fashion across the landscape. Finally, neither SECR nor trapping webs can currently make use of ancillary telemetry information to delineate animal movements relative to the grid.

Here I formalize a density estimator that addresses geographic closure by using auxiliary telemetry data. My method allows home range shifts or irregular movements induced by sampling. Conceptually, the approach can be traced to the idea of estimating fractions of animals or “animal equivalents” within an area as described by Marten (1972), and later Boutin (1984). I describe the basic form of the estimator, which is similar to that proposed by White and Shenk (2001) and implemented by Grant and

Doherty (2007), then extend it to allow for individual covariates and to admit more useful designs. I then apply the estimator to an example for illustration.

## **1.2 ESTIMATOR**

Conceptually, I begin with the notion that each animal occupies some defined area on the landscape, and these areas occur irrespective of the boundaries of a sampling grid (Figure 1). Some animals may occur completely within the grid, others partially overlap the grid, and still others may occupy areas completely outside the grid. During a sampling session, individuals are captured, marked, and released on multiple occasions. Note that if the sampling device is baited traps, animals that normally occupy areas completely outside the grid may make unusual movements to take advantage of bait, and they can become part of the mark-recapture dataset.

To implement the method, I radio-tag animals captured during a trapping session. Immediately following the session, I remove traps and bait from the site and collect a sample of locations from each radio-tagged individual, recording the proportion of those locations on the area formally occupied by the grid (Figure 1). I use traditional mark-recapture estimators to estimate the super population of animals that used the grid during sampling. I then use telemetry to estimate the portion of the super population (i.e., total animal equivalents) that occurred within the boundaries of the grid. This quantity divided by the area of the grid is an unbiased estimate of density corrected for the lack of geographic closure. Put differently, I start with the super population estimate derived from conventional closed-capture methods then disregard those animals completely off of the grid, partially discount edge animals, then tally the whole animals and partial animals left before dividing by the grid area. In order to work well, practitioners should ensure

that telemetry location error is small relative to the size of the grid. Also, the telemetry sampling scheme should be appropriate for the species of interest such that locations can be assumed to be independent and representative of how animals use their home range.

Mathematically, I construct the estimator based on the Huggins (1989, 1991) closed capture estimator for abundance :

$$\hat{N}_s = \sum_{i=1}^{M_{t+1}} \frac{1}{p_i^*}$$

where  $\hat{N}_s$  is the super population of animals that could have used the grid during the trapping session,  $p_i^*$  is the probability animal  $i$  is captured one or more times during the trapping session (i.e., if  $p_i$  is the probability animal  $i$  is captured on any given occasion,  $p_i^* = 1 - (1 - p_i)^n$ , where  $n$  is the number of occasions), and  $M_{t+1}$  is the total number of animals captured. Note that  $p_i^*$  can be modeled using individual-specific covariates. I recommend considering “distance to edge of the grid” (DTE) based on the mean capture location for each individual as one such covariate. Presumably individuals near the edge of the grid have fewer traps in their home range and a diminished probability of capture compared to animals captured near the center of the grid. The DTE covariate accounts for this heterogeneity.

Next, I make a substitution in the numerator of the Huggins estimator:

$$\hat{N}_g = \left( \sum_{i=1}^{M_{t+1}} \frac{\tilde{p}_i}{p_i^*} \right)$$

where  $\tilde{p}_i$  is the proportion of time animal  $i$  spent on the area formally covered by the grid (estimated via tracking of radio tags) and  $\hat{N}_g$  is now the estimated sum of the portions of animals on the grid. Note that animals trapped on the grid, but never located on the

former grid area again are assigned  $\tilde{p}_i = 0$ , and thus do not contribute to the density estimate. Those individuals that are always located on the former grid area contribute fully to the density estimate and are assigned  $\tilde{p}_i = 1$ . All other individuals receive a fractional  $\tilde{p}_i$  and partially contribute to density.

Finally, I divide  $\hat{N}_g$  by the area of the trapping grid in order to obtain an estimate of density:

$$\hat{D} = \left( \sum_{i=1}^{M_{t+1}} \frac{\tilde{p}_i}{p_i^*} \right) / A$$

where  $\hat{D}$  is density (number of animals per unit area),  $A$  is the area of the trapping grid, and  $\tilde{p}_i$ ,  $p_i^*$ , and  $M_{t+1}$  are as defined previously.

### 1.3 VARIANCE

For the simple case where  $\tilde{p}$  is estimated directly from telemetry data as an overall “mean proportion on grid” across individuals and no individual covariates are used, the estimator reduces to

$$\hat{D} = \left( M_{t+1} \cdot \frac{\tilde{p}}{p^*} \right) / A$$

and variance of  $\hat{D}$  can be approximated using the delta method (Seber 1982 p. 7) as

$$\text{Var}(\hat{D}) = \hat{D}^2 \left( \frac{(1 - p^*)}{M_{t+1}} + \frac{\text{Var}(\tilde{p})}{\tilde{p}^2} + \frac{\text{Var}(p^*)}{p^{*2}} \right)$$

where  $(\tilde{p})$  is assumed binomial (i.e., estimated  $\text{Var}(\tilde{p}) = \tilde{p}(1 - \tilde{p})/M_{t+1}$ ),  $\text{Var}(p^*)$  is estimated from the Huggins estimator (Huggins 1989, 1991), estimates of  $\tilde{p}$  and  $p^*$  are substituted for the true parameter values, and  $\hat{D}^2$  and  $M_{t+1}$  are as defined previously.

However, I expect the use of individual covariates to be common and desirable. In such

cases, the delta method approximation is much more complex, and analytic solutions are possible but not practical. Numerical approximations are much more tractable and I provide guidance for this approach in Appendix A.

#### **1.4 ASSUMPTIONS**

Assumptions for this estimator include the usual closed mark-recapture assumptions (Otis et al. 1978, Williams et al. 2002) as well as 3 additional assumptions specific to this method:

- 1) Individually identifiable marks are not lost during the sampling session.
- 2) All marks are recorded correctly during each sampling occasion.
- 3) The population is demographically closed such that no birth, death, immigration, or emigration events occur during the sampling session. Note that violations to geographic closure (i.e., temporary movements on and off the sampling grid) are allowed.
- 4) The radio-tagged sample is representative of the population of animals that use the grid.
- 5) There is no difference between the pre-trapping and post-trapping distribution or movement patterns of radio-tagged animals (i.e., radio tags do not effect movements and there are no lingering effects of trapping on animal movements).
- 6) Telemetry location error is small relative to the size of the grid and assignment (on/off) of locations near the edge of the grid is unbiased.

#### **1.5 USEFUL VARIANTS**

It may not be possible to radio-tag all individuals captured during a sampling session. In such cases, the estimator described above can be modified to model the use of

the grid area by individuals that were captured and marked, but not radio-tagged. Specifically one can estimate  $\tilde{p}_i$  by fitting a logistic model to the data from radio-tagged animals, then applying this model to untagged animals to predict their equivalent. Again, I suggest DTE as the main covariate in such a model to account for heterogeneity induced by location of individuals relative to the grid. Multiple candidate models can be formulated and compared using an information theoretic approach such as  $AIC_c$  (Burnham and Anderson 2002). For example, if sampling multiple grids and/or multiple sessions, grid effects, session effects, as well as habitat characteristics, and environmental covariates can be considered along with an “intercept only” model, which simply assigns each untagged individual the mean proportion-on-grid calculated across all tagged animals.

In most cases, the sampling grid is designed to be large enough to encompass numerous activity ranges of the target species. In these instances, the (DTE) covariate is only important for mean capture locations relatively near the edge of the sampling grid. Activity ranges that are fully “on grid” expose animals to an equal number of traps regardless of whether the range is just inside the grid or exactly in the middle. Thus, it may also be useful to consider a “threshold model” for the estimation of  $\tilde{p}_i$  and/or  $p_i^*$  such that the DTE covariate is only operational up to a point, after which animals are “on grid” and the proportion or capture probability is estimated accordingly. Mathematically, threshold models are represented as

$$\text{logit}(\tilde{p}_i) = \beta_0 + \beta_1(\min(\beta_2, \text{DTE}))$$

where  $\beta_0$  and  $\beta_1$  are the usual intercept and slope terms for a logistic model using distance to edge as a covariate, and  $\beta_2$  is the threshold parameter.

## 1.6 EXAMPLE

I trapped snowshoe hares (*Lepus americanus*) in central Colorado during August 11–15, 2006 using a 6×7 trapping grid with 50-m spacing. I captured 14 adult-sized hares 25 times during the 5-day sampling session (Colorado State University IACUC Protocol 06-062A-03). Of these, 8 were fitted with 28-g radio collars (Model TW5SM, BioTrack, LTD, Wareham, Dorset, United Kingdom). Traps and bait were removed following trapping on August 15. Telemetry sampling commenced on August 17 and occurred daily through August 30. I obtained locations via triangulation at relatively close range (within 250m), resulting in accuracy of  $\pm 60\text{m}$ . Hares were alternately sampled during nighttime (active) and daytime (resting) hours to obtain a representative sample of locations. I obtained 5.7 locations/individual during daytime and 4.7 locations/individual at night. There was significant movement on and off the grid during the telemetry sampling period, and one hare was never located on the grid (Fig. 2).

I used the Huggins estimator (Huggins 1989, 1991) in Program MARK (White and Burnham 1999) to model  $p_i$  using both a simple mean (intercept only) model and a second model including the DTE covariate. I compared similar models for  $\tilde{p}_i$  using PROC LOGISTIC in SAS (Version 9.2, SAS Institute Inc., Cary, NC, USA). In both cases,  $\text{AIC}_c$  selected the DTE model ( $\text{AIC}_c$  weight = 0.99 in both cases). I calculated  $p_i^*$  and  $\tilde{p}_i$  for each individual using parameter estimates from the selected models, summed  $\tilde{p}_i/p_i^*$  across all individuals as described above, then divided by the area of the grid to arrive at a corrected density estimate ( $\pm\text{SE}$ ) of  $1.99 \pm 1.16$  hares/ha (Table 1). Note that failing to account for lack of geographic closure results in a naïve density estimate ( $\hat{N}/A = 5.07$  hares/ha) that is 155% of the telemetry-corrected value.



## 1.7 DISCUSSION

The estimator presented here has several advantages over other traditional and contemporary density estimation techniques. First, it does not require estimation of a buffer strip using ad hoc approaches. Second, it is free from the assumption that animals occupy a stationary home range during the sampling period and do not make forays into the baited grid. Third, implementation of the telemetry estimator can generally be accomplished with far fewer traps and in much smaller patches than can web-based distance sampling approaches. Fourth, it allows users to make full use of ancillary telemetry locations. Finally, the estimator is intuitive and relatively easy to implement.

A disadvantage is that purchasing and sampling radio tags, in addition to the required mark-recapture sampling, is likely cost-prohibitive when the only goal is density estimation. However, practitioners routinely apply radio tags for home range estimation, quantification of habitat use, and/or survival estimation at the same time they obtain density estimates. In fact, many authors (e.g., Di Betti et al. 2006, Soisalo and Cavalcanti 2006, Dillon and Kelly 2008, Balme et al. 2009, Sharma et al. 2010,) have used location data to correct mark-recapture density estimates by first calculating average home range size for animals in the study, then applying a buffer to their sampling grid based on this home range estimate. I suggest that a better use of these location data to correct density estimates would be the more direct approach outlined in this paper. GPS technology provides an excellent opportunity to implement this approach as potentially more locations can be collected with better precision but without the additional cost of physically sampling the collars after deployment.

I presented an example from a single sample unit laid out in a regular grid, but other designs are possible. Traps can be set in virtually any configuration as long as a) the distance between neighboring traps remains roughly equal, and b) the inter-trap distance is such that several traps are likely to occur within a single home range of the species of interest. Also, data from several grids can be pooled so that researchers can use model selection procedures to determine whether  $\tilde{p}_i$  and  $p_i^*$  can be modeled in common across grids, years, habitat types, etc., or whether additive offsets are appropriate, or whether each should be modeled separately (e.g., Grant and Doherty 2007). Potentially large gains in precision can be realized when combining information across sample units.

In my example, I obtained about 10 locations per individual to estimate proportion on grid. Presumably, estimator performance improves with additional locations up to some asymptote. However, simulations suggest that performance of the estimator is more sensitive to sampling error among individuals than sampling error within individuals. Thus, relative bias can be minimized more efficiently by sacrificing number of locations/individual in favor of radio-tagging more individuals (See Chapter 2). For example, the estimator is likely to be less biased when 100% of the captured animals are radio-tagged and only 5 locations are obtained per animal than when 25% are collared and 20 locations per animal are obtained.

Unique assumptions of this estimator include 1) post-sampling movements of radio-tagged individuals are reflective of their pre-sampling movements, and 2) the sample of radio-tagged animals should represent the population of animals that use the grid. Sound design can assist in meeting these assumptions. With respect to the first

assumption, it is imperative that researchers remove all bait at the end of the trapping session so there is no unnatural attractant to influence movements. Also, it may be appropriate to wait 1–2 days post-trapping before collecting location data to allow animals to revert to their “normal” activity patterns. However, telemetry sampling should be completed within a reasonable time after trapping to avoid biasing estimates of  $\tilde{p}_i$  due to seasonal movements, migration, or dispersal.

If the study design requires radio-tagging a subset of the animals captured during a traditional live-trapping session, one can help assure that radio-tagged individuals are representative of the population of interest by checking traps from a random starting point on each occasion. Following this strategy, interior animals and edge animals would be equally likely to be radio-tagged, on average. In addition, holding back some radio tags for deployment during the latter half of a sampling session can facilitate the inclusion of trap-shy individuals in the radio-tagged sample in addition to trap-happy individuals that are captured early and often. Despite these design features, it is plausible that the sample of radio-tagged individuals could be biased toward those with a higher proportion of their range on the grid as they presumably stand a better chance of capture on any occasion. This phenomenon would inflate the numerator ( $\tilde{p}_i$ ) of the estimator, resulting in a positively biased density estimate. However, animals with a greater portion of their range on the sampling grid should also have a higher capture probability ( $p_i^*$ ) which would inflate the denominator of the estimator and functionally cancel out the bias to a degree. Simulations to assess the performance of the estimator indicate that it is relatively unbiased compared to other estimators, although it tends to exhibit positive bias when capture probability is low, possibly due in part to this phenomenon (See Chapter 2).

Density is a fundamental parameter used in a variety of contexts in the field of ecology. Here I described an intuitively appealing method for estimating animal density from trapping grids. The method accounts for lack of geographic closure using ancillary information and makes no assumptions about stationarity of home ranges during trapping sessions. It can be easily implemented in the field, especially within studies where radio-tags are already deployed for other purposes. Additionally, the method can now be fully implemented within Program MARK ("Density with Telemetry" data type) to obtain estimates and associated sampling variances (White and Burnham 1999).

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Table 1. Calculation of density using radio telemetry locations to correct for bias. Data are individual snowshoe hares (*Lepus americanus*,  $n = 14$ ) trapped in central Colorado on a 7.5-ha grid, August 2006.

Hare	DTE (m)	$p_i$	$p_i^*$	$\tilde{p}_i$	$\frac{\tilde{p}_i}{p_i^*}$
1	50.0	0.34	0.87	0.53	0.61
2	40.0	0.24	0.75	0.49	0.66
3	50.0	0.34	0.87	0.53	0.61
4	100.0	0.84	1.00	0.71	0.71
5	0.0	0.05	0.21	0.34	1.61
6	0.0	0.05	0.21	0.34	1.61
7	0.0	0.05	0.21	0.34	1.61
8	50.0	0.34	0.87	0.53	0.61
9	25.0	0.14	0.52	0.43	0.83
10	0.0	0.05	0.21	0.34	1.61
11	0.0	0.05	0.21	0.34	1.61
12	50.0	0.34	0.87	0.53	0.61

13	0.0	0.05	0.21	0.34	1.61
14	83.3	0.71	1.00	0.66	0.66
$\hat{N}_g$					14.92
$\hat{D}$					1.99
$\hat{N}_s$					37.99
$\hat{D}_{naive}$					5.07

DTE (m) = Distance from mean capture location of individual  $i$  to the edge of the grid

$$p_i = \frac{1}{1+e^{-(\alpha_0+\alpha_1 \cdot DTE_i)}}, \text{ where } \alpha_0 = -3.014 \text{ and } \alpha_1 = 0.047 \text{ as estimated from Program}$$

MARK

$$p_i^* = (1 - (1 - p_i)^5)$$

$$\tilde{p}_i = \frac{1}{1+e^{-(\beta_0+\beta_1 \cdot DTE_i)}}, \text{ where } \beta_0 = -0.654 \text{ and } \beta_1 = 0.016 \text{ as estimated from SAS}$$

$$\hat{N}_g = \sum_{i=1}^{M_{t+1}} \frac{\tilde{p}_i}{p_i^*} = \text{estimate of the number of hares on the grid corrected by telemetry}$$

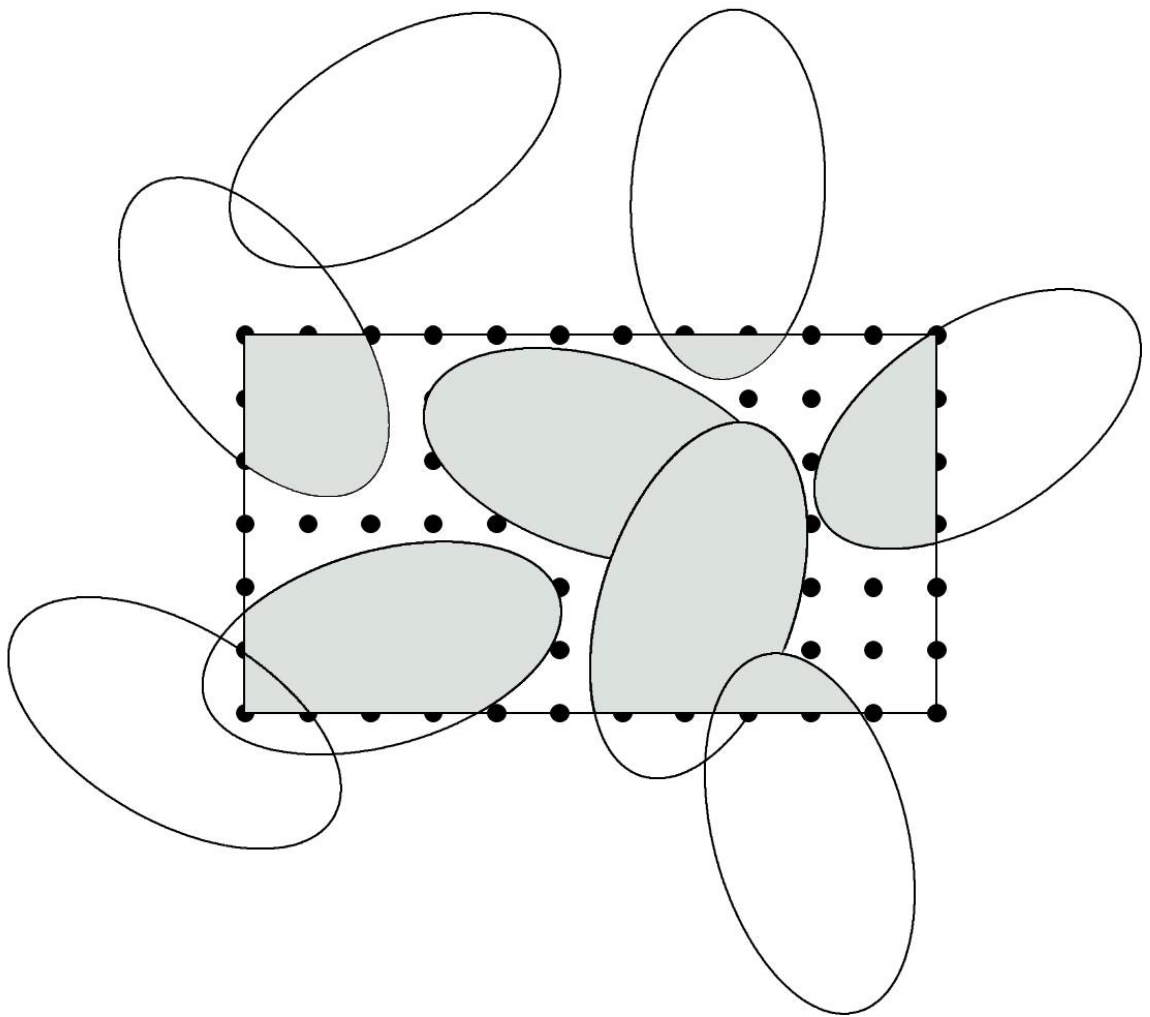
$$\hat{D} = \hat{N}_g / A = \text{corrected density estimate where } A = 7.5 \text{ ha}$$

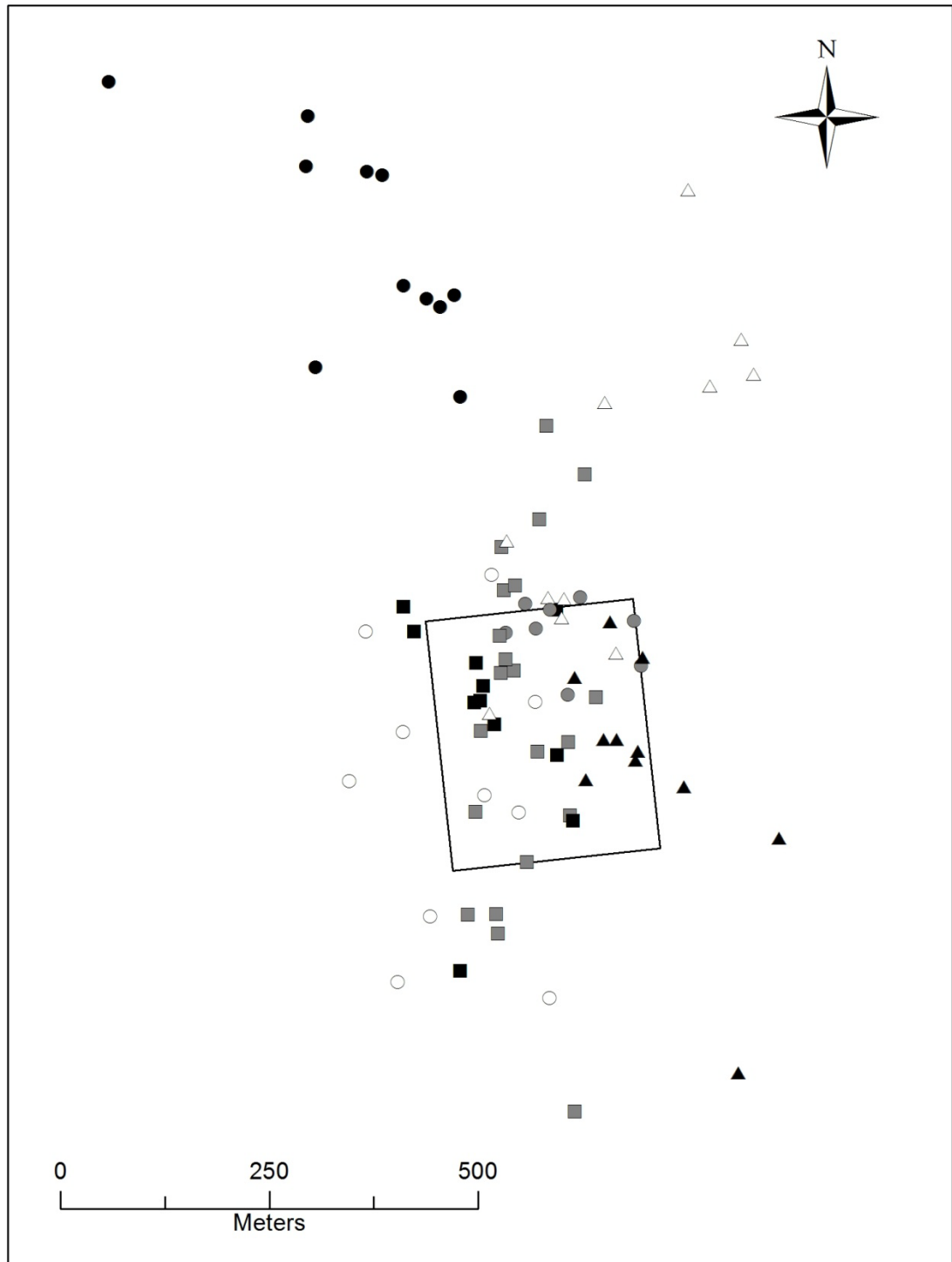
$$\hat{N}_s = \sum_{i=1}^{M_{t+1}} \frac{1}{p_i^*} = \text{estimate of the super population of hares that could have used the grid}$$

$$\hat{D}_{naive} = \hat{N}_s / A = \text{naïve density estimate based on super population and } A = 7.5 \text{ ha}$$

Figure 1. Conceptualization of animal activity ranges (ovals) overlaid on a hypothetical trapping grid. Lack of geographic closure results from some animal activity ranges being partially on the grid such that animals can move on and off the grid during a sampling session. The sum of the proportion of each animal on the grid (gray areas) divided by the grid area is an unbiased estimate of density. Note that activity ranges are depicted as equally-sized ovals for illustration only; the method makes no restrictions about home range shape or size.

