The Implications of Animal Movement on Camera Detections as a Means to Monitor Density

by

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ABSTRACT

Camera traps are an increasingly popular tool for wildlife management. Studies that use detection rates as a simple index of relative abundance assume that movement is not density-dependent. More complex techniques such as spatially-explicit capture recapture models, occupancy models, or N-mixture models make various assumptions about animal home range size in relation to camera spacing. While some assume individual animals can visit multiple camera sites, others assume sites are independent such that no individual can be detected at more than one camera. In all these methods, variation in space use has the potential to confound population estimates and compromise current applications of camera trapping as a monitoring tool. To assess this problem, I quantified how movement rate and home range size vary both between and within populations, and investigated the implications of this variation for camera trap data analysis. To quantify the relationship between space use and population density, I conducted a meta-analysis of studies reporting movement rate, home range size, or density for at least two populations of terrestrial mammals. I found that movement rate and home range size are significantly negatively correlated with density and positively correlated with each other. Using simulations of animal movement and density, I found that density-dependent movement can obscure trends in density indexed by detection rates. True changes in density may be underestimated by up to 30%. I then investigated space use within populations using telemetry datasets for white-tailed deer, moose, and wolves. Patterns between individuals were similar to those patterns seen between populations, where individuals with larger home range sizes generally had faster movement rates. Variation between individuals within a population was an order of magnitude greater than variation between the mean movement rates and home range sizes of different populations. Carnivores in particular exhibited much greater variation between individuals than herbivores. These findings indicate that choosing camera spacing appropriate for a given model is not straightforward, as some individuals are likely violating the model assumptions regarding site independence. I recommend that practitioners treat camera trap detection rate indices of relative abundance as good indicators of directional population trends and as partially accurate indicators of the actual magnitude of density changes. Furthermore, I urge that practitioners be aware that individual variation in space use is considerable, and that assumptions regarding camera spacing relative to animal home range size are likely often violated. Animal space use is an important subject for the ongoing development of robust camera trap analyses, and I hope that this thesis will encourage a more careful consideration of its role in the design of future camera trapping studies.

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CHAPTER I: General Introduction

Effective wildlife management depends on accurate abundance and density estimation, but traditional estimation methods are labor-intensive. Camera traps are an increasingly popular alternative (O'Connell *et al.* 2011), as they provide a less expensive and less invasive way to monitor wildlife populations (Kucera and Barrett 2011). Due to their passive nature, they can be used to collect data on multiple species simultaneously (Tobler *et al.* 2008). For these reasons, camera traps are becoming an increasingly ubiquitous tool in wildlife management.

Analytical methods for estimating density or relative abundance from camera trap data are numerous and diverse. While density and abundance are not the same – density is abundance over a unit of area and requires more information – relative abundance in a monitoring context typically serves as a proxy for density, and so for the purposes of this thesis I will treat them as interchangeable. Individual identification of "marked" species has allowed the successful use of capture-recapture methods (Karanth and Nichols 1998), with accurate density estimation made possible through spatially explicit capture-recapture (SECR, Efford 2004). For unmarked species, density estimation is more difficult, and a popular substitute is the use of detection rates as an index of relative abundance (Burton *et al.* 2015). More sophisticated alternatives include density estimation from spatially correlated detections (Chandler & Royle 2013), abundance estimation from repeated presence-absence surveys (N-mixture models, Royle & Nichols 2003), and density estimation by combining detection rates with *a priori* estimates of animal movement rate and camera detection zone area (Rowcliffe *et al.* 2008).

What all these methods have in common is that they make underlying assumptions about the target species' space use, which for the purpose of this study, I am defining as movement rate and home range size. How animal space use relates to camera trapping is a fundamental issue that deserves more attention. Detection rates are a function of both abundance and movement, so as long as space use remains consistent, changes in detection reflect changes in abundance (O'Brien 2011). However, this core assumption of constant encounter probability is likely untrue (e.g.: Harmsen *et al.* 2010; Sollmann *et al.* 2013). Thus, there is potential for patterns of space use to confound estimates of density or relative abundance (O'Brien 2011; Marcus Rowcliffe *et al.* 2011). Despite this, underlying assumptions regarding animal behavior are often not acknowledged in camera trapping studies, and there is rarely any indication that *a priori* information on the target species' space use was incorporated into the study design process (Burton *et al.* 2015).