Figure 2. Telemetry locations obtained on 8 snowshoe hares (*Lepus americanus*) previously trapped on a 7.5-ha grid (black rectangle) in central Colorado, August 2006. Different symbols indicate unique individuals. Locations were obtained during both day and night over a 13-day period immediately following trapping.





## 1.10 Appendix A

As described in the text, the basic forms of the estimator and its variance without individual specific covariates are:

$$\hat{D} = M_{t+1} \cdot \frac{\tilde{p}}{p^*} \cdot \frac{1}{A}$$

$$\text{Var}(\hat{D}) = \hat{D}^2 \left[ \frac{\text{Var}(M_{t+1})}{M_{t+1}^2} + \frac{\text{Var}(\tilde{p}/p^*)}{(\tilde{p}/p^*)^2} \right]$$

where  $\hat{D}$  is density (number of animals per unit area),  $M_{t+1}$  is the total number of animals captured during a sampling session,  $\tilde{p}$  is the proportion of time an animal spent on the trapping grid,  $p^*$  is the probability an animal is captured one or more times during the trapping session (i.e., if  $p$  is the probability an animal is captured on any given occasion,  $p^* = 1 - (1 - p)^n$ , where  $n$  is the number of occasions), and  $A$  is the area of the trapping grid.

However, I expect use of individual-specific covariates to be both helpful and common. To accommodate individual covariates the estimator becomes:

$$\hat{D} = \left( \sum_{i=1}^{M_{t+1}} \frac{\tilde{p}_i}{p_i^*} \right) / A$$

where  $\tilde{p}_i$  is the proportion of time animal  $i$  spent on the trapping grid,  $p_i^*$  is the probability animal  $i$  is captured one or more times during the trapping session, and other parameters are as defined above (i.e.,  $\tilde{p}_i$  and  $p_i^*$  can now be different for each individual).

Analytical solutions for variance of this individual-specific expression are complex. Approximate variance can be estimated more simply using numerical methods. To accommodate individual-specific covariates, make the following 3 substitutions for the appropriate quantities in  $\text{Var}(\widehat{D})$  above:

- 1) Assuming  $M_{t+1}$  is a binomial random variable,  $\text{Var}(M_{t+1})$  can be approximated by  $N^*p^*(1 - p^*)$ , where  $N^*$  is the number of animals actually using the grid and at risk of capture. The number of individuals captured ( $M_{t+1}$ ) is an estimate for  $N^*p^*$ , therefore:

$$\text{Var}(M_{t+1}) = M_{t+1}(1 - p^*)$$

However, if  $p^*$  is to be specific to each individual, the above expression is not appropriate. Instead:

$$\text{Var}(M_{t+1}) = \sum_{i=1}^{M_{t+1}} (1 - p_i^*)$$

- 2) Use the delta method approximation (Seber 1986 p. 7) to compute  $\text{Var}(\tilde{p}/p^*)$ :
  - a) Compute a  $(1 \times n)$  vector of approximate partial derivatives for each of the  $n$  parameters in the density expression (i.e., all parameters used to estimate both  $\tilde{p}_i$  [ $\beta_0, \beta_1, \dots, \beta_j$ ] and  $p^*$  [ $\alpha_0, \alpha_1, \dots, \alpha_j$ ]). To accomplish this, successively change (one at a time) each parameter ( $\beta_j$  or  $\alpha_j$ ) in the density expression  $(\widehat{D} = (\sum_{i=1}^{M_{t+1}} \tilde{p}_i/p_i^*)/A)$  by  $\Delta\beta_j$  (where  $\Delta$  is very small) and calculate the difference quotient  $([f(\beta_j + \Delta\beta_j) - f(\beta_j)]/\Delta\beta_j)$  for the density expression with each change. The value of the difference quotient at each step is the partial derivative for that parameter and becomes an element in the vector  $a$ .



$$a = \begin{bmatrix} \frac{\partial \widehat{D}}{\partial \beta_0} & \frac{\partial \widehat{D}}{\partial \beta_1} & \cdots & \frac{\partial \widehat{D}}{\partial \beta_i} & \frac{\partial \widehat{D}}{\partial \alpha_0} & \frac{\partial \widehat{D}}{\partial \alpha_1} & \cdots & \frac{\partial \widehat{D}}{\partial \alpha_i} \end{bmatrix}$$

- b) Assuming the partial derivatives for the  $\tilde{p}_i$  parameters ( $\beta_0, \beta_1, \dots, \beta_j$ ) appear first in the vector, the variance-covariance matrix ( $b$ ) for the density expression consists of the variance-covariance matrix of the  $\tilde{p}_i$  parameters in the upper-left quadrant and the variance-covariance matrix of the  $p_i^*$  parameters ( $\alpha_0, \alpha_1, \dots, \alpha_j$ ) in the lower-right quadrant. Remaining quadrants are populated by zeros. The variance co-covariance matrix for the  $\tilde{p}_i$  parameters is output from the statistical package used to compute the logistic regression. The parameters for  $p^*$  come from abundance-estimation software such as Program MARK (White and Burnham 1999).

$$b = \begin{bmatrix} \text{Var}(\beta_0) & \text{Cov}(\beta_0, \beta_1) & \text{Cov}(\beta_0, \beta_j) & 0 & 0 & 0 \\ \text{Cov}(\beta_1, \beta_0) & \text{Var}(\beta_1) & \text{Cov}(\beta_1, \beta_j) & 0 & 0 & 0 \\ \text{Cov}(\beta_j, \beta_0) & \text{Cov}(\beta_j, \beta_1) & \text{Var}(\beta_j) & 0 & 0 & 0 \\ 0 & 0 & 0 & \text{Var}(\alpha_0) & \text{Cov}(\alpha_0, \alpha_1) & \text{Cov}(\alpha_0, \alpha_j) \\ 0 & 0 & 0 & \text{Cov}(\alpha_1, \alpha_0) & \text{Var}(\alpha_1) & \text{Cov}(\alpha_1, \alpha_j) \\ 0 & 0 & 0 & \text{Cov}(\alpha_j, \alpha_0) & \text{Cov}(\alpha_j, \alpha_1) & \text{Var}(\alpha_j) \end{bmatrix}$$

- c) Multiply the vector of partial derivatives by the variance-covariance matrix then by the transpose of the vector of partials, such that:

$$\text{Var}(\tilde{p}/p^*) = a \cdot b \cdot a^T$$

- 3) Because  $\tilde{p}$  and  $p^*$  are specific to an individual:

$$(\tilde{p}/p^*)^2 = \left( \sum_{i=1}^{M_{t+1}} \tilde{p}_i/p_i^* \right)^2$$

The final expression for  $\text{Var}(\widehat{D})$  when using individual-specific covariates:

$$\text{Var}(\widehat{D}) = \widehat{D}^2 \left[ \frac{\sum_{i=1}^{M_{t+1}} (1 - p_i^*)}{M_{t+1}^2} + \frac{a \cdot b \cdot a^T}{(\sum_{i=1}^{M_{t+1}} \tilde{p}_i / p_i^*)^2} \right]$$

where  $\widehat{D}$  is the form of the estimator that allows for individual covariates.

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## CHAPTER 2

### COMPARISON OF METHODS FOR ESTIMATING DENSITY FROM CAPTURE–RECAPTURE DATA

**Abstract.** Estimation of animal density is fundamental to wildlife research and management. Contemporary methods for estimating density using mark–recapture data include 1) estimators that approximate the effective area sampled by a grid of detectors based on the mean maximum distance moved (MMDM) by animals during the sampling session, 2) spatially explicit capture–recapture (SECR) methods that formulate the problem hierarchically with a process model for animal density and an observation model in which detection probability declines with distance from a trap, and 3) telemetry estimators (TELEM) which use animal locations to estimate the total number of whole and “fractional” animals on the sampling grid. I used simulation to compare relative performance of these methods. First I held animal home ranges at a moderately complex configuration and examined estimator performance under a variety of conditions in which I varied capture probability, number of sampling occasions, and number of animals released into the simulation (i.e., true density). Next, I held these latter parameters at an intermediate level, and varied home ranges from regular to irregular shapes to examine the influence of this factor on estimator performance. I used percent relative bias as the primary assessment of estimator performance and found variations of TELEM (especially those in which  $\geq 75\%$  of captured animals are radio–tagged) performed best across most

combinations of capture probabilities, sampling occasions, true densities, and home range configurations. Performance of TELEM was largely unaffected by the number of locations obtained per radio-tag (5, 10, or 20). SECR outperformed MMDM estimators in nearly all comparisons and may be preferable to TELEM at low capture probabilities. However, MMDM performance improved dramatically, eclipsing that of SECR, given certain home range configurations. In general, estimator performance was most sensitive to changes in capture probability, followed by animal density and number of capture occasions; SECR was least sensitive to changes in these parameters and performed most consistently across the range of conditions tested. Estimated sampling variance of density estimates did not match well with empirically derived estimates for any of the estimators.

**Key Words.** *density; closure; geographic closure; mean maximum distance moved; simulation; spatially explicit capture–recapture; trapping grid; telemetry; temporary immigration.*

## 2.1 INTRODUCTION

Animal density is a fundamental parameter of interest in ecology, and practitioners often estimate density using mark–recapture techniques in conjunction with grids of live traps, cameras, hair snags, or other detection devices. Under such a sampling framework, estimates of animal abundance can be obtained using a variety of “closed–capture” models (Otis et al. 1978, White et al. 1982, Huggins 1989, 1991, Williams et al. 2002). These models assume no births, deaths, immigration, or emigration during the sampling period (i.e., the population is “closed” demographically) and that animals do not move on and off the grid during sampling (i.e., the population is closed geographically; Otis et al.

1978, Williams et al. 2002). Short sampling sessions appropriately timed with the natural history of the species of interest can ensure achievement of demographic closure.

However, outside of a few exceptions (e.g., sampling small islands or ponds), geographic closure is unlikely (White et al. 1982).

Without geographic closure, abundance estimates obtained through closed-capture models do not reflect the number of animals within the boundaries of the sampling grid. Rather, they reflect the “super population” of animals that could have used the grid at any time over the course of the sampling period (Schwarz and Arnason 1996, Kendall et al. 1997). Such estimates are difficult to convert to density because the area effectively trapped by the grid (i.e., the area used by the super population) is unknown.

The most common strategy for managing the geographic closure issue has been to attempt estimation of the effective area sampled by the grid, then divide this into the super population estimate obtained from closed capture models to obtain a corrected estimate of density. Usually the maximum distance moved by each individual during the sampling session, as revealed by capture events, is averaged across all individuals captured more than once, and the grid is buffered by this distance (or one-half this distance), to estimate the effective area sampled (Wilson and Anderson 1985). There are a number of concerns regarding this strategy: 1) movements of animals may be constrained by the trapping process itself, 2) movements of animals residing near the edge of the grid may not be well represented, 3) baited detectors (if used) may induce immigration into the grid or otherwise bias normal movement patterns, 4) movement distances revealed through capture events are dependent on the number of times an individual is re-captured, and 5) trap-spacing and grid size can influence movement

estimates (Parmenter et al. 2003). Despite these potential difficulties, the method has performed reasonably well in both simulations (Wilson and Anderson 1985) and field experiments (Parmenter et al. 2003) and is still widely used (e.g., Karanth and Nichols 1998, Trolle and Kery 2003, Zahratka and Shenk 2008, Balme et al. 2009, Tioli et al. 2009, Wang and Macdonald 2009, Sharma et al. 2010).

Recently, spatially explicit capture–recapture (SECR) techniques have been introduced to address lack of geographic closure (Efford 2004, Borchers and Efford 2008, Royle et al. 2009b). Like the MMDM approach, SECR makes use of information contained in the spatial capture history of each individual. However, the SECR approach does not attempt to estimate effective area sampled; rather, spatial information and movement distances are used to estimate parameters of an observation model in which detection probability declines as a function of the distance between an animal’s home range center and a given trap in the sampling grid. The density of home range centers is represented as a separate process model (usually a Poisson model) and the 2 sub–models are combined hierarchically such that density is estimated directly given the data (Efford 2004, Borchers and Efford 2008, Royle et al. 2009a, Royle et al. 2009b). Other than usual capture–recapture assumptions concerning demographic closure and accurate reporting of marks, the main assumptions of this method are that 1) individuals occupy stationary home ranges during the sampling session; home ranges do not shift in response to sampling, and 2) home range centers occur randomly on the landscape at a reasonably constant density (or at least varying in some way that can be modeled) according to a Poisson process. Estimation of the observation portion of the model is based on information from capture locations. Thus, this portion of the model may be susceptible to

some of the potential MMDM biases if movements and detection are unnaturally effected by the trapping process. Early versions of SECR (inverse prediction) performed well in simulation (Efford 2004) and field experiments (Efford et al. 2005). Currently SECR analyses can be accomplished using inverse prediction (Efford 2004), maximum likelihood (Borchers and Efford 2008) or Bayesian (Royle et al. 2009a, Royle et al. 2009b) approaches.

Ancillary radio–telemetry data has been suggested as yet another means to address geographic closure (Boutin 1984, White and Shenk 2001, See Chapter 1). With this method, captured animals are radio–tagged and monitored for a brief period immediately after sampling to estimate the proportion of time they spend on the sampling grid. These proportions are used to scale the super population estimate back to only those animals and “fractions of animals” that use the area of the sampling grid. The corrected super population estimate divided by the grid area provides a theoretically unbiased estimate of density. This approach is appealing because the process of interest (movement of animals on and off the grid) is sampled directly using telemetry rather than addressed via models and assumptions. Implementation requires more resources than either of the previous methods, which may preclude its use in some studies. However, radio tags are routinely deployed for other purposes (e.g., estimation of survival, habitat use), and density estimates could likely be obtained with little additional costs in such cases. Also, recent development of this estimator allows deployment of radio–tags on <100% of captured animals, which makes it more practical (See Chapter 1). The method makes no assumptions regarding stationary home ranges and allows temporary forays to the grid. It does assume, however, that 1) telemetry error is small relative to the size of

the grid, 2) the radio-tagged sample of animals is representative of all animals using the grid, and 3) there is no difference in the pre- and post-trapping distribution and movement of radio-tagged animals. Usual assumptions regarding demographic closure and retention of marks also apply.

These 3 classes of contemporary density estimators have yet to be formally compared against each other. Here I provide a simulation-based comparison to evaluate relative performance under a variety of sampling conditions, identify circumstances under which estimators are likely to fail, and identify the design features to which they are most sensitive. I hypothesized that 1) the telemetry estimator would generally perform best because it makes use of ancillary information about animal movement on and off the grid, which is unavailable to other estimators, and 2) in the absence of ancillary information, SECR would perform better than MMDM due to a more sound theoretical basis.

I use the terms TELEM, MMDM, and SECR to refer generally to the 3 classes of density estimators based on ancillary telemetry information, mean maximum distance moved, and spatially-explicit capture-recapture, respectively. Additional modifiers to these terms indicate a specific form of the estimator. For example, TELEM50 refers to the telemetry estimator where 50% of the captured animals received a radio-tag;  $\frac{1}{2}$  MMDM refers to estimates based on approximating effective area sampled as one-half of the mean maximum distance moved between trapping events; ML SECR references estimates from the maximum likelihood version of SECR.



## 2.2 METHODS

### 2.2.1 Simulation Specifications

The simulation arena consisted of a  $16 \times 16$  grid of cells in which I centered a  $10 \times 10$  trapping grid (Figure 1). An animal home range was initially simulated as a  $4 \times 4$  square randomly located within the arena. I created a utilization distribution within the home range by randomly assigning probability of use to each of the 16 cells comprising the home range under the constraint that the probabilities summed to one (i.e., each home range was a 16-cell multinomial distribution). This design departs from usual simulation procedures in which animals are typically assigned bivariate normal home ranges.

Although forcing animals to have square home ranges with “hard edges” beyond which they are not permitted may be unrealistic for some species, this approach allowed me to produce an array of uniform, unimodal, and multimodal utilization distributions within home range borders that more closely resemble utilization distributions constructed from real data (Figure 1).

Once the first animal was placed in the simulation arena and assigned a utilization distribution, I simulated a capture history for that individual. For the first capture occasion, I drew a uniform random number and compared it to the product of the capture probability specified for the simulation and the probability that the animal was on the grid (sum of probability of occurrence for all home range cells overlapping the trapping grid). Products less than the uniform random number resulted in a “capture.” Thus, animals with a larger proportion of their home range on the grid were more likely to be captured than those only marginally overlapping the grid. If a capture occurred on occasion 1, I assigned the trap of capture probabilistically based on the utilization distribution for that

animal, such that traps in cells where the animal was more likely to occur were more likely to capture the animal. I repeated this process across the specified number of occasions to construct a complete capture history. I then proceeded to simulate a home range location, utilization distribution, and capture history in a similar manner for the remaining animals in the simulation.

Each simulation was governed by a specific combination of capture probability, number of occasions, and animals released into the simulation. I considered 3 levels for each of these 3 factors to represent a range of conditions commonly encountered in field research (capture probability for any single occasion = 0.2, 0.4, 0.6; occasions = 5, 7, 10; animals released into the simulation = 10, 20, 40). I completed 1000 simulations for all 27 possible combinations resulting in 27,000 datasets. Simulations were carried out using SAS 9.2 (Version 9.2, SAS Institute Inc., Cary, NC, USA).

For context, I assumed grid cells were 10m on a side and (thus trap-spacing was 10m), resulting in true densities of 4–16 animals/ha (10–40 animals released into 2.56 ha arena), which is consistent with research on voles, mice, and other small rodents (e.g., Hadley and Wilson 2004, Tioli et al. 2009). However, the absolute spatial scale of the simulation is inconsequential and does not affect the relative performance of the estimators. For example, I could have assumed 50–m cells and 50–m trap spacing resulting in true simulated densities of 0.1–0.6 animals/ha, which corresponds to research on squirrel or rabbit-sized species (e.g., Zahratka and Shenk 2008, Russell et al. 2010).

### **2.2.2 Analysis of Simulated Datasets**

I analyzed each dataset using Full MMDM,  $\frac{1}{2}$  MMDM, ML SECR, and 12 forms of TELEM: 4 levels representing the percentage of captured animals that were radio–

tagged (25%, 50%, 75%, 100%) and 3 levels of telemetry sampling (5, 10, and 20 locations obtained per individual during the post-trapping period). Practically, biologists cannot plan to radio-tag a particular percentage of captured animals. Rather, they typically have an allotment of tags for each grid and apply tags until their allotment is gone, resulting in some percentage of captured animals that receive collars. I simulated this reality by first determining the number of animals captured during a simulation, then assigning radio-tags beginning with the first animal captured and continuing up to the appropriate percentage specified for the simulation. To simulate collection of telemetry locations for each collared individual, I assumed the number of successes (i.e., location on grid) was  $\sim \text{Bin}(N, p_i)$  where  $N$  = number of locations and  $p_i$  = proportion of home range on grid for animal  $i$ . This arrangement does not allow for telemetry error, but if telemetry error in the field is unbiased with respect to on/off grid, such a model is appropriate.

I did not build time or behavioral effects into the simulations, nor did I simulate heterogeneity among individuals except for that induced by the location of home ranges relative to the trapping grid. Therefore, I employed basic forms of each estimator to produce density estimates for each simulation. Specifically I used a conditional likelihood (Huggins 1989, 1991), null closed-capture model (i.e., model  $M_0$ ; Otis et al. 1978) to estimate abundance ( $\hat{N}$ ) under the MMDM approaches. For the observation portion of the ML SECR model, I specified a constant half normal detection function for each trap ( $g_0(\cdot) \sigma(\cdot)$ ), using the conditional likelihood formulation for multi-catch traps, with the default 100-m integration buffer around the traps. For the process portion of ML SECR, I specified that density of home range centers followed a homogeneous

Poisson distribution. For versions of the telemetry estimator in which <100% of captured animals were radio-tagged, I used a single individual covariate (mean distance to the edge of the grid calculated across capture locations) to model capture probability and “proportion on grid” for individuals captured but not radio-tagged (See Chapter 1). This represents the minimum model likely to be implemented in practice when more animals are captured than can be radio-tagged. Estimates for Full MMDM,  $\frac{1}{2}$  MMDM, and TELEM were calculated within the same SAS program that produced the simulated datasets. ML SECR analysis for each simulated dataset was accomplished by creating appropriate input files as datasets were simulated, then submitting these files to the R package ‘secr’ (Efford 2009, Efford et al. 2009) for batch processing. I initially considered examination of Bayesian SECR (Royle et al. 2009a) as well. However, the Bayesian approach was prohibitively time-consuming, and I did not expect maximum likelihood and Bayesian inference techniques to perform significantly differently given the same, relatively simple model formulations used to analyze these data. Therefore, I only considered performance of ML SECR for comparison.

In order to assess estimator performance, I calculated true density for each simulation. Importantly, “truth” varies among the 3 classes of estimators. MMDM estimators operate by tallying the number of animals that fall within the grid plus its buffer. Therefore, I calculated true density for MMDM as the number of animals released into the arena, divided by the area of the arena. ML SECR operates by estimating the number of home range centers that are expected to fall within the area of the sampling grid. Therefore, I calculated the home range center of each animal as a weighted average of the 16 cell probabilities, then tallied the number of home range

centers within the grid and divided by the area of the grid to obtain truth. TELEM estimators seek to estimate the number of whole and partial animals that reside within the grid, so I tallied the proportion of each animal on the grid, summed these proportions across all animals, then divided by the area of the grid. For perfectly symmetric home ranges, the true densities for ML SECR and TELEM would be identical, but because I simulated asymmetric home ranges, the true densities can differ.

Initial simulations were completed with all animals assigned a  $4 \times 4$  home range and I assessed performance across a range of capture probabilities, occasions, and true densities. Next, I assessed the influence of home range shape by holding capture probability, occasions, and true density at intermediate levels ( $p = 0.4$ , occasions = 7, animals released into the simulation = 20) while varying home range shape and use from very regular to completely irregular. Specifically, I completed batches of simulations in which each animal was assigned a circular bivariate normal home range ( $\sigma_x = \sigma_y$ ), a bivariate normal ellipse ( $\sigma_x \neq \sigma_y$ ), a  $4 \times 4$  home range with random utilization distribution as described above, a  $2 \times 8$  home range with random utilization distribution, and a 16-cell irregular home range with random utilization distribution (Figure 1). The latter home range was created for each individual by first selecting a single cell at random within the simulation arena then randomly selecting one of the 4 cells adjacent to the first, forming a home range of 2 cells. I then randomly picked one of the existing home range cells to serve as a temporary reference, added a cell adjacent to the reference, selected another temporary reference from among the new home range cells (now 3), etc. until the home range consisted of 16 cells. Theoretically this procedure could have produced any shape under the constraint that the 16 cells were adjacent. I assigned a

utilization distribution within the 16 cells as before. For bivariate normal home ranges, I assigned  $\sigma$  such that the 95% home range encompassed an area equal to 16 cells. Thus, for this comparison, home ranges varied only in shape, not size. I ran 1000 simulations for each of the 5 home range shapes resulting in 5,000 datasets. Density estimates and truth were calculated for each estimator and each dataset as described above.

### 2.2.3 Assessment of Overall Performance

For each simulation, I calculated percent relative bias ( $\text{PRB} = (\hat{D} - D)/D \times 100\%$ , where  $D$  = density), percent coefficient of variation ( $\text{PCV} = \widehat{\text{SE}}(\hat{D})/\hat{D} * 100$ ), and indicated whether the estimated 95% confidence (95% CI =  $\hat{D} \pm 1.96(\widehat{\text{SE}}(\hat{D}))$ ) interval covered the appropriate true density. My use of realistic parameter inputs complicated summarization as some combinations of parameters resulted in no point estimates (and/or no  $\widehat{\text{SE}}$ s) due to numerical problems with optimizing the likelihood function, or unrealistically large point estimates (and/or unrealistically large SEs). Such results were observed for each class of estimator, estimators did not always fail in concert and no estimator routinely produced estimates when others failed. Usual data summaries involving measures of central tendency, dispersion, mean squared error, or evaluation of linear models relating performance to input parameters (i.e., ANOVA or AIC) were not possible without censoring unrealistic results, but censoring could not be accomplished objectively. Thus, I opted to present findings graphically as follows.

To assess bias of estimators, I ordered the simulations by PRB in ascending fashion, then plotted these values against their percentile (e.g., the  $x$ -axis value for the smallest PRB was  $1/27,000 = 3.7\text{E-}05$ ; the  $x$ -axis value for the largest value for PRB

was  $27,000/27,000 = 1.0$ ) forming a cumulative distribution plot (Figure 2). The cumulative plot of PRB for a perfect estimator would be unbiased for each simulation and its curve would never deviate from the zero. Intuitively, then, curves that approach the zero-bias line “quickly” and remain near it for the greatest number of simulations represent the least biased and most desirable estimators. Two curves that track each other nearly perfectly indicate 2 estimators performing similarly; 2 curves that separate quickly indicate disparate performance. Sharp inflections up or down in the distal portions of a curve indicate the percentile of simulations where estimators encountered optimization problems, produced severe outliers, or otherwise resulted in poor estimates (very high or low). Better estimators have relatively “flat” curves and produce unreasonable results in only a small percentage of simulations. Curves in which the 50<sup>th</sup> percentile passes through zero produce as many negatively biased estimates as positively biased estimates. For initial assessments of overall performance, all simulations from all combinations of sampling parameters were included in the curve for each estimator.

Performance can also be assessed by tallying the percentage of simulations that returned summary statistics within an acceptable range. For instance, I subjectively set a cutoff for acceptable values of PRB at  $\pm 20\%$  then tallied the percentage of simulations that returned values within this range. Estimators that are likely to meet such criteria more often are desirable compared to estimators that are less likely to produce estimates meeting the criteria.

To assess precision, I first checked that the estimated sampling variance of each estimator reflected the true sampling variance by comparing mean  $\widehat{SE}(\widehat{D})$  (i.e., the expected value of the SE) against  $SD(D)$  (i.e., the spread of the sampling distribution) for

the 1000 simulations run under the parameter combination that should have provided the richest datasets (animals = 40, occasions = 10,  $p = 0.6$ ). I found that mean  $\widehat{SE}(\widehat{D})$  for TELEM25 to TELEM100 was 29–49% lower than  $SD(D)$ . Similarly,  $\widehat{SE}(\widehat{D})$  for Full and  $\frac{1}{2}$  MMDM were 30–46% low. Mean  $\widehat{SE}(\widehat{D})$  for ML SECR was 155% of  $SD(D)$ . Thus, no estimator behaved as expected relative to precision of estimates. Given this, I abandoned my original intent of 1) comparing PCV of estimators using cumulative plots similar to those constructed for assessing PRB and 2) comparing 95% confidence interval coverage among estimators.

Note that I used all appropriate simulations to create the curves indicated in the preceding paragraphs, but figures are cropped to facilitate judgment and comparison of estimators within meaningful ranges. For instance, maximum observed PRB for each estimator exceeded 1000%, but there is little utility in presenting such poor results and doing so distorts the scale of the graph so badly as to obscure differences among estimators in ranges of interest. Thus, I present cumulative plots of PRB focused on the range of  $-100\%$  to  $+100\%$ .

#### **2.2.4 Sensitivity of Estimators to Sampling Parameters**

I examined sensitivity of estimators to sampling parameters (i.e., capture probability, number of occasions, number of animals released) using cumulative plots of PRB similar to those described above, but I plotted each estimator–parameter combination separately, with curves representing levels of the parameter of interest. Under this framework, estimator sensitivity to a particular parameter can be assessed by focusing on the separation of performance curves. For example, if for a given estimator the 3 curves representing 3 levels of a given parameter are nearly identical, then the



estimator is not sensitive to changes in that parameter (at least over the range of values simulated for that parameter). However, if the 3 curves are quite different, then the estimator is sensitive to that parameter and its performance hinges on which level of that parameter is realized. For simplicity and ease of presentation I present plots of only the best performing MMDM estimator (Full MMDM) from my initial assessment and an intermediate level of the telemetry estimator (TELEM75, 10 locations), along with ML SECR. I define sensitivity as change in performance based on the fixed values I chose for sampling parameters, which were intended to reflect the range of values most likely to be encountered in reality.

### **2.2.5 Interactions of Sampling Parameters**

I used further variations of cumulative PRB distribution plots to explore interactions between parameter levels, which are important with respect to design of field studies. Here I subset the simulations by unique parameter–level combinations (e.g., animals released into the simulation = low, occasions = medium, capture probability = high), then plotted the data parsed by estimator. Twenty–seven combinations of sampling parameter levels are possible and plots of these combinations appear in Appendix A. For illustration, I consider a handful of combinations that may be of interest, including situations in which 1) each sampling parameter occurred at a low level (e.g., reflective of work with rare and/or elusive species in which sampling resources are limited), 2) animals are relatively easy to capture, and occur at moderate densities, but can only be trapped over a limited number of occasions due to capture myopathy (e.g., reflective of my own experience trapping snowshoe hares (*Lepus americanus*) in Colorado, USA during winter), and 3) animals occur at low densities and are difficult to

capture or detect, but the number of sampling occasions can be high (e.g., reflective of sampling wide-ranging carnivores with hair snags).

## **2.3 RESULTS**

### **2.3.1 Overall Performance**

Across all 27,000 simulated datasets, the mean percent difference between true density for TELEM and true density for ML SECR was  $-1.07\%$  ( $SD = 15.8$ ), but true density for MMDM was substantially lower than TELEM (mean difference =  $-32.7\%$ ,  $SD = 10.07$ ). Thus, while the quantities estimated by TELEM (partial home ranges on grid) and ML SECR (number of home range centers on grid) are quite different, I expect similar estimates on average. However, those estimates should differ markedly from those produced by the MMDM approach.

With respect to PRB (Figure 2),  $\frac{1}{2}$  MMDM performed poorly as over 80% of estimates were severely biased high ( $PRB > 50\%$ ). Full MMDM performed better (curve stayed closer to 0 longer), but was inferior to ML SECR and TELEM. The least biased estimators were TELEM100 and TELEM75; approximately 75% of estimates fell within  $\pm 20\%$  PRB. ML SECR produced estimates within  $\pm 20\%$  PRB in  $\sim 53\%$  of simulations. All estimators were more likely to produce estimates that were biased high than low (0% of estimates were  $< -100\%$  PRB, but  $> 5\%$  of estimates were  $> 100\%$  PRB for MMDM, TELEM, and SECR).

### **2.3.2 Sensitivity of Estimators to Sampling Parameters**

For ease of presentation, I examined the main effects of simulation parameters by plotting only the better performing of the MMDM estimators (Full MMDM), and an intermediate version of the telemetry estimator (TELEM75, 10 locations/radio tag), along

with ML SECR (Figure 3). While the absolute trajectory of omitted curves may differ from those plotted, the relative response to main effects within classes of estimators was similar and well-characterized by the representative estimators plotted here.

Using “separation of curves” as an indicator of sensitivity and PRB as the performance measure of interest, estimators were generally most sensitive to capture probability (Figure 3g–i), followed by number of animals released (Figure 3a–c) and number of occasions (Figure 3d–f). Sampling parameters influenced the likelihood of positively biased results more so than the likelihood of observing negatively biased results (more separation occurs in the positive bias quadrant than occurs in the negative bias quadrant for each parameter and each estimator). Overall, performance of ML SECR was least sensitive to varying levels of sampling parameters compared to Full MMDM or TELEM75.

When capture probability was low, none of the estimators performed well (Figure 3g–i; when  $p = 0.2$ , no estimator tracks the zero bias line for any distance). PRB was  $\pm 20\%$  in  $\sim 50\%$  of simulations for TELEM75,  $\sim 40\%$  of simulations for ML SECR, and  $\sim 25\%$  of simulations for Full MMDM. However, outside of the  $\pm 20\%$  window of interest, both TELEM and MMDM were likely to produce highly positively biased estimates. ML SECR, on the other hand, was not as prone to severe high bias and was equally likely to give both positively and negatively biased results (i.e., its curve passes through the intersection of the zero and 50<sup>th</sup> percentile). Large gains in performance occurred with each estimator as capture probability was increased from 0.2 to 0.4, but relatively smaller gains were realized as capture probability was increased further to 0.6.

Under these higher levels of capture probability, TELEM75 performed best, followed by ML SECR then Full MMDM.

As expected, PRB decreased with increasing animal density (Figure 3a–c).

Contrary to changes in capture probability, increasing the number of animals released into the simulation resulted in a more stepwise response in estimator performance; the difference between the lines representing 20 and 40 animals released was about the same as the difference between the lines representing 10 and 20 animals released. Increasing the number of occasions decreased estimator bias (Figure 3d–f) in a similarly stepwise fashion, but the chance of observing negatively biased results did not change appreciably with number of occasions.

### **2.3.3 Interactions of Sampling Parameters**

No estimator performed well with respect to PRB given low levels of each sampling parameter (Figure 4a). For the case reflective of winter studies of snowshoe hares (Figure 4b), TELEM performed best (~70% of simulations resulted in  $-20\% < \text{PRB} < 20\%$  for TELEM75) followed by ML SECR (~55% of simulations give  $-20\% < \text{PRB} < 20\%$ ), and Full MMDM (~36% of simulations give  $-20\% < \text{PRB} < 20\%$ ). For the case representative of carnivore sampling using hair snags (Figure 4c), ML SECR gave equal numbers of positive and negatively biased density estimates, whereas TELEM and MMDM estimators were slightly to severely biased high, respectively. However, TELEM returned  $-20\% < \text{PRB} < 20\%$  in ~47% of simulations, whereas ML SECR returned  $-20\% < \text{PRB} < 20\%$  in 36% of simulations and Full MMDM in only 29% of simulations. Plots of estimator performance under 24 other combinations of sampling parameters

appear in Appendix A, and I suggest practitioners engaged in study design consult these plots to examine performance under conditions expected in the field.

#### **2.3.4 Radio tag vs. Location trade-off**

There is an obvious trade-off in cost that bears on study design when considering use of the TELEM estimator: number of radio tags deployed vs. the number of locations obtained per radio tag. Plots of PRBs parsed by number of locations indicated that it makes little difference whether 5, 10, or 20 locations were obtained per animal (Figure 5a). Separation between curves is larger, but still minimal when results were parsed by percentage of captured animals that were radio-tagged (Figure 5b). Thus, larger gains in bias reduction can be realized by radio-tagging more animals than can be realized by obtaining more locations per animal. Not surprisingly, TELEM25 was most likely to produce biased results followed successively by TELEM50, TELEM75, and TELEM100. Note, however, that the jump in performance between TELEM75 and TELEM100 was relatively small compared to the jump from TELEM25 to TELEM50 and TELEM50 to TELEM75. Also, most of the difference in bias occurred in the negative quadrant.

#### **2.3.5 Influence of Home Range**

With respect to PRB, TELEM75 performed best across the range of simulated home range shapes and its performance appeared unaffected by home range configuration (Figure 6;  $-20\% < \text{PRB} < 20\%$  in ~82–90% of simulations for each shape). ML SECR performed well for circular and square home ranges (Figure 6a,c;  $-20\% < \text{PRB} < 20\%$  in ~60% of simulations), but was more likely to produce negatively biased results when home ranges were elongated or irregular (Figure 6b,d,e;  $-20\% < \text{PRB} < 20\%$  in ~43–53% of simulations). Performance of Full MMDM estimators improved dramatically given

bivariate normal circles,  $2 \times 8$ , or irregular home ranges (Figure 6a,d,e;  $-20\% < \text{PRB} < 20\%$  in  $\sim 63\text{--}70\%$  of simulations), compared to  $4 \times 4$  or bivariate normal ellipses (Figure 6b,c;  $-20\% < \text{PRB} < 20\%$  in  $\sim 39\text{--}43\%$  of simulations).

## 2.4 DISCUSSION

Prior to testing, uncertainty existed regarding performance of TELEM and at least 2 valid issues were raised. First, animals with a greater proportion of their home range on grid are more likely to be captured and radio-tagged than animals with a home range near the periphery of the grid. This phenomenon would inflate the numerator of the TELEM estimator (See Chapter 1:  $\hat{D} = \left( \sum_{i=1}^{M_{t+1}} \frac{\tilde{p}_i}{p_i^*} \right) / A$ , where  $M_{t+1}$  = number of animals capture,  $\tilde{p}_i$  = estimated proportion of home range on grid for animal  $i$ ,  $p_i^*$  = probability animal  $i$  was captured at least once during the sampling session, and  $A$  = area of the grid), resulting in a positively biased density estimate (Efford 2004). Under conditions where TELEM began to perform poorly (e.g., low capture probability) and exhibited bias, it did so in the positive direction, possibly due to this phenomenon. However, animals with a greater proportion of their range on the sampling grid should also have a higher capture probability ( $p_i^*$ ) which would inflate the denominator of the estimator as well as the numerator, functionally canceling out the bias to a degree. The positive bias I observed was more likely due to underestimating the denominator of the density expression, rather than overestimating the numerator.

Second, questions have been raised regarding the number of locations necessary to accurately assess proportion of time on grid for each animal (Efford 2004). I found that collecting 5, 10, or 20 locations per radio-tag made little difference with respect to bias. The more influential factor was the number of individuals sampled with a radio tag.

I recommend that limited resources be used to sample more individuals rather than sampling more locations per individual. If practitioners can radio-tag at least 50–75% of animals captured, reasonable results can be obtained with as few as 5–10 locations per animal assuming at least intermediate levels of capture probability, occasions, true density.

I recognize that costs associated with obtaining ancillary telemetry data may be prohibitive and preclude use of TELEM in many cases. For those situations, I favor ML SECR (or Bayesian SECR, assuming it performs similarly) as it outperformed both MMDM estimators in nearly all comparisons I considered and has a stronger theoretical background. However, Efford (2004) noted that SECR may not perform well given elongated home ranges and my simulations substantiate this claim. In fact, simulations suggest Full MMDM may be a better choice if home ranges are suspected to be highly asymmetric or elongated. Practitioners should proceed with caution given a system in which heterogeneous habitats and/or animal behaviors could produce such home ranges.

Like Parmenter et al. (2003), I found that Full MMDM performed better than  $\frac{1}{2}$  MMDM, but the degree of positive bias expressed by the MMDM estimators was surprising. Wilson and Anderson observed  $PRB < 22\%$  across all of their simulations using  $\frac{1}{2}$  MMDM, and Parmenter et al. (2003) observed  $PRB = 38$  to  $55\%$  in their field trials. However, 95% of my simulations resulted in  $\frac{1}{2}$  MMDM estimates in which  $PRB$  exceeded 20%. This bias was reduced substantially when simulations were based on bivariate normal or irregular home ranges and I suspect overall performance would have been much improved had I chosen one of these home range shapes for the bulk of the simulations. With a  $4 \times 4$  home range representation, animals were never allowed to

occur outside of the 16 cells I initially selected for them, whereas bivariate normal home ranges are technically infinite in all directions and a small probability exists that an animal could be located a fair distance from its usual area of use. Thus, I expect the mean maximum distance moved between trapping events to be larger, on average, given a bivariate normal home range than one with a hard edge. Increased movements would lead to increased estimates of the effective area sampled and decreased estimates of density. To the degree that one is willing to assume bivariate normal or “irregular” home ranges, are adequate representations of a study system, Full MMDM may perform adequately. However, hard-edged home ranges may be a fair abstraction of animal movements over short sampling sessions as the daily routine of an individual may be confined to a fairly discrete area.

For simulation purposes, I used a null closed capture model ( $M_0$ ) to calculate  $\hat{N}$  used in MMDM estimates. A heterogeneity estimator ( $M_h$ ) may have been more appropriate given that heterogeneity in capture probability was induced by the location of an animal’s home range in relation to the sampling grid. However, using a null model when heterogeneity is present results in underestimation of true abundance (White et al. 1982 p. 63). MMDM suffered substantial positive bias in nearly all of the comparisons I considered, thus use of a heterogeneity estimator would only hinder already poor performance. Jett and Nichols (1987) suggested a correction based on the premise that maximum movement would be better estimated by individuals captured more often than those captured only a few times. I did not evaluate the performance of that correction here, but its performance relative to other estimators should be evaluated.



I did not design any simulations to examine the influence of home range size (relative to grid size) on estimator performance. I do not expect this factor to have a significant effect on any of the estimators as long as the number of traps within a home range remains at or above a reasonable level, say 4–6 traps per home range. Wilson and Anderson (1985) found that MMDM estimators were fairly robust to changes in home range size relative to grid size and trap spacing. A handful of post hoc simulations (J. Ivan, unpublished data) suggest this may be the case not only for MMDM estimators, but for others as well. However, formal testing of this assertion should be completed.

Sampling variance of  $\hat{D}$  for TELEM and MMDM was underestimated for “rich” datasets (i.e., high capture probability, large number of occasions, large number of animals released into the simulation). I calculated sampling variance based on the delta method approximation (Seber 1982 p. 7) and it is not clear why this approached performed so poorly. In contrast, sampling variance of  $\hat{D}$  was overestimated by ML SECR. I accepted default settings for the ML SECR routine, meaning that sampling variance was based on a Poisson distribution for the number of animals caught. This explains why mean  $\widehat{SE}(\hat{D})$  for ML SECR was much larger than that of other methods and may preclude direct comparisons. However, I expect mean estimated sampling variance to approximate the empirical variance of the realized  $\hat{D}$ . That this was not the case for any estimator is disturbing and more should be done to explore this issue.

Implementation of the TELEM estimator in Program MARK (White and Burnham 2001) includes an option to obtain estimates of sampling variance by bootstrapping across the individual encounter histories in the dataset. This approach produces somewhat larger

sampling variances than those derived empirically, and may be a more robust option than the analytical formula (J. Ivan, unpublished data).

In general, estimator performance was most sensitive to changes in capture probability, followed by animal density and of capture occasions. However, my simulations are based on only a few design points typical of traditional live-trapping studies. I did not simulate special cases where detectors such as cameras or hair snags are deployed for  $\gg 10$  occasions. I expect a large number of occasions to better aid in overcoming potentially low capture probability and/or animal density, but I cannot say how this might effect performance of the estimators relative to each other.

My simulations perfectly met some of the critical assumptions of TELEM, namely that 1) the radio-tagged sample was representative of the population of animals that use the grid, 2) there was no difference between the pre-trapping and post-trapping distribution or movement patterns of radio-tagged animals (i.e., radio tags do not affect movements and there are no lingering effects of trapping on animal movements), and 3) telemetry location error was small relative to the size of the grid and assignment (on/off) of locations near the edge of the grid was unbiased. Fully meeting these assumptions likely bolstered the performance of this estimator and I cannot speculate on the degree to which it may be robust to violations. However, rigorous study design can help assure the assumptions are met in field applications as well (See Chapter 1).

My simulations did not allow animals to shift their home ranges or make temporary forays out of their usual home range in response to sampling. No doubt this occurs in reality when bait is used in the sampling process, and such events violate assumptions of SECR and MMDM. Theoretically, temporary forays or range shifts

should not affect TELEM, assuming that the phenomenon disappears when bait is removed from the sampling site. Further work in this area would be useful to evaluate the robustness of estimators relative to these violations.

My simulations represent the first tests of the telemetry estimator across a wide range of conditions as well as the first comparison among the 3 contemporary estimators of density using sampling grids. I found variations of TELEM performed best across a range of capture probabilities, sampling occasions, true densities, and home range configurations, although it is prone to returning positively biased results at low capture probability. That TELEM performed well was not surprising given it uses ancillary information that provides a direct measure of the process leading to lack of geographic closure (i.e., movement of individuals on and off of the sampling grid) which is unavailable to other estimators.

## **2.5 ACKNOWLEDGMENTS**

I thank P. Lukacs for assistance in formulating the telemetry estimator. M. Efford and J. A. Royle provided insightful discussions regarding density estimation in general and spatially explicit capture–recapture in particular. I particularly appreciate M. Efford’s assistance with implementation of the R package ‘secr’. Logistical support was provided by the Colorado Cooperative Wildlife Research Unit. Funding was provided by the Colorado Division of Wildlife. I thank M. Efford and the “Wagar 113 Superpopulation” for comments on previous drafts of this manuscript.

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Figure 1.  $10 \times 10$  simulated trapping grid centered within a  $16 \text{ cell} \times 16 \text{ cell}$  simulation arena. For a majority of simulations, home ranges were represented by a  $4 \times 4$  square within which probability of use of any given cell was assigned randomly under the constraint that all probabilities within a home range summed to 1.0 (a). For simulations exploring the role of home range shape on estimator performance, I maintained home range size, but varied shapes to include  $2 \times 8$  (b), 16-cell irregular (c; shape is random for each animal under the restriction that each of the 16 cells is adjacent to at least one other cell), bivariate normal “circles” (d;  $\sigma_x = \sigma_y$ ), and bivariate normal “ellipses” (e;  $\sigma_x \neq \sigma_y$ ), in addition to the  $4 \times 4$ . I assumed 10-m spacing between traps.

Figure 2. Cumulative percent relative bias (PRB) of density estimators. Curves represent estimates from  $n = 1000$  datasets simulated for each combination of capture probability (0.2, 0.4, 0.6), occasions (5, 7, 10), and true density (10, 20, 40 animals released into arena) for a total of 27,000 datasets. PRB was calculated for each simulation, then values were ordered smallest to largest and plotted against their percentile.

Figure 3. Cumulative percent relative bias for 3 classes of density estimator plotted by the number of animals released into the simulation (a–c), number of occasions (d–f), and capture probability (g–i). Results for the TELEM75 estimator were based on obtaining 10 locations per radio-tagged individual.