Given the potential for space use to interfere with camera trapping methods, it is important to investigate the relationships between movement rate, home range size, and density. Quantifying the degree to which these parameters are related and how much they are likely to vary will illuminate potential sources of trouble for camera trap study design and data interpretation.

This thesis aims to investigate animal space use and how it relates to camera trapping. More specifically, I will attempt to answer these two questions:

1. *What is the relationship between density, movement rate, and home range size in mammals?*
2. *Given this, what are the implications for camera traps as a monitoring tool to assess changes in mammalian population density or abundance?*

Chapter II focuses on implications for comparatively straightforward detection rate indices of relative abundance. As these indices are a popular choice, particularly among managers

(Sollmann *et al.* 2013a), it is critical to determine the degree to which they may be confounded by movement. This is investigated in Chapter II through both a meta-analysis to determine how movement rate and home range size relate to density, and simulated data to determine how changes in space use affect camera detection rates. Chapter III uses telemetry data to investigate how movement rates and home range sizes vary within populations. As different techniques for analyzing camera trap data make different assumptions regarding camera spacing relative to animal movement, heterogeneity in space use makes fulfilment of these assumptions difficult. It is hoped that this thesis will illuminate the potential for space use to act as a confound in camera trap studies, and will provide some helpful recommendations for camera trap study design and interpretation, and fruitful directions for further research.

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CHAPTER II: Density-Dependent Space Use and its Effect on Detection-Rate Indices

Introduction:

Population Estimation with Camera Traps

Accurate abundance and density estimation is at the core of wildlife management, and camera traps are an increasingly popular monitoring tool (O'Connell *et al.* 2011). Camera traps are triggered by temperature changes and movement across their field of view, thus capturing images of animals that pass by. Compared to traditional live-trapping, camera trapping is less expensive and less invasive (Kucera and Barrett 2011), and it can be used for the simultaneous collection of data on multiple species (Tobler *et al.* 2008). This makes camera traps very attractive to those wishing to conduct large-scale, multi-species monitoring programs. The camera trapping technique has been particularly successful in the study of large species whose coat patterns allow individuals to be identified. Identification of such "marked" species allows for standard capture-recapture methods to be applied (Karanth and Nichols 1998), and accurate density estimation of such populations has been further improved with the development of spatially explicit capture-recapture methods (SECR, Efford 2004).

However, most species cannot be reliably identified individually by unique markings. This presents a challenge to those wishing to monitor these populations, and so scientists and managers must rely on alternatives to capture-recapture methods for estimation of density or abundance. Indices that document relative changes are one such alternative to more formal methods of density estimation (Williams, Nichols & Conroy 2002). In fact, indirect measures of population trends like relative abundance and presence/absence represent the most common ways camera trap data are analyzed; a recent review indicated that such indices were the most common measures reported from camera studies, with relative abundance being reported in 43.6% of studies, changes in presence/absence in 41.4%, density or absolute abundance in 15.8%, and changes in occupancy in 15.4% (Burton *et al.* 2015). Relative abundance indices typically consist of detections standardized by effort (number of detections per 100 camera trap days is most common, but indices vary widely – e.g. detections per camera trap hour, per survey week, etc.) (Burton *et al.* 2015). Often, detections clustered in time are lumped into a single "detection event." This represents an attempt to count "independent" detections for the purpose of calculating the index, but criteria for delineating events vary widely between studies. The spatial scales across which relative abundance indices are applied also vary. They may be used to track trends over broad spatial scales, combining data from all cameras within the study to make population-level inferences; alternatively, they may be used at a much finer spatial scale to compare local abundance at individual sites or habitats (Burton *et al.* 2015). Despite variation in protocol, however, all relative abundance indices operate on a shared assumption that detection rates are correlated with abundance.