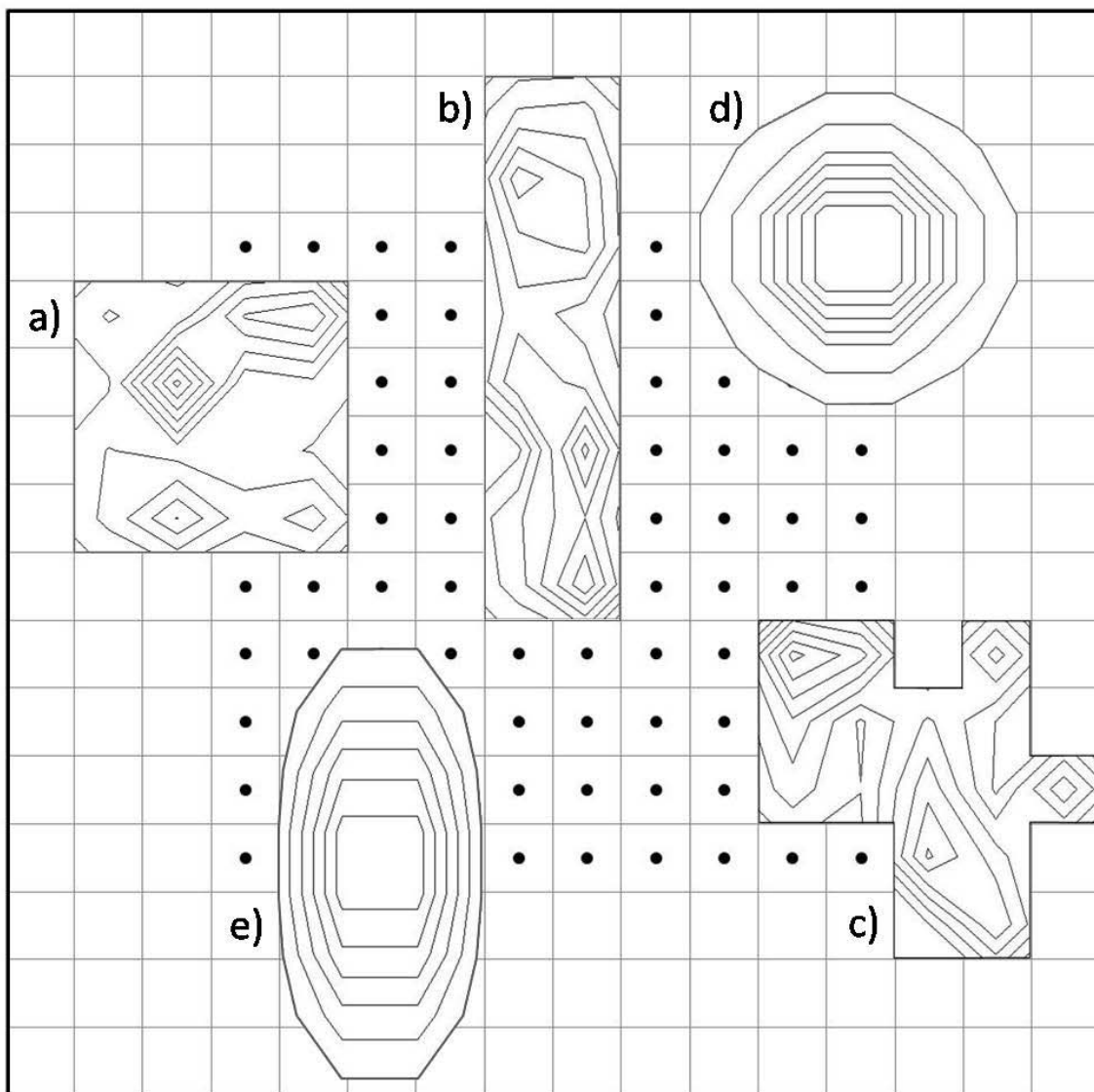
Figure 4. Cumulative percent relative bias for simulated datasets in which each factor was set to a) the lowest level simulated (capture probability = 0.2, occasions = 5, animals

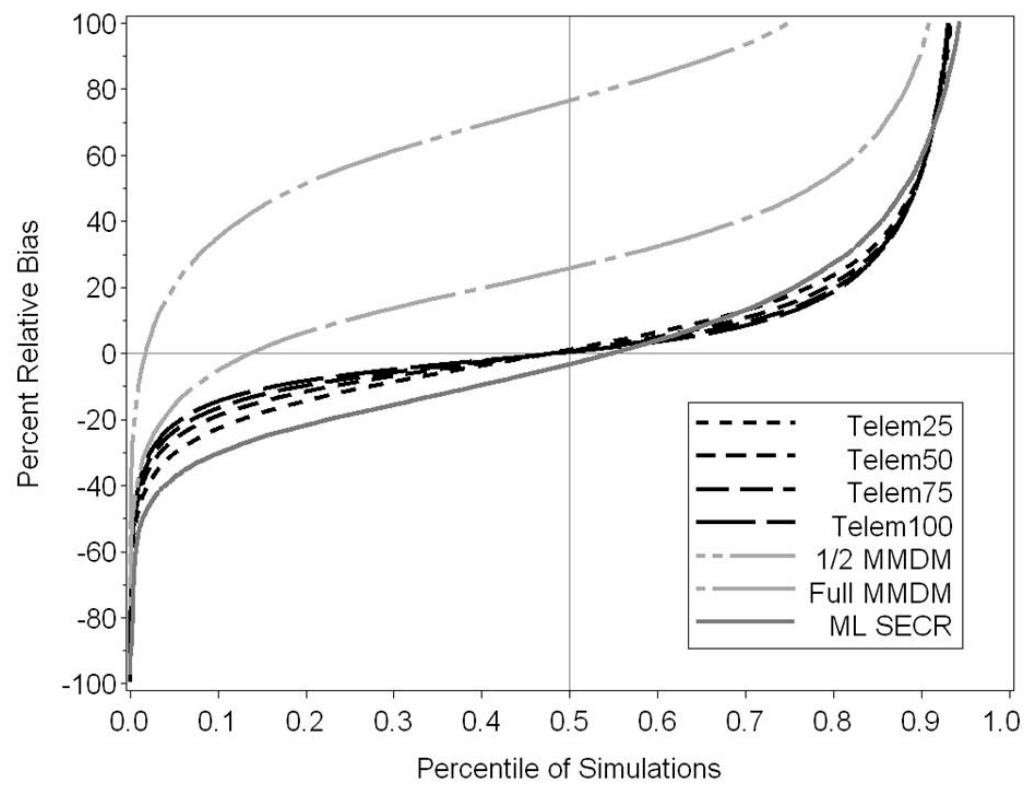


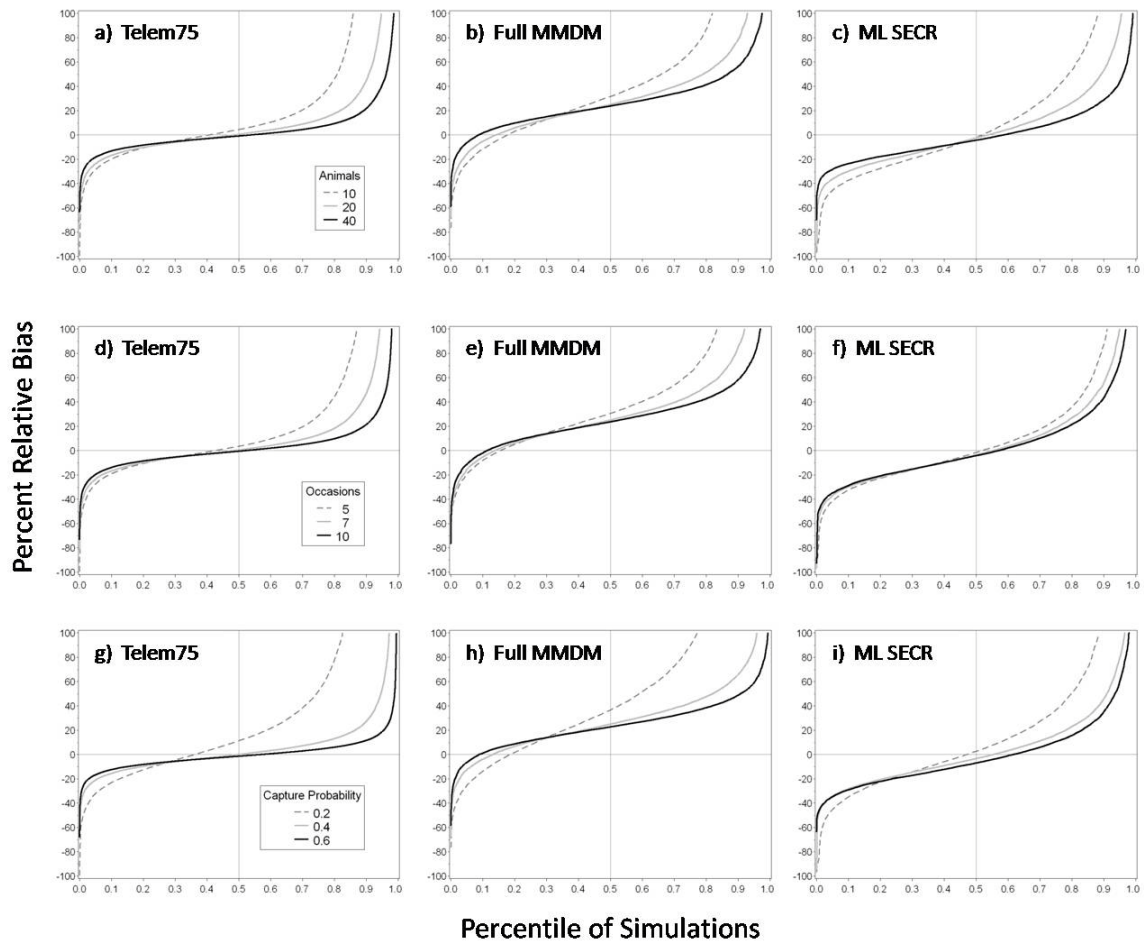
released into simulation = 10), b) capture probability = 0.4, occasions = 5, animals released into simulation = 10, and c) capture probability = 0.2, occasions = 10, animals released into simulation = 10.

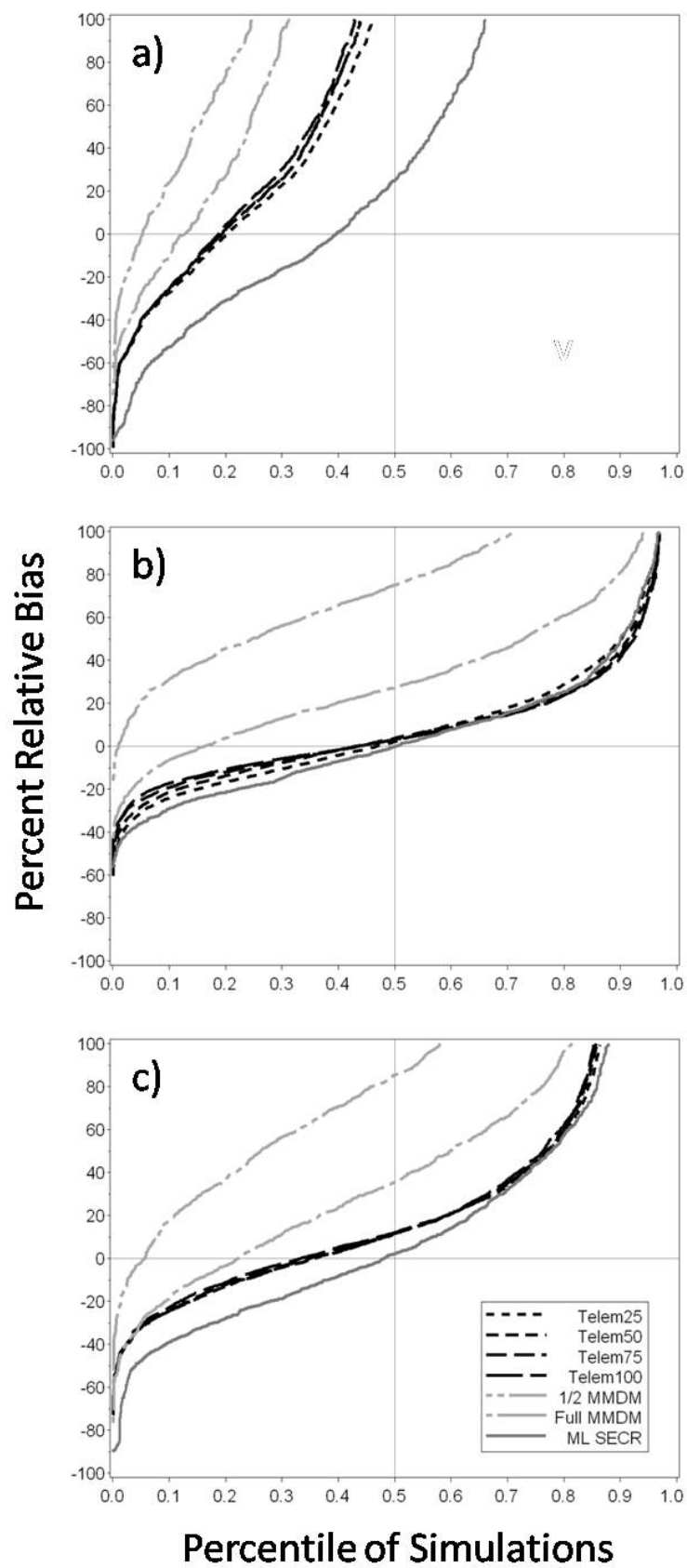
Figure 5. Cumulative percent relative bias of telemetry estimators parsed by a) number of radio locations obtained per radio-tagged individual and b) percent of captured individuals radio-tagged.

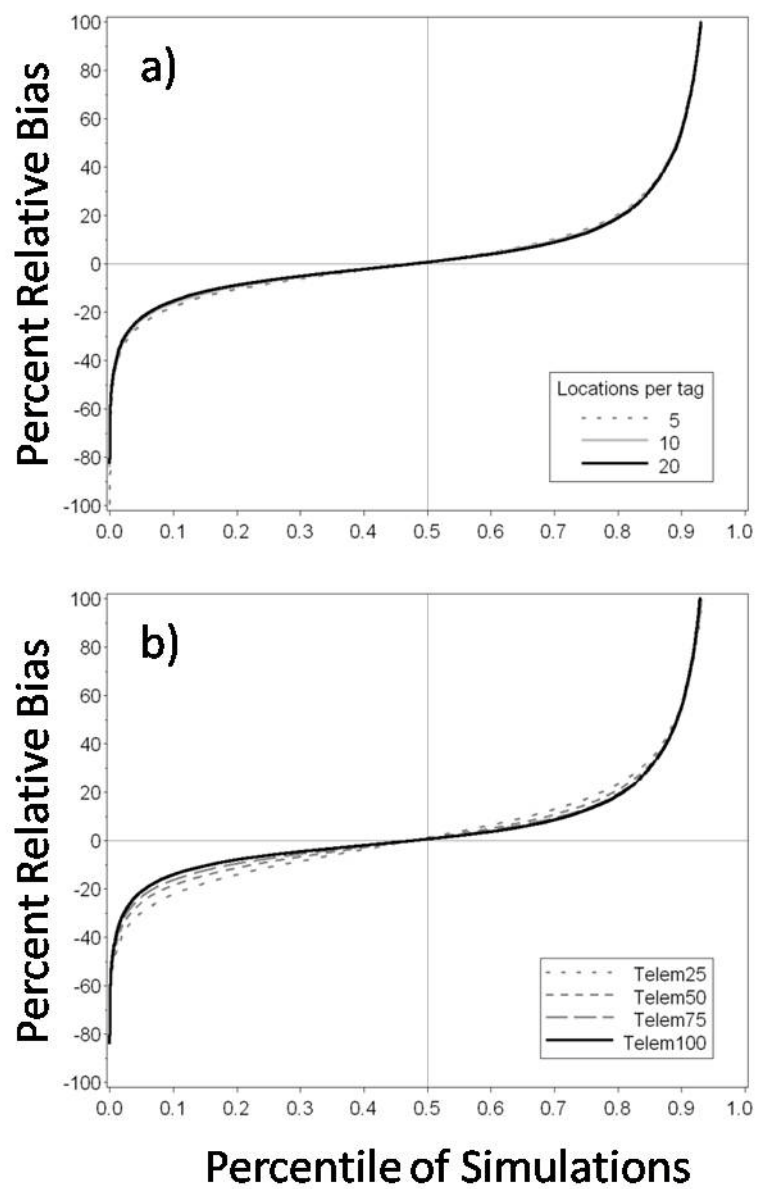
Figure 6. Cumulative percent relative bias for simulated datasets in which capture probability, occasions, and number of animals released into the simulation were fixed to intermediate levels (0.4, 7, and 20, respectively) and home range size varied vary from regular (bivariate normal circle) to highly irregular (16 cells allowed to take any shape in which each cell is adjacent to  $\geq 1$  other cell).

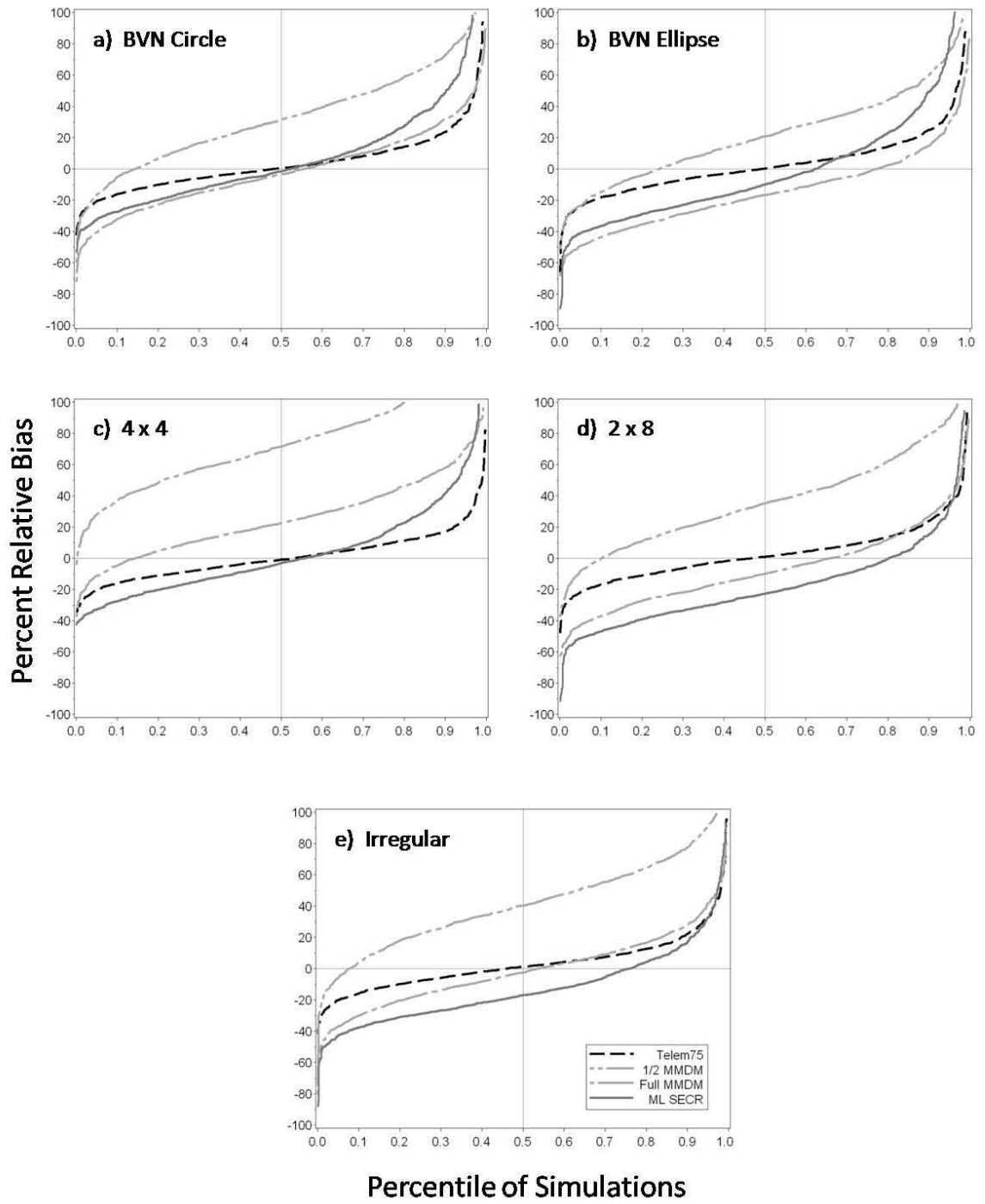












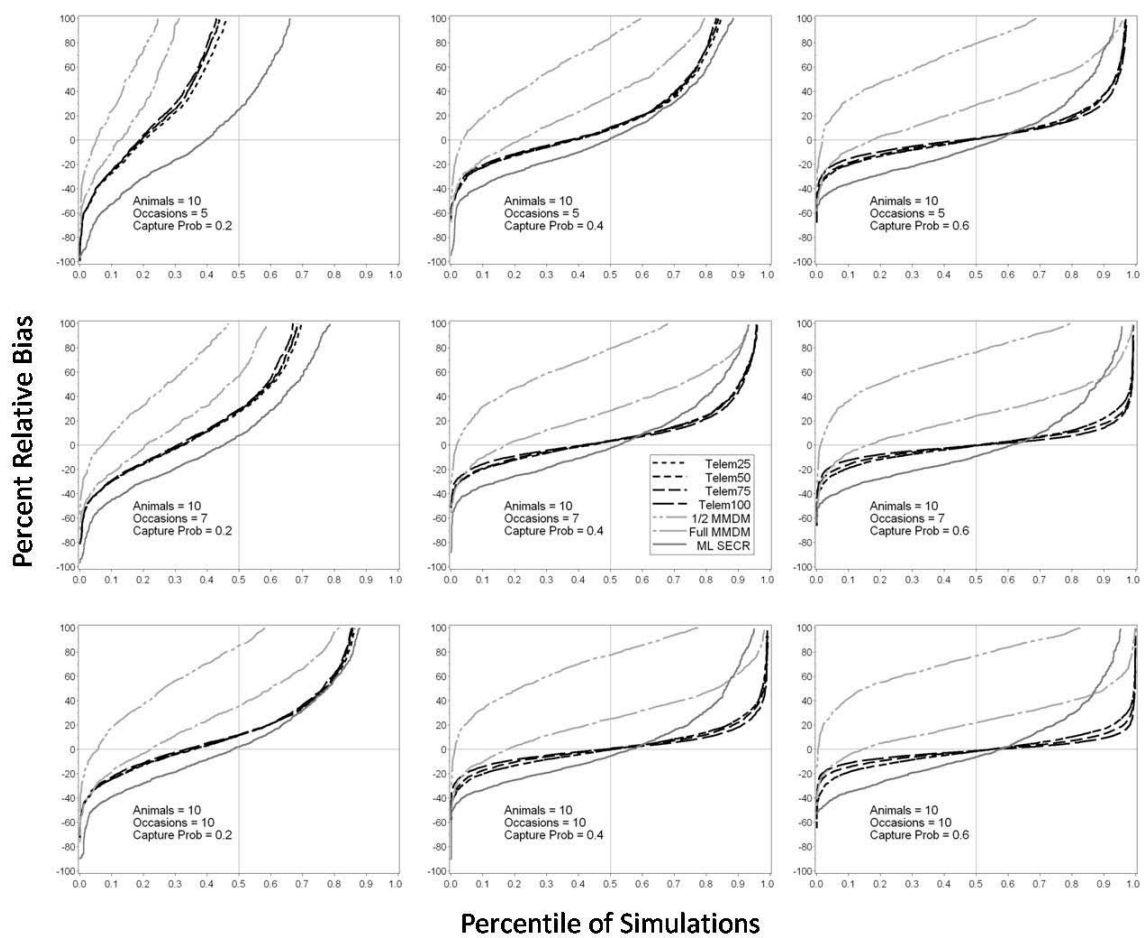
## **2.7 APPENDIX A**

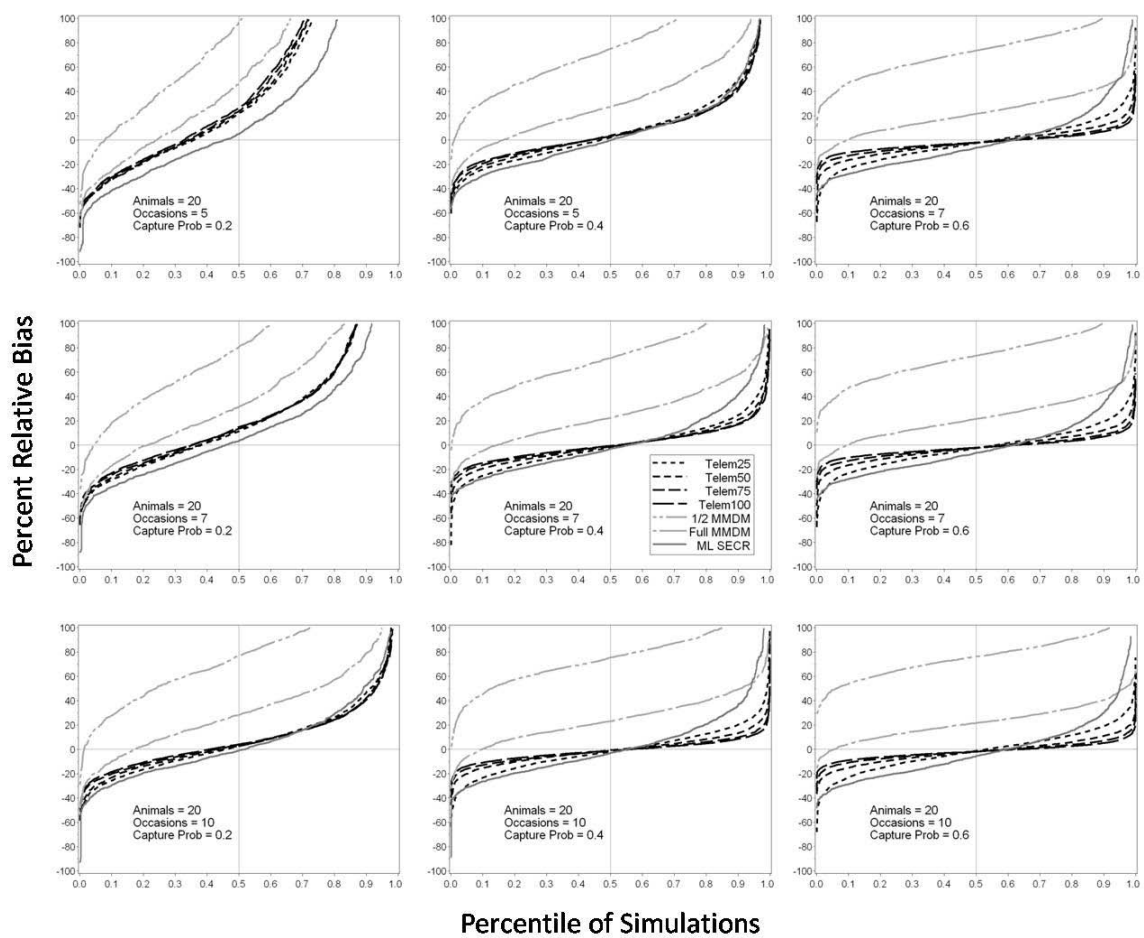
Figure 1. Cumulative percent relative bias of for simulated datasets in which 10 animals were released into each simulation (density = 4 animals/ha for 10–m trap–spacing, 0.16 animals/ha for 50–m spacing) and all levels of capture probability (0.2, 0.4, 0.6) were crossed with all levels of sampling occasions (5, 7, 10).

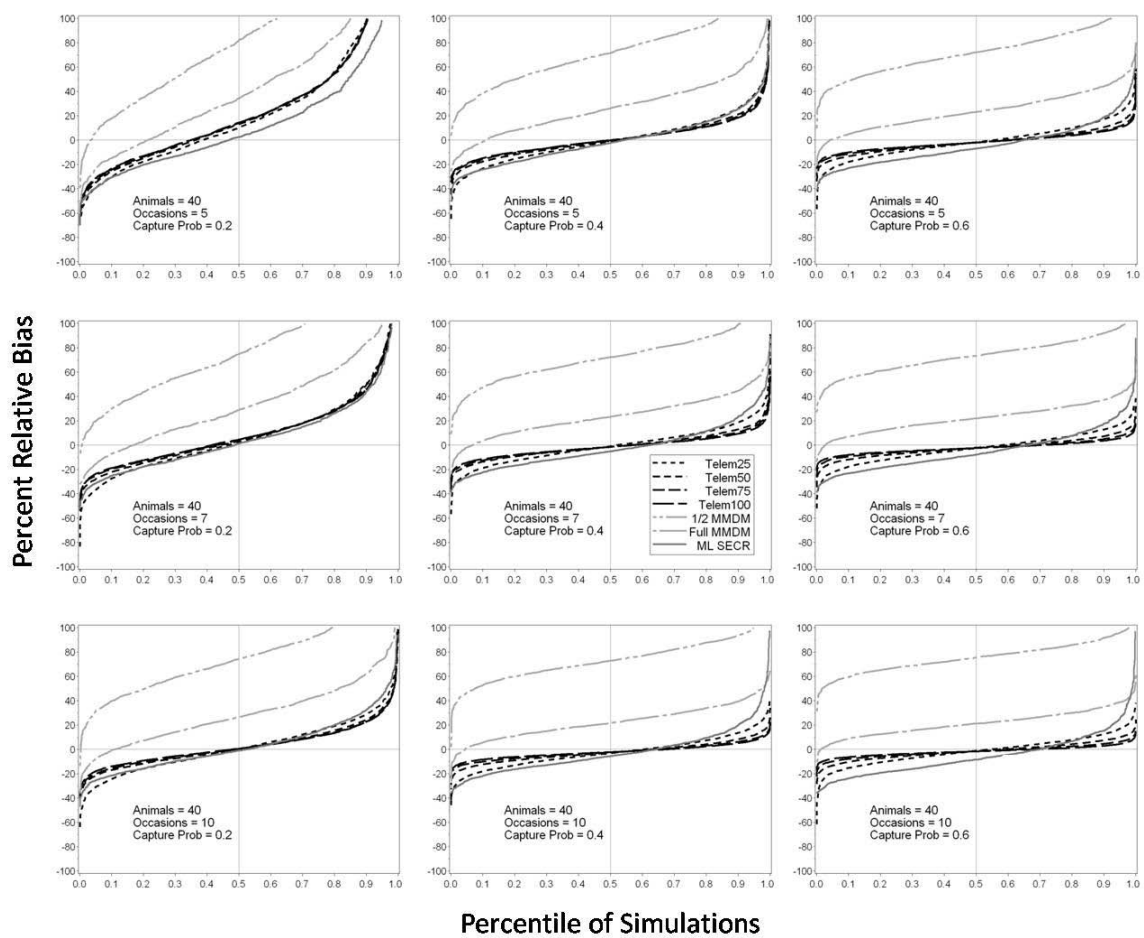
Figure 2. Cumulative percent relative bias of for simulated datasets in which 20 animals were released into each simulation (density = 8 animals/ha for 10–m trap–spacing, 0.3 animals/ha for 50–m spacing) and all levels of capture probability (0.2, 0.4, 0.6) were crossed with all levels of sampling occasions (5, 7, 10).

Figure 3. Cumulative percent relative bias of for simulated datasets in which 40 animals were released into each simulation (density = 16 animals/ha for 10–m trap–spacing, 0.6 animals/ha for 50–m spacing) and all levels of capture probability (0.2, 0.4, 0.6) were crossed with all levels of sampling occasions (5, 7, 10).









## CHAPTER 3

### DENSITY AND DEMOGRAPHY OF SNOWSHOE HARES IN CENTRAL COLORADO

**Abstract.** Using a combination of mark-recapture and radio telemetry, I estimated snowshoe hare (*Lepus americanus*) density, survival, and recruitment in west-central Colorado, USA from July 2006–July 2009. I sampled 3 types of forest stands that purportedly provide good habitat for hares: 1) mature Engelmann spruce (*Picea engelmannii*)/subalpine fir (*Abies lasiocarpa*), 2) early seral, even-aged lodgepole pine (*Pinus contorta*), and 3) mid-seral, even-aged lodgepole pine that had been pre-commercially thinned. In all stand types and all seasons, snowshoe hare densities were <1.0 hares/ha. During summer, hare densities were highest in early seral lodgepole pine ( $0.20 \pm 0.01$  (SE) to  $0.66 \pm 0.07$  hares/ha), lowest in mid-seral lodgepole pine ( $0.01 \pm 0.04$  to  $0.03 \pm 0.03$  hares/ha), and intermediate in mature spruce/fir ( $0.01 \pm 0.002$  to  $0.26 \pm 0.08$  hares/ha). During winter, densities became more similar between the 3 stand types. The hare population apparently declined from winter 2007 through summer 2008, then began to increase. Annual survival of hares was highest in mature spruce/fir ( $0.14 \pm 0.05$  (SE) to  $0.20 \pm 0.07$ ) and similar among the 2 lodgepole stand types ( $0.10 \pm 0.03$  to  $0.16 \pm 0.06$ ). Across stand types, summer-winter survival was nearly twice as high as winter-summer survival. Furthermore, winter-summer survival during the first 2 years of the study (coinciding with the decline in abundance) was lower than survival during the

third winter-summer period, although precision was poor. Recruitment of juvenile hares occurred during all 3 summers in early seral lodgepole stands, 2 of 3 summers in mature spruce/fir stands, and in only 1 of 3 summers in mid-seral lodgepole. Stand attributes indicative of dense cover were positively correlated with density estimates and explain relatively more process variance in hare densities than other attributes. These same attributes were not positively correlated with hare survival. Both density and survival of hares in early seral lodgepole stands were positively correlated with the occurrence of similar stands in the surrounding landscape. Based on stand-specific estimates of density and demography, I conclude that thinned, mid-seral lodgepole stands are probably less important than mature spruce/fir and small lodgepole stand types. Management for snowshoe hares (and lynx) in central Colorado should focus on maintaining the latter. Given the more persistent nature of spruce/fir compared to small lodgepole, and the fact that such stands cover considerably more area, mature spruce/fir may be the most valuable stand type for snowshoe hares in the state.

**Key Words.** *Barker model; Colorado; density; demography; Lepus americanus; population ecology; recruitment; robust design; snowshoe hare; survival; trapping grid; telemetry.*

### 3.1 INTRODUCTION

In an effort to restore a viable population of federally threatened Canada lynx (*Lynx canadensis*) to the southern portion of their former range, 218 individuals were reintroduced into Colorado from 1999–2006 (Devineau et al. 2010). Snow tracking of released individuals and their progeny from 2000–2009 indicated that approximately 70% of lynx diet in Colorado was comprised of snowshoe hares (*Lepus americanus*,

Shenk 2009). Thus, as in the northern portions of their range where lynx demography is famously tied to snowshoe hare population cycles (Hodges 2000a, Krebs et al. 2001), existence of lynx in Colorado and long-term success of the reintroduction effort hinges, at least partly, on maintaining adequate and widespread populations of hares in the state.

Generally, snowshoe hares are associated with dense understory vegetation that provides both browse and protection from elements and predators (Wolfe et al. 1982, Litvaitis et al. 1985, Hodges 2000b, Ellsworth and Reynolds 2009). In montane regions of the conterminous U.S., this understory can be provided by young, even-aged conifer stands regenerating after stand-replacing fires or timber harvest (Koehler 1990, Koehler and Brittell 1990, Bull et al. 2005) as well as mature, uneven-aged stands (Beauvais 1997, Berg 2009, Griffin and Mills 2009). Hares may also take advantage of seasonally abundant browse and cover provided by deciduous cover (e.g., riparian willow [*Salix* spp.], aspen [*Populus tremuloides*]; Wolff 1980, Miller 2005). In contrast to the continuous expanse of boreal forest at the heart of lynx and hare ranges at northerly latitudes, purported hare habitat in the U.S. Rocky Mountains is naturally fragmented due to strong topographic and climatic variation. In fact, many have suggested that the fragmented nature of the habitat in this region may dampen or even eliminate the famous cyclic behavior of hare populations (Howell 1923, Dolbeer and Clark 1975, Wolff 1980, Keith et al. 1993), although snowshoe hare demography and population dynamics in the southern portion of their range are not well known (Hodges 2000b).

In Colorado, Dolbeer and Clark (1975) postulated that mature Engelmann spruce (*Picea engelmannii*)/ subalpine fir (*Abies lasiocarpa*) forest was preferred hare habitat and used live-trapping data to estimate density, survival, home range, and productivity in

such stands during summer. Similarly, Zahratka and Shenk (2008) showed that winter snowshoe hare densities were generally greater in mature spruce/fir forests compared to mature lodgepole pine stands. In contrast, Miller (2005) concluded from annually collected pellet plot data that mid-seral spruce/fir and lodgepole pine (*Pinus contorta*) stands were most consistently occupied by snowshoe hares in northern Colorado. However, understory and structural complexity were important predictors of pellet occurrence, suggesting that early or late-seral stands may also have the capability of providing hare habitat, depending on their structure (Miller 2005).

Recent snowshoe hare research in the U.S. Rocky Mountains has focused on density estimation or indices to density (Miller 2005, Malaney and Frey 2006, Zahratka and Shenk 2008, Berg 2009, Hodges et al. 2009) which have resulted in the patterns of association described above. However, density may not necessarily reflect fitness, and density can be high even in “sink” habitats (Van Horne 1983). For instance, Griffin and Mills (2009) documented high hare densities in dense young conifer stands in western Montana. They also found that only uneven-aged, mature stands held as many hares in winter as in summer, hares using mature stands had higher survival rates, and only uneven-aged mature stands functioned as sources over the course of their study; all other stand types sampled, including dense young stands, were population sinks.

In sum, habitat associations of snowshoe hares in the Rocky Mountains of the conterminous U.S. have been described, but habitat-specific demographic estimates, in addition to density, are sparse. Thus, considerable uncertainty exists regarding the types of stands necessary for persistence of snowshoe hares (and lynx) in these landscapes. Here I identify 3 types of stands associated with snowshoe hares in the Southern Rockies,

then evaluate the importance of each stand type using a combination of mark-recapture and radio telemetry data to rigorously estimate stand-specific snowshoe hare density, survival, and recruitment. In contrast to previous hare research in Colorado, I concurrently sampled early, mid-, and late-seral stands during both summer and winter. Based largely on Griffin and Mills (2009), I expected that 1) snowshoe hare densities would be highest in early seral lodgepole stands, but most consistent in mature spruce/fir stands, 2) survival and recruitment would be highest in mature spruce/fir, and 3) density, survival, and recruitment would be highly correlated with understory cover.

## **3.2 METHODS**

### **3.2.1 Study Area**

The study area encompassed roughly 1200 km<sup>2</sup> around Taylor Park and Pitkin, Colorado, USA (39°50'N, 106°34'W; Figure 1), and included a portion of the “Core Reintroduction Area” occupied by reintroduced Canada lynx (Shenk 2009). Open sagebrush (*Artemisia tridentata*) parks dissected by narrow riparian zones of willow and potentilla (*Potentilla* spp.) dominated the relatively low elevation (~2800–3000m) parts of the study area. Extensive stands of lodgepole pine occupied low and mid-elevation slopes (~3000–3300m), giving way to narrow bands of Engelmann spruce/subalpine fir in the sub-alpine zone (~3200–3600m). Alpine tundra topped the highest parts of the study area (~3300–4200m). Moist spruce/fir forests also occurred on north-facing slopes at mid-elevations. Some human habitation occurred, mostly in the form of seasonal residences. The area received considerable recreational use during summer in the form of dispersed camping and off-highway vehicle traffic.



Climate was typical of continental, high-elevation zones with relatively short, mild summers and long, harsh winters. Mean July temperature was 14°C; mean January temperature was -11°C. The area receives approximately 51–64 cm of precipitation annually, mostly in the form of winter snow and late summer monsoons (Koch and Barger 1988). Maximum snow depth on the study area averaged 80 cm but ranged from 22–163 cm depending on year, elevation, and aspect. Snowpack generally persisted from November through May (low elevations) or June (high elevations and north-facing slopes).

### **3.2.2 Sampling**

From the literature, I identified early and mid-seral, even-aged lodgepole pine stands as potential habitat for snowshoe hares, along with mature, uneven-aged, spruce/fir (Dolbeer and Clark 1975, Hodges 2000b, Miller 2005, Zahratka and Shenk 2008, Ellsworth and Reynolds 2009). Thus, I selected “small” (early seral) and “medium” (mid-seral) lodgepole stands and “large” (mature) spruce/fir stands for sampling, where the classes “small”, “medium”, and “large” refer to the diameter at breast height (dbh) of overstory trees as defined in the United States Forest Service R2VEG database (small = 2.54–12.69 cm dbh, medium = 12.70–22.85 cm dbh, and large = 22.86–40.64 cm dbh; J. Varner, United States Forest Service, personal communication). Small lodgepole stands were clear cut approximately 20–25 years prior to sampling and had regenerated into densely stocked stands (6231 stems/ha, Appendix A). Trees in these stands had not started to self-prune and tree canopies generally extended to ground level. Medium lodgepole stands were clear cut approximately 40–60 years prior to sampling and were pre-commercially thinned to 3-m spacing at approximately 20 years pre-sampling.

Trees in these stands were beginning to self-prune with lower branches starting an average 0.83 m above ground. Spruce/fir stands had some evidence of historical logging, but were largely unmanaged and structurally complex due to down logs and their uneven-aged nature.

I intended to randomly select 3 replicates of each stand type to sample for snowshoe hare density and demography using live-trapping grids. However, due to logistical constraints I subjectively selected sites that best typified the 3 stand types of interest. Additionally, few small lodgepole stands were of sufficient size to hold a full trapping grid so I sampled twice as many of these sites using half-sized grids. Thus, I sampled 3 mature spruce/fir sites, 3 medium lodgepole sites, and 6 small lodgepole sites within the study area.

I used a combination of mark-recapture and telemetry data to estimate snowshoe hare density and demography at each site during both summer (mid-July through September, 2006–2008) and winter (mid-January through March, 2007–2009). Colorado State University and Colorado Division of Wildlife Animal Care and Use Committees approved all sampling methods (Colorado State University IACUC Protocol 06-062A-03). For mark-recapture sampling, I used Tomahawk Model 204 live traps deployed on  $7 \times 12$  (medium lodgepole and large spruce/fir) or  $6 \times 7$  (small lodgepole) grids with 50-m spacing. I covered traps with pine boughs and bark to protect entrapped animals from elements; additionally, during winter sampling sessions, I encased traps in several inches of snow to provide further protection. Traps were baited with apple slices, commercial rabbit chow, and cubed timothy hay (*Phleum pratense*). I pre-baited traps for 3 nights, followed by 5 nights of trapping. Several hares died during my initial winter sampling

session, apparently due to capture myopathy (Lisa Wolfe, DVM and Laurie Baeten, DVM, Colorado Division of Wildlife, personal communication). Thereafter, I reduced my trapping effort by locking traps open on the third night of each 5-night trapping effort. This eliminated the possibility that hares could be trapped >2 nights in a row (most deaths occurred after individuals were captured on 3 consecutive nights) without deterring individuals from using the sampling grid. Altering my protocol in this manner alleviated the capture myopathy issue, and I used the altered trapping schedule for the remainder of the winter trapping sessions.

I concurrently sampled 1 spruce/fir grid, 1 medium lodgepole grid, and 2 small lodgepole grids. Upon completion, I moved to a second set of 4 grids, then on to the third. I sampled the same 12 grids each season, but rotated the order in which I sampled the groups of replicates so that no set of grids was routinely sampled early or late in a sampling season.

I aged, weighed, sexed, and individually marked captured hares with a passive-integrated transponder (PIT) tag (Biomark Inc., Boise, Idaho, USA), all without anesthesia. Additionally, I radio-marked up to 10 hares per grid using a 28-g collar (Model TW5SM, BioTrack, LTD, Wareham, Dorset, United Kingdom) equipped with a 6-hr mortality sensor. I anticipated being unable to radio-mark every hare I captured. Furthermore, I expected heterogeneity in the use of the trapping grid (hares with home ranges near the edge of the grid were theoretically less likely to be captured than those near the interior) as well as heterogeneity in response to trapping (some hares were captured early and often, others were only captured once toward the end of a session). To account for these sources of heterogeneity and attempt to radio-mark a representative

sample of hares on each grid, I checked grids using random starting points each day so that hares near the edge were as likely to be encountered and receive a collar as hares near the center. Also, I retained 2 of the allotted 10 collars per grid for application during the last 2 days of trapping. After trapping, I carefully removed all bait from the area, in addition to traps, so that animal movements post-trapping were not influenced by the grid.

Using radio telemetry, I sampled hare movements for a 7–10 day period beginning 1–3 days post-trapping. I attempted to obtain 10 locations per individual. Hares are generally most active during nighttime (Keith 1964, Foresman and Pearson 1999), so I tried to obtain equal daytime and nighttime locations to representatively locate hares during resting and active periods. Most locations were obtained via triangulation. I prioritized hares that remained near the grid where they were captured, and worked to obtain accurate locations (in or out of the trapping grid) by triangulating at short range (usually <250 m from receiver to transmitter). Hares that strayed far from the grid after trapping were located via triangulation as well, but often at distances of >500 m. All locations were estimated using the maximum likelihood procedure (Lenth 1981) in Program LOAS (Version 4.0, Ecological Software Solutions LLC, Sacramento, CA, USA). Sometimes it was logistically more efficient to forgo triangulation and home in on individuals until I obtained a visual or heard the radio signal without an antenna. I only homed during daytime when hares were inactive and holding tight to their hiding spots; I did not record a location if it was apparent from the signal that the animal had moved as I approached. A few times per grid per session, I assessed accuracy of “short-range”

locations by triangulating on hares during daytime when they were inactive, then immediately homing on them to obtain their true location.

Hares made larger movements than I anticipated at the onset of the study and individuals initially trapped in spruce/fir, medium lodgepole, and small lodgepole stands, often did not remain exclusively in those stands during sampling. I was able to account for this phenomenon when estimating density (see below), but could not account for it when estimating survival or recruitment. Therefore, I re-defined the area to which survival and recruitment estimates applied in the following manner. I identified the 90<sup>th</sup> percentile of the distance hares were located from the center of their grid of capture during each sampling session (range = 715–1175 m), buffered the trapping grids by these distances, and defined the area included in this buffer as the “landscape” in which sampled hares lived their lives. Thus survival and recruitment estimates for hares in “spruce/fir” stands actually reflect survival and/or recruitment of individuals that used a landscape comprised of approximately 85% spruce/fir, 7% medium lodgepole, 6% willow, and 2% other. Estimates for “medium lodgepole” reflect use of landscapes comprised of 64% thinned, even-aged medium lodgepole, 15% large lodgepole, 13% aspen, and 8% other. Estimates for “small lodgepole” reflect landscapes comprised of about 7% small lodgepole, 83% large lodgepole, and 10% willow. Note that “small lodgepole” landscapes contain little small lodgepole on a percentage basis (small lodgepole stands occur as small patches [mean size = 4.9 ha] strewn throughout a matrix of larger, unharvested lodgepole), but these stands are the signature component of these landscapes as large lodgepole provides almost no understory cover and willow provides understory only seasonally. No individual moved between these 3 landscape types

during the study. With respect to survival or recruitment, any reference to spruce/fir, medium lodgepole, and small lodgepole “stands” from here forward refers to hares sampled in the 3 landscapes described above.

In addition to the relatively short telemetry sampling periods that occurred post-trapping, I also checked the status of collared hares (live or dead) from the air and/or ground during intervals between summer and winter trapping sessions. Because hares were capable of remaining still long enough to set off the mortality sensor in their collar, animals were not considered dead until they were recovered as such in the field or until mortality signals were obtained on  $\geq 3$  consecutive checks. Hares that were not captured during a given session but retained working transmitters from previous sessions were located regularly while working on the current sample of hares from a given grid.

### **3.2.3 Covariates**

To characterize the sampled stands and generate covariates for explaining variation in density or demographic rates of hares, I systematically sampled structural attributes of each replicate stand at 15 of the 84 trap locations (or 9 of the 42 trap locations for small lodgepole stands) using protocols developed for previous lynx and hare work in the region (Zahratka 2004, Shenk 2006). Specifically, at each sampled trap location I measured 1) stem density, 2) canopy cover, 3) horizontal cover, 4) crown height, and 5) down wood. I estimated stem density by measuring distance from the trap location to the nearest stem 1.0–7.0 cm, 7.1–10.0 cm, and >10.0 cm in diameter. I then applied the “closest individual method” of Cottam and Curtis (1956) to convert these measurements to density. I estimated canopy cover using vertical densitometer readings from a subsample of 25 points centered at each of the 15 trap locations (Stumpf 1993).

Both canopy cover and stem density were measured at heights of 0.1 m and 1.0 m above the ground to capture summer and winter conditions, respectively. I used a cover board (read from a distance of 6 m) to characterize horizontal cover in 0.5-m increments above the ground up to 2 m following Nudds (1977). Crown height was measured as the distance from the ground to the lowest live branch on the nearest tree. I estimated metric tons of down wood ( $\geq 2.54$  cm in diameter) per hectare according to Brown (1974). All structural measurements were averaged across the 15 trap sites to characterize the stand.