Abundance, however, is not the only factor that influences detection rates. Other factors are related to the camera and its immediate environment, such as the camera's settings, the size of its detection zone, vegetation cover, the time of day, etc. (Burton *et al.* 2015). Animal body size, space use, and population density will also influence detectability. As long as camera and site conditions are appropriately controlled for, variation in detections will be driven solely by animal-specific factors, and as long as space use remains consistent, population density changes should be the primary factor responsible for changes in detection rate (number of detections over space and time). That is, if individual encounter rates (i.e.: the probability that a given individual will encounter a camera per unit time) remain constant across space and time, detection rate serves as a valid index of abundance (O'Brien 2011). When comparing detections across space or time, an index of relative abundance assumes that a difference in detection rate reflects a difference in the number of individuals present in the study area; an average change in the index is assumed to correlate with an average change in the population (O'Connell *et al.* 2011). Such relative abundance indices have been employed in many studies (e.g.: Carbone *et al.* 2001; O'Brien 2011, O'Brien *et al.* 2003; Bengsen *et al.* 2011), while others have noted their frequent use within the grey literature of wildlife management reports and conservation strategies (Sollmann *et al.* 2013a). While some camera studies have investigated the performance of detection indices against independent measures of density (e.g. Villette *et al.* 2016; Villette, Krebs & Jung 2017), indices are usually employed without any prior validation (Williams *et al.* 2002). The widespread popularity of relative abundance indices over more complex analyses can be largely attributed to their being easy to apply and straightforward to interpret (Sollmann *et al.* 2013a).

The validity of population indices has long been debated in wildlife ecology (see Anderson 2001, 2003; Engeman 2003), and indices using camera data are no exception. Despite the widespread usage of detection rate as a relative abundance index, the core assumption of constant encounter probability is likely untrue (e.g.: Harmsen *et al.* 2010; Sollmann *et al.* 2013). Violation of this assumption poses a problem for the use of detection rates as an index of relative abundance when encounter probability co-varies with density (Jennelle *et al.* 2002; Harmsen *et al.* 2010). Because of this assumption, there is great potential for animal behavior to confound relative abundance estimates (O'Brien 2011; Marcus Rowcliffe *et al.* 2011). Consider the effect of home range size. Given a camera array design, an individual's home range determines the number of different camera sites it is likely to overlap with. Individuals with larger home ranges are likely to encounter more cameras but may have lower probability of encountering any given camera within their home range. Conversely, individuals with small home ranges are likely to encounter fewer cameras; in the extreme, an individual with a small home range may not overlap a single camera. Movement rate can likewise have a strong effect. The greater an individual's movement rate, the more encounters it is likely to have with cameras within its home range over a given period of time. When passive traps like cameras are distributed randomly over large spatial scales, both the mean encounter rate and time to first encounter are strongly affected by movement rate, particularly when the detection zone of the camera is small (Gurarie & Ovaskainen 2013). If home range size and movement rate are density-dependent, this could obscure true change in abundance inferred from a relative abundance index. This is particularly problematic if home range and movement rate are negatively correlated with density. At best, a relative abundance index will underestimate the true change in abundance. At worst, increased movement rates and home range sizes at low densities could result in those individuals producing the same or more total detections than a high density population, despite there being fewer individuals.

Relationship Between Animal Movement and Density

Since home range size and movement rate could adversely affect the reliability of relative abundance indices, it is important to understand their relationship with each other and with density. There is a logical link between movement rate and resource availability. The more an animal stops to feed, the lower its movement rate, therefore more productive patches should be associated with less movement (Owen-Smith *et al.* 2010) – a response observed in a number of species (e.g. Novellie 1978; Owen-Smith 1979; Fryxell *et al.* 2008). It follows that where population density is correlated with habitat quality (i.e. higher density in higher quality habitats), one would expect a negative relationship between movement rate and population density. Low densities can also result in the need for increased movement to search for rarer mates (Kokko & Wong 2007), which could further contribute to the density-dependence of movement rate.