In addition to structural covariates, I also considered covariates that described potentially important landscape features around the stand of interest. I quantified the hectares of willow and small lodgepole within the landscape (as defined previously) around each trapping grid, along with the distance to the nearest patch of each.

I recorded temperature (HOBO Pro Series Temp, Onset Computer Corporation, Pocasset, MA, USA) at each grid during mark-recapture sampling as minimum temperature has been shown to influence capture probability of hares in winter (Zahratka and Shenk 2008). I constructed other weather covariates using data from the National Weather Station in Crested Butte, Colorado, which is approximately 20 km west of the study area at 2700 m elevation (National Climatic Data Center, Ashville, NC, USA). Specifically, I extracted “departure from normal precipitation,” “departure from normal days with snow cover” (based on 25-year average), and total precipitation for appropriate periods. Finally, during winter trapping sessions, I recorded snow depth at each trap where structural measurements were taken.

### 3.2.4 Density

Geographic closure of the sampling grid is critical to performance of models used to estimate abundance (and density) from mark-recapture data (Otis et al. 1978). However, this assumption is rarely met as animals routinely move on and off of grids during sampling periods. Such movement imposes a positive bias on abundance estimates (which reflect the “super population” of animals that could have used the grid during the sampling session) and makes conversion of such estimates to density difficult because the area actually sampled by the grid is unclear (White et al. 1982 p. 120, Kendall et al. 1997).

I addressed this issue using a telemetry-augmented approach (See Chapter 1). Under this approach, capture probability ( $p_i^*$ ) is modeled as a function of time, behavior, heterogeneity, or any combination of individual covariates using the traditional Huggins closed-capture formulation (Huggins 1989, 1991). Additionally, I define a second parameter ( $\tilde{p}_i$ ) as the estimated proportion of locations (or estimated proportion of time) animal  $i$  spends on the trapping grid. Estimation of  $\tilde{p}_i$  is based on telemetry data collected immediately after trapping and can include the use of covariates. Summing  $1/p_i^*$  across all captured individuals gives an estimate of the super population. Including  $\tilde{p}_i$  in the numerator of this summation corrects the estimate to reflect only the estimated “whole” and “partial” animals residing on the sampling grid. This quantity can then be divided by the area of the sampling grid to obtain an unbiased estimate of density:

$$\hat{D} = \left( \sum_{i=1}^{M_{t+1}} \frac{\tilde{p}_i}{p_i^*} \right) / A$$



where  $\hat{D}$  = estimated density,  $M_{t+1}$  = number of unique animals captured,  $A$  = area of the grid, and  $\tilde{p}_i$  and  $p_i^*$  are as defined above.

Such an estimator is available in Program MARK (White and Burnham 1999) and simulations suggest that under conditions I expected to encounter in the field, it is relatively unbiased compared to other available estimators (See Chapter 2). Simulations also suggest that given limited resources, maximizing the number of collars deployed, at the expense of obtaining a large number of locations per collar, is preferable to maximizing the number of locations at the expense of collars. Therefore, I took the former approach, and only attempted to obtain 10 locations per individual. I adjusted the nominal area of trapping grids to account for topography using the Surface Tools for Points, Lines, and Polygons Extension for ArcView 3.x, version 1.6b (Jenness Enterprises, <http://www.jennessent.com>).

I considered season (winter or summer), trapping session, stand type, grid, and distance of the mean trap location for individual  $i$  to the edge of the trapping grid ( $DTE_i$ ) as potentially important predictors of  $\tilde{p}_i$ . In addition to these covariates, I also considered age, behavior, heterogeneity, and minimum daily winter temperature as potential predictors of  $p_i^*$ . Because the likelihoods for  $\tilde{p}_i$  and  $p_i^*$  are factorable and do not influence each other, I identified the best models for each in stepwise fashion. First, I fixed  $p_i^*$  to be constant across grids and time, and considered all possible additive models using the 5 covariates for  $\tilde{p}_i$  under the constraint that redundant variables could not occur in the same model (e.g., a model with a grid effect could not also include the nested effect of stand type). I identified the best structure for  $\tilde{p}_i$  using  $AIC_c$  (Burnham and Anderson 2002). I then fixed this structure for  $\tilde{p}_i$  and built 60 models to estimate density using all additive

combinations of covariates for  $p_i^*$ , omitting models that included redundant variables. Heterogeneity and  $DTE_i$  were included in every model for  $p_i^*$  because trapping experience suggested strong heterogeneity in capture probability and simulations suggested a strong effect of  $DTE_i$ . I compared and evaluated models using  $AIC_c$ , then model-averaged (Burnham and Anderson 2002) grid-specific estimates and used the delta method (Seber 1982 p. 7) to obtain average density estimates by stand type through time.

### **3.2.5 Survival**

I estimated survival across intervals between mark-recapture sessions using a Barker model (Barker 1997, 1999) adapted for robust design (Pollock 1982, Kendall et al. 1995, Kendall et al. 1997). The Barker model incorporates dead recoveries, live resightings during mark-recapture sampling, and resightings of marked animals outside of mark-recapture sessions into the same likelihood in order to improve survival estimates and precision. Here, both dead recoveries and live “resightings” during the interval between mark-recapture sessions came in the form of live/dead data from radio signals.

The robust design is a sampling scheme in which  $\geq 1$  secondary sampling occasions (in my case, 4–5 days per trapping session) occur for each primary period of interest (i.e., summer and winter). Intervals between primary periods over which survival is estimated are relatively long, whereas intervals between secondary periods are short so populations can be assumed closed, at least demographically. Such a sampling scheme allows estimation of more survival parameters than would be possible otherwise, and increases precision of estimates by incorporating information on capture probability from secondary closed capture sessions (Kendall et al. 1995).

In addition to closed capture parameters used to model mixtures ( $\pi$ ), initial capture probabilities ( $p$ ), and recapture probabilities ( $c$ ), the parameters in the Barker robust design include:

$S_t$  = probability an individual survives interval ' $t, t + 1$ ' given that it was alive at  $t$ .

$r_t$  = probability an animal that dies in the interval ' $t, t + 1$ ' is found dead and the tag is reported.

$R_t$  = probability an animal that survives ' $t, t + 1$ ' is resighted alive during that interval.

$R'_t$  = probability an animal that dies in the interval ' $t, t + 1$ ,' without being found dead, is resighted alive in that interval before it died.

$\gamma''_t$  = probability of being on the sampling grid and available for capture during primary session  $t$ , given that the animal was present during primary session  $t - 1$ .

$\gamma'_t$  = probability that an animal returns to the sampling grid during primary session  $t$  given that the animal was not present on the study area during  $t - 1$ .

$F_t$  = probability an animal at risk of capture at time  $t$  does not permanently emigrate before  $t + 1$ .

$p_t^*$  = probability that an individual is captured at least once during primary session  $t$ , given it was alive and on the study area. Note that this parameter includes the usual closed capture parameters such as those representing mixtures ( $\pi$ ), probability of initial capture during a secondary sampling occasion ( $p_i$ ), and probability of recapture during a secondary sampling occasion ( $c_i$ ).

A priori, I hypothesized that  $S_t$  might vary with age, time, season, grid, and stand type (survival may vary among all stand types, or more simply, spruce/fir may differ from lodgepole). Also, during the first two years of sampling, anecdotal field evidence suggested an apparent decline in hare numbers. Therefore, I postulated that survival may have been especially poor during these winters and added such an effect to the list of covariates. I constructed 56 models using all additive combinations of these covariates except those that would have resulted in redundant variables in the same model. I modeled  $p_t^*$  using the best structure from the density estimation procedure.

I modeled survival with 2 groups: animals that were radio-collared and those that were not. For the radio-collared group, I specified  $r_t$ ,  $R_t$ , and  $R_t'$  to be constant across grids and time because all hares were fitted with radio tags of the same make/model and were sampled under the same protocol (including attainment of locations from the air) during each session or interval. Thus, I had no reason to suspect that the probability of being “seen” alive (or dead), or being recovered, varied through time, across grids, with stand type, etc. Setting  $r_t$  constant across time also enabled me to estimate  $S_6$  using dead recoveries collected during the 6-month interval after mark-recapture sampling ended in March 2009. This last survival estimate would have been unidentifiable otherwise. For the group that did not receive radio collars, I fixed  $r_t$ ,  $R_t$ , and  $R_t'$  to zero as it was impossible to observe or recover uncollared individuals from this group during intervals between mark-recapture sampling.

I constructed models that allowed the probability of leaving or returning to a sampling grid within  $(\gamma_t'', \gamma_t')$  or between  $(F_t)$  seasons to vary between large and small grids and between habitat types. However, initial results using such structures were not

well supported (i.e., incorporating these effects reduced AICc scores), those parameters were not well estimated, and they were tangential to my goal of estimating survival. Therefore, I fixed  $\gamma_t''$ ,  $\gamma_t'$ , and  $F_t$  to be constant across grids and time for the final analysis.

### 3.2.6 Recruitment

Because I sampled under a robust design framework and obtained age-specific (juvenile or adult) estimates of abundance and survival, I was able to estimate recruitment (number of adults in the population at time  $t + 1$  that were not in the population at time  $t$ ) following Nichols and Pollock (1990). Using their ad hoc approach, recruitment from in situ reproduction ( $B'$ ) was estimated as the product of the number of estimated juveniles alive at time  $t$  and the estimated proportion of these animals that survived to  $t + 1$ .

Recruitment from immigration ( $B''$ ) was obtained by subtracting the estimated number of adult and juvenile survivors over the interval  $(t, t + 1)$  from the estimated number of adults at  $t + 1$ . I altered their equations by substituting  $\sum \tilde{p}_i$  everywhere they required absolute abundance of animals. Thus, my estimates were standardized to reflect the number of hares recruited per hectare, rather than the total number of hares recruited per grid, and estimates of recruitment were directly comparable to estimates of density.

Density and survival were derived separately; therefore I could not directly estimate the covariance between them. I assumed this quantity to be zero and calculated SE for these estimates using the delta method (Seber 1982, p. 7).

### 3.2.7 Variance Components

To assess the influence of habitat and weather variables on density and survival of hares, I analyzed components of variance in density and survival estimates using Program MARK (Burnham and White 2002). Generally this type of analysis proceeds by

producing a set of parameter estimates from a general (fully time and/or spatially specific) fixed effects model, followed by application of a random effects model to those estimates. This allows estimation of the true process variation among the original estimates separate from sampling variation (Franklin et al. 2002). I sampled 12 grids across 6 sessions (or intervals in the case of survival), which under a general fixed effects model produces 72 estimates of density (or survival). However, these 72 estimates were not independent as multiple grids were sampled during a single session, and multiple sessions were sampled at a single grid. Therefore, for the random effects portion of the procedure, I first fit “session” (or interval in the case of survival) as a fixed effect within the random effects model to estimate the process variation among the 72 estimates after accounting for the effect of session ( $\sigma_s^2$ ). I then added habitat variables (one at a time) to this “session” model to estimate the process variation left after accounting for both session and the habitat variable of interest ( $\sigma_{s+h}^2$ ). The quantity  $(\sigma_s^2 - \sigma_{s+h}^2)/\sigma_s^2$  is an estimate of the percent variation in density or survival estimates due to the habitat variable, after accounting for variation due to session. Similarly, I fit grid as a fixed effect, then added session-specific variables (i.e., weather variables) one at a time to estimate the percent variation in density or survival due to the session variable, after accounting for variation among grids.

I considered 7 habitat variables as potentially important predictors of variation in snowshoe hare density. Because hares tend to be associated with dense cover, I expected density to be positively related to horizontal cover (mean value 0–2 m above ground), stem density (for stems 1–7 cm in diameter), canopy cover, down wood, and willow hectares; I expected a negative relationship between crown height and distance to willow.

Also, because willow is deciduous and unavailable during winter, I assigned the covariate “hectares of willow” a value of zero for winter sessions. Similarly, I assigned “distance to willow” the maximum observed for any stand in the study. These adjustments functionally made the willow covariates important only during summer sampling sessions. Finally, I isolated the small lodgepole stands ( $n = 36$  estimates) and analyzed variance components by fitting “hectares of small lodgepole” as well as “distance to small lodgepole” as fixed effects, reflecting my hypothesis that density in these stands might be dependent on the amount of similar habitat in the surrounding landscape.

I considered 2 weather variables as potentially important predictors of variation in snowshoe hare density across sampling sessions. I expected total precipitation for the 1 year period immediately preceding summer sampling to be positively correlated with hare density because increased precipitation should result in increased browse, cover, survival, and productivity during the 12 months leading up to the year of interest. I also considered a 2-year lag in precipitation effects.

I postulated similar relationships with habitat variables for survival. However, I hypothesized that precipitation would have more immediate effects on survival, so I considered total precipitation during the interval of interest (rather than 1 year prior) as well as a 6-month lag (rather than 2-year lag) as covariates to evaluate. Additionally, departures from normal snowfall may influence survival by facilitating mismatches between hare pelage (which changes during fall and spring based on photoperiod) and surroundings (L. S. Mills, Personal Communication). Therefore, I included “departure from average days of snow cover” (based on 25-year average) and “departure from normal precipitation” for the interval of interest.

### 3.3 RESULTS

I captured 305 hares (132 males, 151 females, 22 unknown sex; 246 adults, 59 juveniles) 740 times over the course of the study. I radio-tagged 223 (73%) of these hares, obtained 2,252 total locations, and averaged 8.3 locations/hare/season (range = 3–12). Ninety-one percent of locations were obtained via triangulation; the remainder were obtained by homing. Fifty-four percent of locations were obtained during daytime (~10am to 1 hour before official sunset), 46% during nighttime (1 hour after official sunset to ~2:00am). Based on  $n = 100$  trials over the 6 sampling sessions, mean estimated location error was 63 m (range 3–330), slightly more than 1 trap width.

#### 3.3.1 Density

The top model for  $\tilde{p}_i$  was the general, additive structure in which  $\tilde{p}_i$  varied by trapping session, grid, and  $DTE_i$  ( $AIC_c$  weight = 0.99). Capture probability ( $p_i^*$ ) was strongly influenced by behavioral effects (recapture probability was lower than initial capture probability), age (adults were more difficult to capture than juveniles), trapping session, and grid. These effects appeared in the only models that held any weight (Table 1), and slope parameters for these effects were strongly divergent from zero. Minimum daily temperature during winter trapping also appeared in the top models, but its inclusion increased  $AIC_c$  scores of base models and the slope for this effect was zero, indicating that it is not an important variable. My assertion that heterogeneity and  $DTE_i$  were important enough to include in every model was well-founded. Removing heterogeneity from the top model added 170 units to its  $AIC_c$  score; removing  $DTE_i$  added 50 units.



I estimated snowshoe hare densities in all stand types and all seasons to be  $<1.0$  hares/ha (Figure 2). During summer, densities were generally highest in small lodgepole stands ( $0.20 \pm 0.01$  (SE) to  $0.66 \pm 0.07$  hares/ha), lowest in medium lodgepole ( $0.01 \pm 0.04$  to  $0.03 \pm 0.03$  hares/ha), and intermediate in spruce/fir stands ( $0.01 \pm 0.002$  to  $0.26 \pm 0.08$  hares/ha). Summer 2008 was an exception as spruce/fir grids appeared virtually uninhabited. However, telemetry information and direct observation indicated that several hares were available but never captured. This phenomenon did not occur for other stand types or during other seasons and its cause is unclear. Regardless, I likely underestimated hare density in the spruce/fir stand type during summer 2008 by an unknown amount. During winter, density estimates generally became more similar among stand types compared to summer estimates. Small lodgepole stands lost hares from summer to winter, medium lodgepole stands gained hares (although inference here is weak given the poor precision of these estimates), and spruce/fir stands retained nearly as many hares as during summer (except during 2008 as noted above). The bulk of hares in the system occurred in either small lodgepole or spruce/fir stands. Hares in these stands apparently underwent a decline that began in winter 2007 and ended in either summer 2008 (small lodgepole) or winter 2009 (spruce/fir).

### **3.3.2 Survival**

I found strong support for seasonal differences in hare survival (summer–winter survival was higher than winter–summer) and depressed survival during the first 2 winters of the study (Table 2). These effects pervade the top models in the set (cumulative  $AIC_c$  weight for “season” across all models in the set was 0.66, cumulative  $AIC_c$  weight [2-winter decline] = 0.44) and slopes for these parameters were non-zero.

The spruce/fir effect appeared moderately important (cumulative AIC<sub>c</sub> weight [spruce/fir] = 0.41) as addition of this effect to seasonal or decline models slightly improved their AIC<sub>c</sub> scores and the 95% confidence intervals on the spruce/fir slope only slightly overlapped zero. Hares in spruce/fir stands tend to have higher survival than hares residing in either of the lodgepole stand types. There was little evidence that age or stand type (in this case “stand type” meant that survival was allowed to differ among all three stand types rather than simply by spruce/fir or not spruce/fir) impacted survival; these effects appeared in some of the top models, but their addition increased the AIC<sub>c</sub> score of the parent model, cumulative AIC<sub>c</sub> weights were lower (0.17–0.25), and 95% confidence intervals on their slopes included zero. Model-averaged estimates reflected seasonal differences, depressed survival early in the study, and relatively high spruce/fir survival as noted above. Annual survival ranged from  $0.10 \pm 0.03$  SE to  $0.20 \pm 0.07$  SE depending on year and stand type (Table 3).

### 3.3.3 Recruitment

Recruitment of juvenile hares (*in situ* recruitment) was most consistent in small lodgepole stands (Figure 3b). Juveniles were recruited into spruce/fir populations during 2 of the 3 years of the study, but were minimally recruited into medium lodgepole in only 1 year (Figure 3b). Hares tended to immigrate into spruce/fir and medium lodgepole stands during each summer–winter interval, but immigration estimates were zero or slightly negative (i.e., emigration occurred) during winter–summer intervals (Figure 3a). Conversely, hares tended to immigrate into small lodgepole during winter–summer. However, precision was poor for all immigration estimates and 95% CIs for all estimates overlapped zero.

### 3.3.4 Variance Components

Of the habitat variables I considered for the variance components analysis, horizontal cover explained the greatest portion of variation in hare densities (after accounting for variation due to trapping session), followed by stem density, canopy cover, and down wood (Table 4). Hectares of willow, crown height, and distance to willow accounted for little variation. Estimated slopes for habitat variables generally followed my hypotheses (hare densities tended to be positively associated with horizontal cover, stem density, canopy cover, and hectares of willow in the surrounding landscape, but negatively associated with distance to willow and height of tree crowns above the forest floor), but only horizontal cover and stem density had slopes that differed strongly from zero based on 95% confidence intervals. For the sub-analysis involving only small lodgepole stands, process variance could not be estimated, likely because it was swamped by large sampling variance. However, the slopes and associated 95% CIs of the random effects models indicated strong positive relationships between hare density and both the amount of small lodgepole surrounding the patch of interest and distance to the nearest small lodgepole patch. The former relationship is consistent with my prediction, but the latter is contradictory. Of the weather variables I considered, total precipitation 1 year prior to the year of sampling accounted for more session to session variation than total precipitation 2 years prior. Precipitation was positively correlated with density at both scales, but the effect was stronger (CI did not include zero) for the year immediately preceding sampling.

With respect to survival, no habitat variable explained much variation in the estimates and none of the slopes were in the direction I predicted (Table 5). For the

analysis involving small lodgepole stands only, I found evidence that survival was positively related to the amount of small lodgepole in the immediate landscape, and negatively related to the distance to the nearest neighboring small lodgepole. Total precipitation in the current interval was positively associated with survival and explained a substantial portion of session-to-session variation in survival. Other weather variables explained relatively little, if any variation, although the slopes for departure from normal snowfall and departure from normal precipitation were as predicted.

### **3.4 DISCUSSION**

Snowshoe hare densities in Colorado were <1.0 hares/ha in all seasons and in all types of stands, and in most cases were <0.3 hares/ha. These results tend toward the low end of those reported elsewhere in the U. S. Rocky Mountains (Zahratka and Shenk 2008, Berg 2009, Ellsworth and Reynolds 2009, Griffin and Mills 2009) and correspond to densities observed during the low phase of population cycles in boreal Canada (Hodges 2000b). This is partly due to the method I used to estimate density. In Chapter 2, I found that density estimation based on “mean maximum distance moved” (MMDM, Wilson and Anderson 1985), which was used in the previously-listed studies, tends to be positively biased whereas the telemetry estimator I employed here is relatively unbiased. Indeed, re-calculating densities in my study area using the popular  $\frac{1}{2}$  MMDM or full MMDM methods (Wilson and Anderson 1985, Parmenter et al. 2003), increased estimates by an average of 100% and 33%, respectively.

I observed lower hare densities in small lodgepole stands during winter compared to summer, whereas medium lodgepole stands experienced the opposite. My estimates of recruitment due to immigration are consistent with these changes: hares tended to move

into medium lodgepole stands during the summer-winter interval, but moved into small lodgepole stands during the winter-summer. The most obvious explanation for this apparent movement is the interaction between snow depth and tree canopy. Medium lodgepole stands were mature enough that lower limbs were largely inaccessible to hares during summer, but winter snows brought those canopies within reach for use as browse and/or cover. Conversely, heavy winter snows exacerbated by a “snow fence” effect could have filled small lodgepole stands to a degree, making them less desirable. Mature spruce/fir forests exhibited less dramatic changes in seasonal density estimates, likely because their complex structure provided cover under a variety of conditions. Beyond stand type, the variance components analysis confirmed that hare density was positively correlated with dense cover (e.g., horizontal cover, stem density, down wood) as has been shown consistently throughout the snowshoe hare literature (Hodges 2000b, Ellsworth and Reynolds 2009). I also found that precipitation during the 12 months preceding sampling explained a fair amount of variation in hare density. Presumably more precipitation translated to more herbaceous forage and cover, which may have promoted better survival and reproduction leading to more hares. However, this correlation is tenuous given the short duration of the study.

The cyclic nature of hare populations has fascinated ecologists for decades and is a well-documented phenomenon in the boreal forest. Hodges (2000b) concluded from time series of harvest data that hares likely cycle in the southern portion of their range as well, albeit at diminished amplitudes. However, Dolbeer and Clark (1975) and Hodges et al. (2009) determined that hares were acyclic. This study was only 3 years in length and thus cannot provide conclusive evidence for or against cycling. Density estimates in

spruce/fir and small lodgepole stands declined then partially recovered during the study, consistent with a low amplitude cycle. Anecdotal evidence from lynx tracking crews in Colorado suggested that hare densities were higher prior to this study and have rebounded further since its conclusion, also consistent with a population cycle (T. Shenk, unpublished data).

However, the pattern I observed could be explained in other ways. For instance, some models suggest that predator-prey systems can have multiple equilibria (Ricklefs 1993 p. 378). Lynx were only recently reintroduced to this landscape after being absent for decades. Possibly the hare population was released from a lower equilibrium when lynx were extirpated from Colorado, and I observed the population returning to this state in response to the recent return of lynx (e.g., the "predation model," Messier 1994).

Alternatively, the decline I observed could have been due to reduced survival as a result of abnormal winters (minimal snow cover during the first winter followed by heavy, persistent snow cover during the second winter). Hares turn color during spring and fall based on photoperiod. Thus during winters that deviate strongly from normal, many hares would be white when their environment lacks snow cover or vice-versa. Random effects models indicated that hare survival was indeed correlated with deviations from normal precipitation and snow cover. However, these models explained relatively little variation in hare survival and other factors appeared more important. Finally, the pattern in hare abundance I observed could represent an acyclic fluctuation in hare populations in the region due to unmeasured factors. Any combination of these explanations is plausible as well, and they cannot be teased apart without further extending the time series of the study.

Regardless of the cause of the apparent decline, it may have had important ramifications for lynx ecology and management. The Colorado Division of Wildlife documented reproduction by reintroduced lynx in the 4 years leading up to and including summer 2006, the first summer of this hare work (Shenk 2009). Anecdotal information suggests that hare numbers were high during these years (T. Shenk, personal communication). No reproduction was recorded during the 2 summers of apparent hare decline during this study, but reproduction resumed following winter 2009 (Shenk 2009) when hares apparently rebounded. Thus, as has been shown elsewhere (e.g., Brand et al. 1976, Poole 1994), snowshoe hares may play a critical role in successful lynx reproduction.

Relationships between survival and vegetation attributes of each stand were largely opposite of predictions based on previous work. I offer 2 explanations for this discrepancy. First, hares utilized larger areas than I anticipated at the onset of the study. I was able to tie density estimates directly to the stands where covariates were measured using ancillary telemetry information, but survival could not be similarly corrected. Perhaps the habitat measurements made on my relatively small trapping grids were not representative of the larger areas hares used during the study, leading to counterintuitive results. Second, survival was estimated over long periods in which conditions covered the complete gradient from summer to winter conditions. Habitat covariates were measured at the endpoints of these intervals. Thus there was a mismatch between the time when measurements were taken and the interval to which I tried to apply them. I attempted to address this by averaging summer and winter covariate values and using the

averages to explain variation in survival, but perhaps this approach was too coarse to be meaningful.

No combination of survival and recruitment estimates from any stand type in any year would result in a self-sustaining population. This is somewhat unsurprising given that I sampled during an apparent population decline, but is not consistent with the partial recovery I observed, especially considering that I intentionally sampled purportedly “good” hare habitat. Annual and 30-day survival estimates were within the range of values reported elsewhere for hares (Hodges 2000b, Hodges et al. 2001, Griffin and Mills 2009); survival early in the study is closer to rates reported for populations known to be in decline whereas survival later in the study is consistent with rates reported for increasing populations. This suggests that recruitment estimates, at least in the last year of the study when the population apparently began to recover, were too low. My sampling efforts started in mid-July each summer, corresponding roughly to the timing of the second birth pulse of hares in the area (Dolbeer and Clark 1975). Juveniles born during this pulse may have been unavailable for capture during initial summer sampling sessions. Given that second litters are often larger than first litters (Dolbeer and Clark 1975, Griffin and Mills 2009), and during a recovery hares are more productive than usual (Krebs et al. 2001), I may have missed a substantial number of juvenile hares. Furthermore, in some years, third litters are possible in Colorado (Dolbeer and Clark 1975). If this occurred I likely under sampled the third litter to a greater degree than the second, further biasing my estimate. However, given that I sampled each stand type during each of the 3 sampling sessions conducted each summer, relative differences in



recruitment among stands are probably representative even if overall recruitment was underestimated.

This study did not explicitly assess the importance of juxtaposition or connectivity between stands types, although the variance components analysis suggested that survival of hares in small lodgepole stands was positively related to the amount of small lodgepole in the surrounding landscape and was inversely related with distance to the nearest small lodgepole patch. I found weak evidence suggesting that density in small lodgepole stands followed a similar pattern and that willow in the landscape can positively influence hare density in all stand types. I urge managers to consider juxtaposition when planning for hare and/or lynx conservation in their jurisdictions. During this study, some hares made large movements over short periods, apparently making use of many types of forest habitat including mixed conifer, mature lodgepole, aspen, and willow. Given the structure of these stands, I doubt that they are capable of self-sustaining hare populations, but they may be seasonally important and/or provide connectivity between preferred stands types. I did not observe hares venturing into dry sagebrush valleys or alpine ridges despite their having the opportunity to do so. Work to identify corridors of movement and barriers to dispersal would facilitate better management for hares and should be pursued.

Hares reached their highest densities and recruited juveniles most consistently in small lodgepole stands, followed closely by spruce/fir, but survival was highest in spruce/fir stands. Hare density in medium lodgepole stands was uniformly low (even during winter when snow apparently made these stands more useful to hares), recruitment of juveniles in these stands was largely absent, and survival was relatively low. With the

exception of juvenile recruitment in small lodgepole outpacing spruce/fir, these results are fairly consistent with my original, broad predictions based on work by Griffin and Mills (2009) in Montana. I conclude that thinned, medium lodgepole stands are relatively unimportant as primary habitat for snowshoe hares in central Colorado.

Small lodgepole stands occupied 6,167 ha in the study area whereas mature spruce/fir stands occupied 62,512 ha. Similarly, spruce/fir forests encompass twice the area of lodgepole pine forest statewide (Buskirk et al. 2000) and only a portion of statewide lodgepole pine occurs as “small” stands. Furthermore, the complex structure of late-successional spruce/fir forests can potentially provide hare habitat for many decades, whereas the dense structure of small lodgepole stands is more ephemeral, likely providing good hare habitat for approximately 10 to 30 years post clear-cutting, dependent on site conditions. Thus, while some of my metrics of snowshoe hare population performance favor small lodgepole, the sheer area covered by spruce/fir, along with the consistency and longevity with which it may provide habitat, render it equally important, if not more important as a resource for hares. Timber management for snowshoe hares in Colorado should focus on maintenance of small lodgepole and mature spruce/fir stands on the landscape.

This study represents one of the first in the Southern Rocky Mountains in which stand-specific density and demographic rates were simultaneously estimated during both summer and winter periods and across more than one stand type. However, I temper these findings with the recognition that sampling covered only a small area, and sites were not chosen randomly, which precludes any statistical inference to areas beyond those sampled. Elevation, soils, moisture, and management history vary within the

montane portions of this region which may influence the suitability of regenerating lodgepole and mature spruce/fir stands for hare habitat. Replicate studies are warranted.

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Table 1. Table of model selection results for snowshoe hare density estimation in mature spruce/fir, even-aged small lodgepole, and thinned, even-aged medium lodgepole stands in west-central Colorado, USA, summer 2006–winter 2009. Sixty models were considered for the analysis; the top ten based on  $AIC_c$  (Burnham and Anderson 2002) are shown. Density estimation was implemented in Program MARK using information from telemetry sampling to correct for lack of geographic closure.

Model*	$AIC_c$	$\Delta AIC_c$	$AIC_c$ Wt.	$K$
p(heterogeneity+DTE+age+behavior+grid+session)	3482.2	0.0	0.73	41
p(heterogeneity+DTE+age+behavior+grid+session+wintertemp)	3484.3	2.0	0.26	42
p(heterogeneity+DTE+age+behavior+grid+season)	3492.5	10.3	0.00	37
p(heterogeneity+DTE+age+behavior+grid+season+wintertemp)	3494.2	11.9	0.00	38
p(heterogeneity+DTE+age+behavior+grid)	3494.8	12.6	0.00	36
p(heterogeneity+DTE+age+behavior+session+stand)	3500.9	18.7	0.00	32
p(heterogeneity+DTE+age+behavior+session)	3501.9	19.7	0.00	30
p(heterogeneity+DTE+age+behavior+session+stand+wintertemp)	3502.4	20.2	0.00	33
p(heterogeneity+DTE+age+behavior+session+wintertemp)	3503.1	20.8	0.00	31

p(heterogeneity+DTE+age+behavior+season+stand)	3504.5	22.3	0.00	28
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\*Models names indicate structures applied to capture probability ( $p_i^*$ ) only (DTE is the distance to the edge of the grid from the mean capture location). All models were built using the previously determined best structure for  $\tilde{p}_i$  (DTE + grid + session).

Table 2. Table of model selection results for snowshoe hare survival in mature spruce/fir, even-aged small lodgepole, and thinned, even-aged medium lodgepole stands in west-central Colorado, USA, summer 2006–summer 2009. Forty-two models were considered during the analysis; the top ten based on  $AIC_c$  (Burnham and Anderson 2002) are shown. Survival estimation was implemented via the Barker robust design data type in Program MARK using telemetry sampling to improve precision over mark-recapture alone.

Model*	$AIC_c$	$\Delta AIC_c$	$AIC_c$ Wt.	$K$
S(season + spruce/fir)	2631.9	0.0	0.09	32
S(season)	2631.9	0.0	0.09	31
S(2-winter decline)	2632.0	0.1	0.09	31
S(2-winter decline + spruce/fir)	2632.3	0.4	0.07	32
S(season + spruce/fir + 2-winter decline)	2632.7	0.8	0.06	33
S(season + spruce/fir + 1-winter decline)	2632.8	0.9	0.06	33
S(season + 2-winter decline)	2632.8	0.9	0.06	32
S(season + 1-winter decline)	2633.2	1.3	0.05	32
S(season + stand)	2633.6	1.7	0.04	33

S(season + spruce/fir + age)	2634.1	2.2	0.03	33
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\*Models names indicate structures applied to survival ( $S$ ) only. All models used the best structure for  $p_i^*$  from Table 1. Other model parameters ( $r$ ,  $R$ ,  $R'$ ,  $F$ ,  $\gamma'$ ,  $\gamma''$ ) were fixed to be constant (.) or zero, as specified in the text.

Table 3. Model-averaged adult survival estimates (SE) for snowshoe hares in west-central Colorado, USA, summer 2006–summer 2009.

		Year 1	Year 2	Year 3
Spruce/fir	Summer-Winter	0.52 (0.08)	0.54 (0.07)	0.53 (0.08)
	Winter-Summer	0.28 (0.05)	0.30 (0.05)	0.39 (0.05)
	Annual	0.14 (0.05)	0.16 (0.05)	0.20 (0.07)
	30-day <sup>a</sup>	0.85 (0.02)	0.86 (0.02)	0.88 (0.03)
Med Lodgepole	Summer-Winter	0.47 (0.07)	0.48 (0.07)	0.48 (0.07)
	Winter-Summer	0.23 (0.05)	0.25 (0.05)	0.34 (0.10)
	Annual	0.11 (0.03)	0.12 (0.03)	0.16 (0.06)
	30-day <sup>a</sup>	0.83 (0.02)	0.84 (0.02)	0.86 (0.02)
Small Lodgepole	Summer-Winter	0.46 (0.004)	0.47 (0.004)	0.47 (0.003)
	Winter-Summer	0.23 (0.002)	0.24 (0.003)	0.33 (0.01)
	Annual	0.10 (0.03)	0.12 (0.03)	0.15 (0.05)
	30-day <sup>a</sup>	0.83 (0.02)	0.84 (0.02)	0.86 (0.02)

<sup>a</sup>Represents transformation of annual survival estimate to a generic 30-day interval.

Table 4. Variance components analysis for density estimates ( $n = 72$ ) of snowshoe hares from west-central Colorado, USA, summer 2006–winter 2009. Estimates were not independent of each other, so effects that varied by grid were examined after fitting a fixed effect for trapping session; effects that varied by session were examined after fitting a fixed effect for grid. Percentages represent estimated portion of the total process variation explained by the effect of interest, after accounting for grid or session effects.

Effect	% Variation			
	explained	Slope ( $\hat{\beta}$ )	95% LCL	95% UCL
<b>After accounting for session:</b>				
Horizontal cover	60.4	0.000675	0.000232	0.001118
Stem density	34.1	0.000005	0.000001	0.000009
Canopy cover	22.6	0.043654	−0.005025	0.092333
Down wood	18.5	−0.000351	−0.000772	0.000070
Hectares of willow	8.3	0.001319	−0.000665	0.003303
Crown height	2.4	−0.013963	−0.039057	0.011131
Distance to willow	0.0	−0.000004	−0.000024	0.000016
Hectares of Small lodgepole <sup>a</sup>	0.0	0.006527	0.003115	0.009939
Distance to small lodgepole <sup>a</sup>	0.0	0.000173	0.000022	0.000324
<b>After accounting for grid:</b>				
Total Precipitation (1 yr prior)	58.0	0.000056	0.000021	0.000091
Total Precipitation (2 yr prior)	25.5	0.000033	0.000000	0.000066

<sup>a</sup>Random effects model run using data from small lodgepole stands only ( $n = 36$ ).

Table 5. Variance components analysis for survival estimates ( $n = 72$ ) of snowshoe hares from west-central Colorado, USA, summer 2006–winter 2009. Estimates were not independent of each other, so effects that varied by grid were examined after fitting a fixed effect for trapping session; effects that varied by session examined after fitting a fixed effect for grid. Percentages represent the estimated portion of the total process variation explained by the effect of interest, after accounting for grid or session effects.

Effect	% Variation			
	explained	Slope ( $\hat{\beta}$ )	95% LCL	95% UCL
<b>After accounting for session:</b>				
Down wood	7.1	−0.000376	−0.000711	−0.000041
Canopy cover	3.5	−0.083534	−0.172465	0.005397
Horizontal cover	1.2	−0.000233	−0.000552	0.000086
Hectares of Willow	1.2	−0.000064	−0.000156	0.000028
Distance to willow	1.2	0.000009	−0.000003	0.000021
Stem density	0.0	−0.000002	−0.000006	0.000002
Crown height	0.0	0.013311	−0.012057	0.038679
Hectares of small lodgepole <sup>a</sup>	55.6	0.001509	0.001001	0.002017
Distance to small lodgepole <sup>a</sup>	47.2	−0.000029	−0.000041	−0.000017
<b>After accounting for grid:</b>				
Total precipitation	82.0	0.000278	0.000217	0.000339
Depart normal precipitation	18.3	−0.009708	−0.017685	−0.001731
Depart normal days with snow	0.0	−0.000532	−0.002384	0.000132



Total Precipitation (6 mo. lag)	0.0	−0.000017	−0.000070	0.000036
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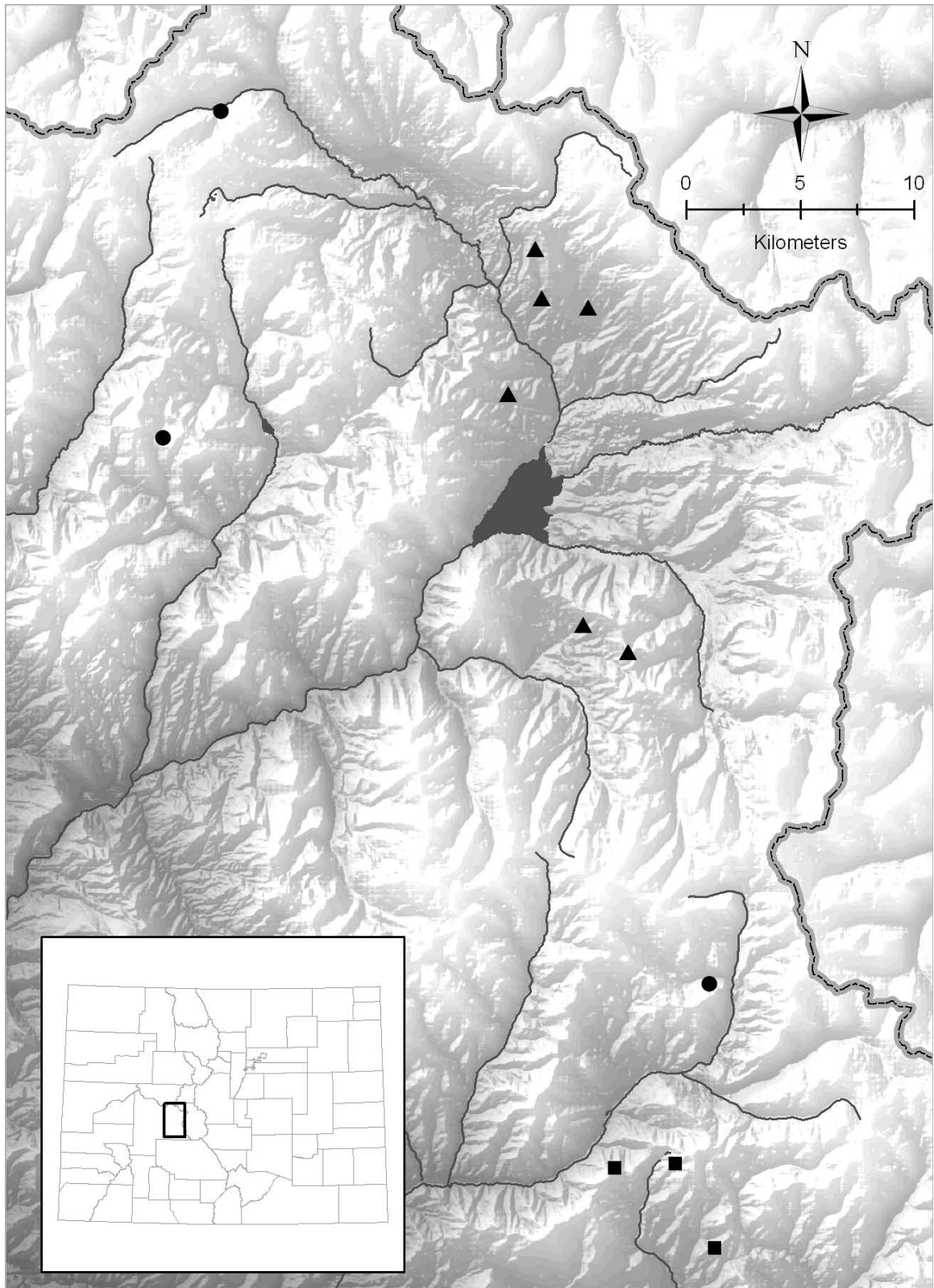
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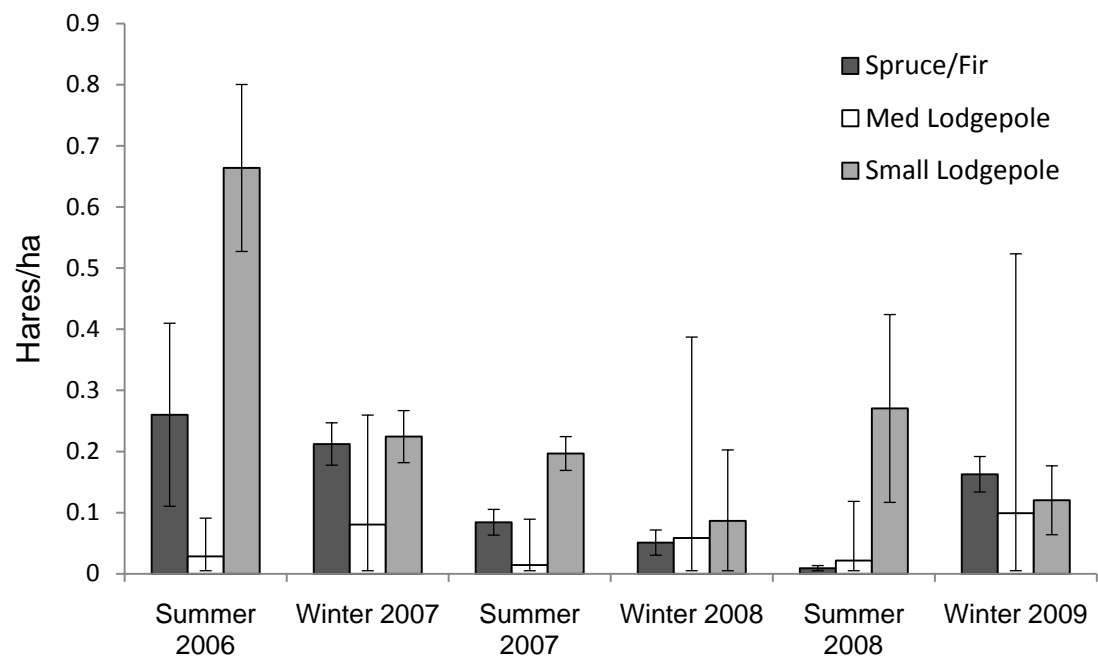
<sup>a</sup>Random effects model run using data from small lodgepole stands only ( $n = 36$ ).

Figure 1. Digital elevation model of the study area near Taylor Park and Pitkin, west-central Colorado. Darker pixels indicate lower elevations; white pixels indicate higher elevations. I estimated snowshoe density and demography in 3 late-seral Engelmann spruce/subalpine fir stands (circles), 3 mid-seral lodgepole stands (squares), and 6 early-seral lodgepole stands (triangles) from summer 2006 through winter 2009.

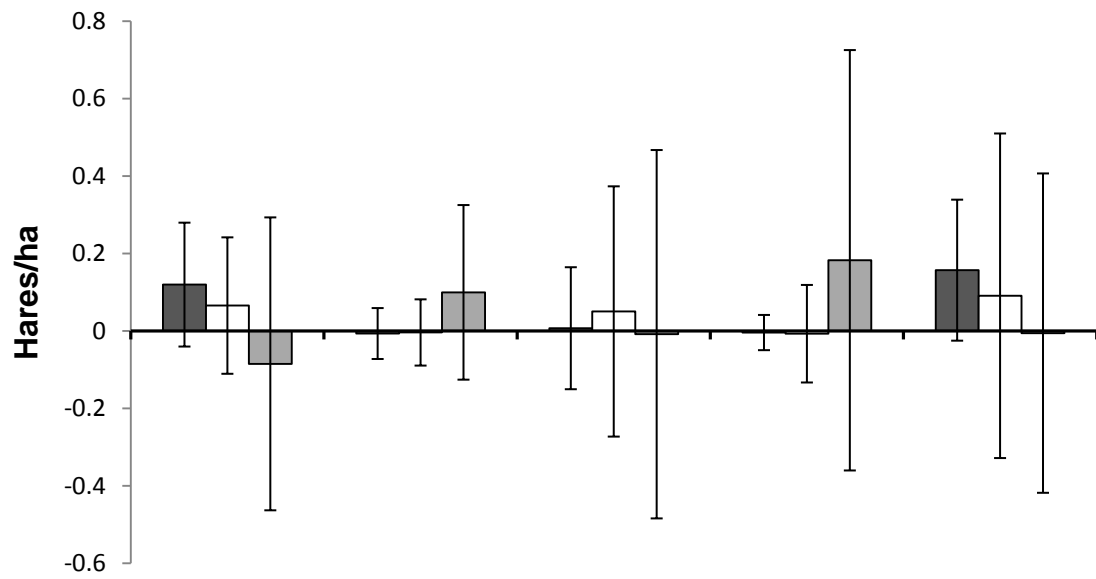
Figure 2. Snowshoe hare density and 95% confidence intervals in 3 types of stands in west-central Colorado, summer 2006 through winter 2009. Estimates were derived using a combination of mark-recapture and radio telemetry in order to correct for lack of geographic closure during sampling periods.

Figure 3. Recruitment of snowshoe hares (hares/ha) by immigration (a) and in situ recruitment (b) in 3 types of stands in central Colorado, summer 2006 – winter 2009. Negative immigration estimates indicate emigration of hares away from the stand of interest.

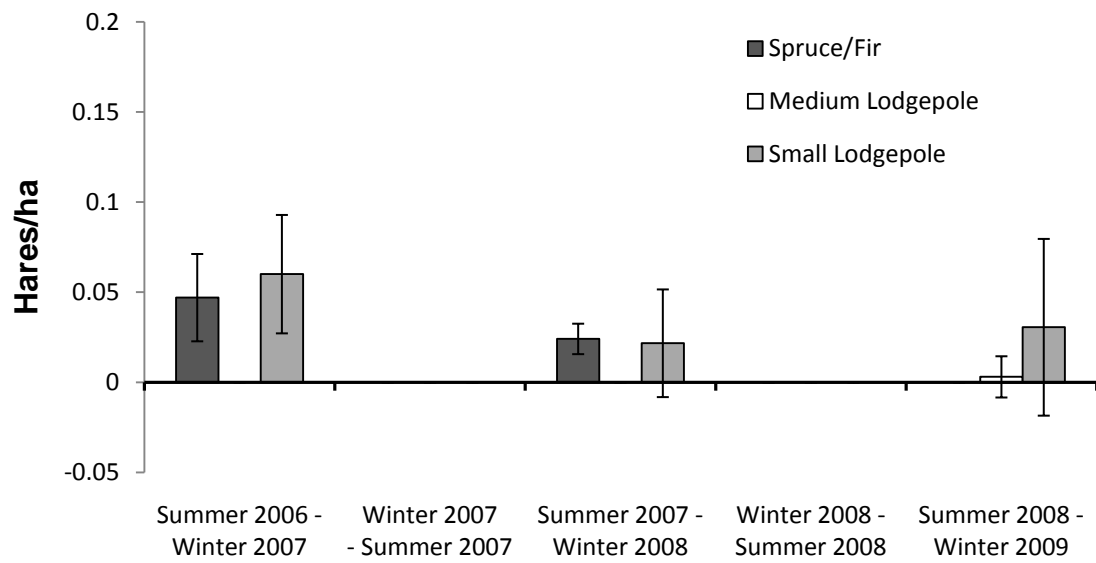




a)



b)



### 3.7 APPENDIX A

Structural characteristics of mature spruce/fir, even-aged small lodgepole, and thinned, even-aged medium lodgepole stands that were sampled for snowshoe hare density and demography, west-central Colorado, summer 2006–summer 2009. Estimates represent means (SD) from  $n = 3$  spruce/fir,  $n = 3$  medium lodgepole, and  $n = 6$  small lodgepole stands. Values for each stand were obtained by averaging measurements from systematic subsampling at  $n = 15$  (spruce/fir, medium lodgepole) or  $n = 9$  (small lodgepole) trap locations within each stand. See text for sampling and measurement details.