As with movement rates, home range size is likewise related to resource availability. Home range is defined generally as the area in which an individual lives, excepting any unusual excursions (Burt 1943; Brown and Orians 1970). The relationship between home range size and resource requirements is apparent at the species level, where larger species generally have larger home ranges (Harestad and Bunnel 1979). Additionally, carnivores with more sparsely distributed prey tend to have larger home ranges than omnivores and herbivores (Harestad and Bunnel 1979). Within a species, it follows that home range size would negatively correlate with population density (as resource-poor habitats necessitate larger home ranges, and support a lower carrying capacity). Indeed, this relationship has been observed in multiple species (e.g. Wolff 1985; Trewhella, Harris and McAllister 1988; Erlinge *et al.* 1990; Kjellander *et al.* 2004). Territoriality may act as a complicating factor, because maintenance of a territory requires defensive behaviors (Krebs *et al.* 1994). Higher density populations necessitate greater defense costs (more time spent patrolling, interacting with conspecifics), leading to smaller territories overall (Both and Visser 2003). These greater efforts spent on defense could maintain high movement rates within these small territories.

As movement rate and home range size are driven by the same underlying ecological processes, it is natural to expect them to be correlated. Indeed, if home range and movement rate are both negatively correlated with density, the logical complimentary relationship is that they are positively correlated.

Chapter Objectives

Despite a strong theoretical grounding for variation and interdependence of these parameters, it remains unknown if and/or how often changes in space use could confound the assumed relationship between camera detection rate and relative abundance, as well as to what degree the assumptions of detection rate indices are violated. If resource availability is the primary driver of movement rate, home range size, and density, one would expect the assumption of static space use to be frequently violated. Specifically, movement rate and home range size would both negatively correlate with density (and be themselves positively correlated), such that opposing forces act on the detection rate. However, until the strength and consistency of these relationships are quantified across taxa and at different scales, one cannot determine the frequency and degree to which detection rate indices for relative abundance are confounded by movement. Therefore, quantifying the relationships between density, movement rate, and home range size is an important step in determining if camera trap detections serve as an accurate measure of changes in relative abundance.

This chapter aims to quantify how home range size, movement rate, and density co-vary between populations of mammalian taxa. If the same factors that drive population density also drive movement rates and home range size, then higher density populations will have on average slower movement rates and smaller home ranges. Populations with a larger average home range size should also exhibit faster average movement rates. In order to quantify the relationships between movement rate, home range size, and density between populations, I conducted a systematic meta-analysis of published studies that have reported any two of these parameters in any terrestrial mammalian taxa.

Once the relationships between movement rate, home range size, and density are quantified, a remaining challenge is determining the impact such relationships will have on detection rates by camera traps. I used simulation to quantify the magnitude of the expected effect of density-dependent movement on interpretation of camera trap detection rates. From a set of available simulation parameters, I chose space use scenarios that would span the range of variation found in the meta-analysis, so as to reveal the full extent by which movement could confound relative abundance estimates from detection rates.

Methods:

Literature Search

Relevant articles were searched for in the Web of Science database using the following search terms: (“movement” OR “distance travelled” OR “distance moved” OR “speed” OR “activity”) AND (“population density” OR “abundance” OR “home range size” OR “territory size”) AND (“mammal” OR “mammalian”). The search was conducted in 2015 and restricted to English-language papers published from 2005 up to 2015. Studies on any terrestrial mammalian taxa were considered. Retained were those studies that reported at least two of either movement rate, (relative) density/abundance, or home range size. The list was further restricted to only papers that reported these parameters for at least two different “populations” (defined spatially or temporally, i.e. the same population in different years), in order to control for study methodology. Excluded were any studies that used a telemetry location interval greater than 24 hours to calculate movement rates, or for which one of the parameters was confounded by the other parameter (for example, a population density calculated as the number of home ranges that could fit in the study area would not be considered valid). Also omitted were studies that only compared single individuals as well as studies that compared islands to mainland areas so as to exclude situations of unusually constrained spatial geography.