Characteristic	Spruce/fir	Medium Lodgepole	Small Lodgepole
Horizontal Cover 0.0–0.5 <sup>a</sup>	69.7 (8.1)	37.1 (11.6)	53.7 (9.7)
Horizontal Cover 0.5–1.0 <sup>a</sup>	37.4 (4.1)	25.3 (9.7)	56.6 (10.2)
Horizontal Cover 1.0–1.5 <sup>a</sup>	24.4 (1.4)	22.3 (4.5)	56.6 (12.4)
Horizontal Cover 1.5–2.0 <sup>a</sup>	31.3 (3.5)	27.9 (6.5)	65.6 (14.9)
Stem Density 0–7 cm <sup>b,s</sup>	3618 (1046)	1431 (912)	4467 (1808)
Stem Density 7–10 cm <sup>b,s</sup>	577 (63)	151 (83)	1117 (469)
Stem Density >10 cm <sup>b,s</sup>	1679 (401)	1600 (198)	647 (317)
Stem Density 0–7 cm <sup>b,w</sup>	1366 (492)	332 (69)	2966 (1427)

Stem Density 7–10 cm <sup>b,w</sup>	586 (129)	173 (79)	920 (621)
Stem Density >10 cm <sup>b,w</sup>	1465 (274)	1447 (347)	527 (301)
Canopy Cover (%) <sup>s</sup>	64.9 (2.7)	49.6 (8.0)	52.3 (5.8)
Canopy Cover (%) <sup>w</sup>	56.6 (3.5)	45.3 (10.0)	46.2 (6.9)
Crown Height (m) <sup>c</sup>	0.65 (0.21, 1.29)	0.83 (0.48, 1.16)	0.53 (0.23, 0.64)
Down wood <sup>d</sup>	57.7 (26.2)	47.7 (9.4)	24.5 (11)
Snow Depth Year 1 (m)	0.77 (0.31)	0.49 (0.13)	0.47 (0.14)
Snow Depth Year 2 (m)	1.37 (0.25)	1.07 (0.13)	0.97 (0.12)
Snow Depth Year 3 (m)	0.97 (0.12)	0.7 (0.13)	0.69 (0.14)

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<sup>a</sup>percent of coverboard obstructed by vegetation in 0.5–m increments up to 2 m.

<sup>b</sup>stems/ha in 0–7, 7–10, and >10 cm diameter classes

<sup>c</sup>median (25<sup>th</sup> percentile, 75<sup>th</sup> percentile) height from ground to lowest live branches.

Median and percentiles were based on pooled data from all replicates within a stand type.

<sup>d</sup>t/ha of down wood  $\geq 2.54$ cm in diameter

<sup>s</sup>summer (measurement taken 0.1m above ground)

<sup>w</sup>winter (measurement taken 1.0 m above ground)

## CHAPTER 4

### SEASONAL MOVEMENTS OF SNOWSHOE HARES IN CENTRAL COLORADO

**Abstract.** The extent and frequency of animal movements can reflect the availability of food in a given habitat, as well as predation pressure and availability of mates. I used radio telemetry to quantify seasonal snowshoe hare (*Lepus americanus*) movements in west-central Colorado from 2006–2009 to better understand snowshoe hare ecology at the southern periphery of their range. I summarized movements at 2 scales in 3 habitat types. Specifically, I calculated 1) the pair-wise distance between all locations collected over a ~10-day sampling period within a season (i.e., summer or winter), which is an index to home range size, and 2) the distance hares moved from their median summer location to their median winter location (between-season movements). I sampled movements in 1) mature Engelmann spruce (*Picea engelmannii*)/subalpine fir (*Abies lasiocarpa*), 2) early seral, even-aged lodgepole pine (*Pinus contorta*), and 3) mid-seral, even-aged lodgepole pine that had been pre-commercially thinned. Within-season movements of hares were larger during winter than during summer and tended to be larger in small lodgepole stands. Within-season movements of males tended to be larger than females during summer, possibly as a means of maximizing mating opportunities; movements were similar between the sexes during winter. Hares in both small and medium lodgepole stands tended to make larger movements between seasons than



hares in spruce/fir stands, possibly reflecting the variable value of these stands as mediated by snow depth.

**Key Words.** *Colorado; home range; Lepus americanus; movements; snowshoe hare; telemetry.*

#### **4.1 INTRODUCTION**

Snowshoe hares (*Lepus americanus*), their famous 10-year population cycle, and close association with Canada lynx (*Lynx canadensis*) have been well-studied in boreal Canada for decades (Hodges 2000a, Krebs et al. 2001a, Krebs et al. 2001b). However, hares range south into the Sierra Nevada, Southern Rockies, Upper Lake states, and Appalachian Mountains (Hodges 2000b) and hare ecology in these areas is not as well understood (Hodges 2000b). Recently, work in the Rocky Mountains of the conterminous U.S. has accelerated (Wirsing et al. 2002, Miller 2005, Malaney and Frey 2006, Zahratka and Shenk 2008, Berg 2009, Griffin and Mills 2009, Hodges et al. 2009). Much of this recent work has focused on density estimation in various habitat types. Relatively high hare densities occur in young, even-aged conifer stands regenerating after stand-replacing fires or timber harvest (See Chapter 3, Wirsing et al. 2002, Berg 2009, Griffin and Mills 2009) as well as mature, uneven-aged conifer stands (See Chapter 3, Beauvais 1997, Berg 2009, Griffin and Mills 2009). Both types of stands are characterized by dense understory vegetation that provides both browse and protection.

While density is an important metric, it can be a misleading indicator of habitat quality as areas with high animal density may function as population sinks (Van Horne 1983). Estimation of habitat-specific demographic rates in addition to density provides a more complete assessment of habitat quality. A handful of recent studies in southern

snowshoe hare range have incorporated both demography and density estimation ( See Chapter 3, Wirsing et al. 2002, Griffin and Mills 2009). Indeed, results from some of these endeavors indicate that habitats with high hare density are not necessarily the habitats where hares have the highest survival or recruitment (See Chapter 3, Griffin and Mills 2009).

Movement is an important and informative aspect of animal ecology as well. Timing, extent, and frequency of movements can reflect predation pressure, food scarcity/abundance, availability of mates, or seasonal changes in any of these parameters (Lima and Dill 1990). Theoretically, differential movement patterns across habitat types could also influence survival and mating opportunities which could influence demography. Thus, movements can provide yet another metric of habitat quality. However, to my knowledge no studies have explicitly examined snowshoe hare movements in the southern portion of their range (but see Wirsing et al. 2002 for effects of dispersal on survival). In southwest Yukon Territory, snowshoe hare movement was quantified in relation to experimental manipulation of predation risk and food availability; hares increased movement with increased predation pressure (Hodges 1999). This could decrease the probability of being discovered in any one place and/or serve to disperse scats which predators may use to locate prey. Also, snowshoe hares typically escape predation by fleeing, thus it would not be surprising to find hares moving more as an artifact of increased predation risk (Hodges 1999). Hares in Yukon also increased (males) or decreased (females) movements to meet reproductive demands, but did not change their movements in responses to food availability or a 5-fold change in density of conspecifics (Hodges 1999).

I describe movement patterns of snowshoe hares at 2 scales (within-season and between-season) in 3 types of stands (mature spruce/fir, early seral even-aged lodgepole pine, and mid-seral even-aged lodgepole pine that had been pre-commercially thinned). The data were collected as part of a larger effort to estimate snowshoe hare density, survival, and recruitment using a combination of mark-recapture and radio telemetry (See Chapter 3). Given Hodges' (1999) findings, I expected males to cover larger areas than females during summer due to differential demands on the sexes during the breeding season. I also expected hares to move more in habitats and/or during seasons when predation pressure was highest (i.e., hare movement would be negatively correlated with survival). In Chapter 3, I found snowshoe hare survival was highest in spruce-fir stands and lower in lodgepole pine stands. Also, survival was substantially lower during winter-summer intervals than for summer-winter intervals. Therefore, I expected within-season movements to be larger for hares in lodgepole stands compared to mature spruce/fir and larger during winter than during summer. Finally, density and recruitment estimates indicate that hares may move into and out of the 2 classes of young lodgepole pine based on snow depth (See Chapter 3). Thus, I expected large between-season movements by hares occupying both types of lodgepole stands.

## **4.2 METHODS**

### **4.2.1 Study Area**

The study area encompassed roughly 1200 km<sup>2</sup> around Taylor Park and Pitkin, Colorado, USA (39°50'N, 106°34'W). Extensive stands of lodgepole pine occupied the low and mid-elevation slopes (~3000–3300m), giving way to narrow bands of Engelmann spruce /subalpine fir in the sub-alpine zone (~3200–3600m). Alpine tundra

topped the highest parts of the study area (~3300–4200m). Moist spruce/fir forests also occurred on north-facing slopes at mid-elevations.

Climate was typical of continental, high-elevation zones with relatively short, mild summers and long, harsh winters. Mean July temperature was 14°C; mean January temperature was –11°C. The area receives approximately 51–64 cm of precipitation annually, mostly in the form of winter snow and late summer monsoons (Koch and Barger 1988). Maximum snow depth on the study area averaged 80 cm but ranged from 22–163 cm depending on year, elevation, and aspect. Snowpack generally persisted from November through May (low elevations) or June (high elevations and north-facing slopes).

#### **4.2.2 Sampling**

I selected “small” (early seral) and “medium” (mid-seral) lodgepole stands and “large” (mature) spruce/fir stands for sampling where the classes “small”, “medium”, and “large” refer to the diameter at breast height (dbh) of overstory trees as defined in the United States Forest Service R2VEG database (small = 2.54–12.69 cm dbh, medium = 12.70–22.85 cm dbh, and large = 22.86–40.64 cm dbh; J. Varner, United States Forest Service, personal communication). Small lodgepole stands were clear cut approximately 20–25 years prior to sampling and had regenerated into densely stocked stands (6231 stems/ha). Medium lodgepole stands were clear cut approximately 40–60 years prior to sampling and were pre-commercially thinned to 3-m spacing at approximately 20 years pre-sampling. Trees in these stands were beginning to self-prune, and lower branches were 0.83 m above ground on average. Spruce/fir stands had some evidence of historical

logging, but were largely unmanaged and exhibited structural complexity due to their uneven-aged nature and numerous down logs.

I subjectively selected 3 replicate stands that best typified the 3 stand types of interest. However, most small lodgepole stands in the area were not large enough to hold a full trapping grid necessary for the mark-recapture portion of the project, so I sampled twice as many of these stands using half-sized grids. Thus, I sampled 3 mature spruce/fir stands, 3 medium lodgepole stands, and 6 small lodgepole stands within the study area.

I captured and radio-tagged hares at each site during both summer (mid-July through September, 2006–2008) and winter (mid-January through March, 2007–2009). Hares were captured using Tomahawk Model 204 live traps deployed on  $7 \times 12$  (medium lodgepole and large spruce/fir) or  $6 \times 7$  (small lodgepole) grids with 50-m spacing. I covered traps with pine boughs and bark to protect entrapped animals from elements. Additionally, during winter sampling sessions, I encased traps in several inches of snow to provide further protection. Traps were baited with apple slices, commercial rabbit chow, and cubed timothy hay (*Phleum pratense*). I concurrently trapped 1 spruce/fir grid, 1 medium lodgepole grid, and 2 small lodgepole grids for 5 days, then conducted a short telemetry sampling session on hares captured on those grids (see below). Upon completion, I moved to a second set of 4 grids to repeat the capture and telemetry work, then on to the third. I sampled the same 12 grids each season, but rotated the order in which they were sampled so that no set of grids was routinely sampled early or late in a sampling season. Colorado State University and Colorado Division of Wildlife Animal Care and Use Committees approved all sampling methods (Colorado State University IACUC Protocol 06-062A-03).

I radio-marked up to 10 hares per grid using a 28-g collar equipped with a 6-hr mortality sensor (Model TW5SM, BioTrack, LTD, Wareham, Dorset, United Kingdom). I anticipated being unable to radio-mark every hare I captured and expected heterogeneity in response to trapping (some hares were captured early and often, others were only captured once toward the end of a session). To account for this heterogeneity, I retained 2 of the allotted 10 collars for application during the last 2 days of trapping. After trapping, I carefully removed all bait from the area in addition to traps so that animal movements post-trapping were not influenced by the grid.

Using radio telemetry, I sampled hare movements for a 7–10 day period beginning 1–3 days post-trapping. I attempted to obtain 10 locations per individual during each season. Hares are generally most active during nighttime (Keith 1964, Foresman and Pearson 1999, Hodges 1999), so I obtained equal daytime and nighttime locations to representatively locate hares in their resting locations as well as during periods of activity. During summer, I generally obtained 1 location/hare/day and alternated daytime and nighttime sampling on consecutive days. During winter, I obtained 2 locations (one daytime, one nighttime)/hare/day, but I only sampled a given hare every other day.

Most locations were obtained via triangulation. I prioritized hares that remained near the grid where they were captured (for the density estimation portion of the study), and worked to obtain accurate locations by triangulating at short range (usually <250 m from receiver to transmitter). Hares that strayed farther from the grid after trapping were located via triangulation as well, but sometimes at distances of 500 m or more. All grids in all stand types included hares that remained close to their grid of capture as well as

hares that moved farther away. All locations were estimated using the maximum likelihood procedure (Lenth 1981) in Program LOAS (Version 4.0, Ecological Software Solutions LLC, Sacramento, CA, USA). To assess accuracy of short-range triangulations, I homed in on a few individuals per grid-season immediately after triangulating their location. I only homed during daytime when hares were inactive. I recorded a location once I obtained a visual or heard the radio signal without an antenna. I did not record a location if it was apparent from the signal that the animal moved as I approached.

Hares made larger movements than I anticipated at the onset of the study and individuals initially trapped in spruce/fir, medium lodgepole, and small lodgepole stands, did not necessarily remain exclusively in those stands during sampling. Thus, metrics for hares in “spruce/fir” stands actually reflect movements of individuals that used a landscape (See Chapter 3 for definition of landscape) comprised of approximately 85% spruce/fir, 7% medium lodgepole, 6% willow, and 2% other. Estimates for “medium lodgepole” reflect use of landscapes comprised of 64% thinned, even-aged medium lodgepole, 15% large lodgepole, 13% aspen, and 8% other. Estimates for “small lodgepole” reflect landscapes comprised of about 7% small lodgepole, 83% large lodgepole, and 10% willow. Note that small lodgepole landscapes contain little small lodgepole on a percentage basis (small lodgepole stands occur as small patches [mean size = 4.9 ha] strewn throughout a matrix of larger, unharvested lodgepole), but these stands are the signature component of these landscapes as large lodgepole provides almost no understory cover and willow provides understory only seasonally. No individual moved between the 3 landscape types during the study.

### 4.2.3 Analysis

Because I obtained relatively few locations per hare ( $\leq 12$ ), I was unable to assess snowshoe hare movements using traditional home range approaches or in the context of resource selection. Instead, I broadly characterized hare movements in each stand using metrics based on distance between locations. Specifically, I quantified within-season movements by identifying the median distance between all possible pairs of locations obtained for each individual in each season. Such a metric is an index to the amount of area used by an individual and should be strongly, positively correlated with minimum convex polygon home range size (e.g.,  $R^2 = 0.86$ , for hares with  $\geq 10$  locations in this study, J. Ivan unpublished data). To quantify between-season movements, I calculated distance between median summer locations and median winter locations for each hare. I characterized movements at each scale using median values because distance metrics can be sensitive to outliers, especially when sample sizes are low. I only included adult hares for which I recorded at least 3 locations per season.

For each movement metric, I constructed a set of linear models to evaluate the effect of stand type, season, and sex on the metric. For within-season model sets, I evaluated all possible additive combinations of the 3 effects ( $n = 8$ ) plus 2 additional models that included a season  $\times$  sex interaction term whenever both effects occurred together as additive combinations. For between-season models, I evaluated all possible additive combinations of stand type and sex ( $n = 4$ ). I collected measures on the same hares during multiple seasons, and the number of locations obtained per hare was not uniform. To account for these issues, I modeled individuals as random effects but



specified the covariates of interest as fixed effects (PROC MIXED, Version 9.2, SAS Institute Inc., Cary, NC, USA).

### 4.3 RESULTS

I monitored 131 adult snowshoe hares (medium lodgepole = 16 males, 13 females; small lodgepole = 39 males, 38 females; spruce/fir = 18 males, 17 females). I obtained 1,128 total locations, an average of 8.0 locations per hare per season (range = 3–12). Ninety percent of locations were obtained via triangulation; the remainder were obtained by homing. Fifty-six percent of locations were obtained during daytime (~10am to 1 hour before official sunset), 44% during nighttime (1 hour after official sunset to ~2am). Based on  $n = 100$  trials, mean estimated location error was 63 m (range 3–330), for hares located at close range.

Median distances between all pair-wise combinations of points within a season were on the order of ~400 m (Table 3, Intercept value). “Season” had the strongest effect on within-season hare movements, which were smaller during summer than during winter. The top model included only this effect (Table 1), it was present in all models that held any weight in the set (cumulative  $AIC_c$  weight for “season” = 0.98), and the estimate of the coefficient of this effect was strongly divergent from zero (Table 3). Females tended to make smaller within-season movements than males, and I did find evidence that the influence of sex on movements varied by season (Table 1; second best model). Overall, however, evidence for this effect was weaker. Cumulative  $AIC_c$  weight was 0.51 and the confidence interval for the female coefficient, while negative, overlapped zero (Table 3). Stand type influenced within-season movements the least (cumulative  $AIC_c$  = 0.35), although I did find weak evidence that hares in small

lodgepole stands tend to move larger distances than those in medium lodgepole or spruce/fir (Table 3).

Evidence was equivocal regarding whether distance between median summer and winter locations differed among stand types; models with and without these effects held roughly equal support from the data according to AIC<sub>c</sub> (Table 2). Coefficient estimates from the fully additive model (Table 3) indicate that hares residing in medium or small lodgepole stands tended to move greater distances between summer and winter locations than did hares residing in spruce/fir stands. There was little support for differences in between-season movements between males and females (Tables 1, 3).

#### **4.4 DISCUSSION**

Hodges (1999) found that males had much larger home ranges than females during summer, but there was little difference between the sexes during winter. She attributed this phenomenon to differential activities associated with the mating season: males cover large areas to maximize mating opportunities with females, whereas females restrict their space use while nursing litters. My results substantiate these findings: there was evidence of a sex  $\times$  season interaction for within-season movements and movements of males tended to be larger than females.

Based on Hodges' (1999) finding that hares make larger movements in response to increased predation pressure, and earlier findings in this study (See Chapter 3), I predicted that snowshoe hare movements would be a) larger in winter than summer and b) larger in lodgepole habitats than spruce/fir. The within-season movements I observed were consistent with prediction a) and partially consistent with prediction b). There was

some indication that within-season movements were larger in small lodgepole than spruce/fir, but movements in medium lodgepole were similar.

Thus, predation pressure alone does not adequately explain the differential pattern of movement I observed between stands. Perhaps hare movements on the study area were mediated by landscape configuration in addition to predation pressure. Spruce/fir and medium lodgepole stands were relatively homogeneous compared to small lodgepole stands, which tend to occur as a series of small patches (<10 ha) within a matrix of mature lodgepole that is poor snowshoe hare habitat. In order for hares to exist in small lodgepole landscapes, they may need to utilize more than 1 small lodgepole stand (indeed I documented this for several hares via telemetry), which increases median within-season movements relative to medium lodgepole or spruce/fir.

In Chapter 3 I noted that density and recruitment rates for snowshoe hares in small and medium lodgepole suggested movement into small lodgepole from winter to summer. Movement into medium lodgepole stands occurred during summer-winter. I hypothesized that this was due to the interaction between crown height and snow depth in these stands – presumably medium lodgepole stands provide little forage or cover during summer, but accumulating snow brings the lower branches of trees within reach of hares during winter. Conversely small lodgepole stands provide dense cover/forage during summer, but “fill in” somewhat with drifting snow during winter. The relatively large between-season movements I observed for hares in small and medium lodgepole stands is consistent with this hypothesis. Accordingly, the complex structure of mature spruce/fir stands may obviate the need for hares to move significant distances to meet needs,

regardless of snow depth, and between-season movements in this stand type were relatively smaller.

This study represents the first to explicitly address snowshoe hare movements using telemetry in the Southern Rockies. I noted apparent differences in movements among sexes, seasons, and habitat types, but inferences are limited by small sample sizes and reliance on relatively crude indices of movement. Further work specifically designed to evaluate how hares use the highly fragmented landscapes in this part of their range would improve general knowledge of hares in the region and aid management decisions that ultimately dictate the type and juxtaposition of forest cover on the landscape.

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Table 1. Model selection results for within-season movements of snowshoe hares in Taylor Park and Pitkin, Colorado, USA, 2006–2009. Stand types were mature spruce/fir, even-aged small lodgepole pine, and thinned, even-aged medium lodgepole pine. Sampling of movements occurred during summer and winter seasons. The response variable was median pair wise distance between all locations during a sampling session.

Model	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	AIC <sub>c</sub> Wt.	<i>K</i>
Season	1966.7	0.0	0.30	4
Season+Sex+Season*Sex	1967.5	0.8	0.19	6
Stand Type+Season	1967.8	1.1	0.17	6
Season+Sex	1968.2	1.5	0.14	5
Stand Type+Season+Sex+Season*Sex	1968.8	2.1	0.10	8
Stand Type+Season+Sex	1969.2	2.5	0.08	7
Intercept Only	1974.9	8.2	0.00	2
Sex	1976.5	9.8	0.00	3
Stand Type	1977.2	10.5	0.00	4
Stand Type+Sex	1978.8	12.1	0.00	5



Table 2. Model selection results for between-season movements of snowshoe hares in Taylor Park and Pitkin, Colorado, USA, 2006–2009. Stand types were mature spruce/fir, even-aged small lodgepole pine, and thinned, even-aged medium lodgepole pine. The response variable was distance between median summer and median winter locations.

Model	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	AIC <sub>c</sub> Wt.	<i>K</i>
Intercept Only	1096.2	0.0	0.38	3
Stand Type	1096.3	0.1	0.38	5
Sex	1098.5	2.2	0.13	4
Stand Type+Sex	1098.7	2.5	0.11	6

Table 3. Estimated coefficients and 95% confidence intervals for fully additive models constructed to explain variation in within-season and between-season movement metrics for snowshoe hares, Taylor Park and Pitkin, Colorado, USA, 2006-2009. Note that these are not the best models according to AIC<sub>c</sub> (see Tables 1, 2). Full models are presented to indicate the magnitude, direction, and precision of all coefficients of interest. Coefficient values were similar for other models.

		95% Confidence Interval	
	$\hat{\beta}$	Lower	Upper
<b>Within-Season Movements:</b>			
Medium Lodgepole	6.6	-117.9	131.1
Small Lodgepole	82.7	-18.5	183.9
Summer	-160.2	-241.7	-78.8
Female	-36.9	-120.3	46.6
Intercept	418.6	318.0	519.3
<b>Between-Season Movements:</b>			
Medium Lodgepole	389.7	-89.8	869.2
Small Lodgepole	422.2	34.3	810.1
Female	-1.8	-325.7	322.1
Intercept	312.8	-44.9	670.5