For the resulting set of papers, the species, taxonomic order, parameters measured, and methods used to measure the relevant parameters were recorded. I defined, movement rate as the average cumulative step length over time, including non-moving steps. If location data could be recorded in a continuous fashion, this parameter reflects the true distance travelled by an animal over time (i.e. km/d) but telemetry data provide locational data at intervals determined by the duty cycle of the collar. Longer location intervals miss finer-scale movements and underestimate the true movement rate, but still provide an approximation. In an example telemetry dataset with 1-hour intervals between locations, movement rate would reflect the summed distances of 24 consecutive steps divided by 24 hours (or one day). Inclusion of non-moving steps is critical, because the more an animal stays in one place, the fewer cameras it will encounter over time. Terminology for this parameter varies widely across movement studies and the label "movement rate" may even be applied to a different parameter (i.e. average speed of moving steps only), so the methods of each individual study were examined carefully. Only the parameter whose description matched the definition for movement rate given above was selected for analysis, regardless of the terminology originally applied in the source.

Magnitude of variation

I considered three relationships: movement rate vs density, home range size vs density, and home range size vs movement rate. To compare the relationships between studies and systems, I calculated the ratio of the higher value to the lower value for the populations in the study. The population with the lowest value for the x-axis parameter was considered the “reference” population, and I then calculated the increase in that parameter from the “reference” to the other population. For studies with more than two populations, I used the populations that offered the greatest difference across the x-axis parameter. I then calculated the value for the y-axis parameter as the percentage of its value in the “reference” population (such that 100% represents no change in value). This was done to quantify and visualize the actual magnitudes of changes in these parameters, rather than simply a positive or negative correlation.

Meta-analysis

A meta-analysis calculates an overall effect size from a set of standardized effect sizes, thereby determining the magnitude of the effect of one variable on another (Rosenthal and DiMatteo 2001). Given that all of the parameters analyzed (density, movement rate, and home range size) are continuous, the correlation coefficient (r) was chosen as the most appropriate measure of effect size. In this context, the overall correlation coefficient represents the strength and direction of the association between a given pair of parameters. Correlation coefficients of individual studies were obtained either from direct reporting, or from converting other test statistics given. When a test statistic other than r was reported (e.g. t, χ^2, F, U,) it was changed using standard conversion formulae into the Fisher’s Z transformation of r (Rosenthal and DiMatteo 2001). For example, a t statistic from a study comparing two mean movement rates can be converted into a correlation coefficient using the formula $r = \sqrt{\frac{t^2}{t^2+df}}$. Once standardized, these effect sizes (weighted by the inverse of their variances) were analyzed together using a random-effects model to determine the overall strength and direction of the effect. A random-effects model is preferable for ecological phenomena because it accounts for random variation in effect sizes across studies and allows generalization to studies outside of the meta-analysis

(Rosenthal and DiMatteo 2001; Cooper *et al.* 2009). Cochran's Q test for heterogeneity was used to assess the significance of variation in effect sizes across studies in the meta-analysis. Significant heterogeneity indicates that sampling error alone cannot explain variance in effect sizes.

Animal Simulations

The effect of density-dependent movement on camera detection rates was examined using a set of computer simulations designed by Tal Avgar. Animal movement was simulated using a "stepping-stone" approach, in which individuals move across a grid of hexagonal cells (Avgar *et al.* 2016). The movement mode comprises a discrete biased random walk, where during each time-step, *t*, an individual could move to an adjacent hexagonal cell, or remain in place. The position of the animal at the next time step is described by the function:

$$p(x_{t+\tau} = x) = \frac{I(\|x - x_t\| \leq 1)\exp\left(-\alpha\|x - x_t\| - \beta\|x - x'\|^2\right)}{\sum I(\|x - x_t\| \leq 1)\exp(-\alpha\|x - x_t\| - \beta\|x - x'\|^2)}. \quad [1]$$

in which $x_{t+\tau}$ represents the next time step where τ is the time step's duration, x' is the individual's home range center, I is an indicator function valued at 1 or 0 based on the immediately following expression, α is the movement cost, and β is a parameter determining attraction to the home range center. This model of animal movement allows for a more realistic simulation of animal paths, as observed patterns in speed and home range size are an emergent property of the movement process, rather than the result of imposed boundaries. By altering the movement cost (α) and the home range attraction ($\beta\|x - x'\|^2$) parameters, different space-use patterns can be simulated. The movement cost parameter (α) is easily converted into a more biologically-relevant parameter: the probability that an animal will move during a time step, $\mu = [1 + (e^{\alpha}/6)]^{-1}$. Modifying this probability in turn modifies the movement rate. The steady-state home range size (i.e. the utilization distribution the animal will eventually produce if given enough time) is approximately $14.4676 \cdot \beta^{-0.5}$ m, if 99% of the utilization distribution is to be included.

Out of a set of available simulated populations, two contrasting movement scenarios were chosen: one with fast movement rates and large home ranges and one with slow movement and small home ranges. These scenarios were chosen to capture the relationship found in the meta-analysis, where movement rate and home range size are both negatively correlated with density and positively correlated with one another. The fast, large home range population had a steady-state home range size of 100 km^2 and $\mu = 1$ (mean realized speed of approx. 180m/h). The slow, small home range population had a steady-state home range size of 1 km^2 and $\mu = 0.1$ (mean realized speed of approx. 57m/h). These scenarios were chosen to reflect a range in movement that would encompass the possible variation found in real populations. For instance, movement rate can more than triple over a 25-fold change in home range size (chacma baboon, Hoffman & O'Riain 2012). By covering the possible range in variation found in nature, the simulation can represent a 'worst-case scenario' and is able to reveal the full extent to which space use can confound population estimates.

The simulated domain comprised ~10^7, 100 m^2, hexagonal cells, making up 1000 km^2 in total. The domain was wrapped around a torus, thus eliminating any edge effects. Individuals were given random home range centers and were allowed to move for 3,153,600 10-second time steps (1 year in total). To remove effects of the initial conditions, only the last 1,576,800 steps (6 months) were used for analysis. One-thousand random cells in the domain were designated as camera trap sites, such that the presence of an individual within that cell during a time-step was counted as a detection on that camera. 100 individuals were simulated for each movement scenario. The final output was a record of how many times a given animal was detected at each camera location over the duration of the simulation. To get the detection rate for a given camera, the detections from all 100 individuals at that camera were summed and then divided by the study duration. In order to simulate variation in density, 25, 50, and 75 individuals were subsampled from the full population of 100, and their detections at a given camera location summed. The mean detection rate in all cases was then obtained by averaging the detection rates of all 1000 cameras. A Tukey HSD test was used to test for significant differences between mean detection rates.

Results:

Meta-analysis

The literature review resulted in 42 studies covering 42 species from 6 orders, with carnivores (13), primates (13), rodents (10), and ungulates (7) being the most common (see Appendix A for detailed study information and Appendix B for cited literature).

Movement rates were included in only 11 studies that reported density (Fig. 2-1), and in 10 of these, the higher density population exhibited a lower movement rate.. There appeared to be a non-linear relationship between the magnitude of the decrease in movement rate and the magnitude of the density change. Movement rates decreased by a maximum of just over 50% despite changes in density of up to 26-fold. Most density changes were on the order of <10-fold.

Increases in density were associated with decreases in home range size in 22 of 27 cases (Fig. 2-2). While the most pronounced decrease was an approximate 90% reduction in home range size over a 2.4-fold increase in density (coyotes; Wilson and Shivik 2011), there was a non-linear pattern between the magnitude of the decrease in home range and the magnitude of the density change (up to 42.2-fold). Three species, (white-tailed deer; Webb *et al.* 2007; chamois; Brambilla *et al.* 2006; and degu; Quirici *et al.* 2010) exhibited an increase in home range size with density.

An increase in home range size was usually associated with an increase in movement rate (Fig. 2-3). Movement rates increased to a maximum of just over 300% of the reference value while home range sizes differed by up to 25-fold. Most home range size changes, however, were on the order of <5-fold.

Meta-analysis of effect sizes using a random effects model revealed a significant negative relationship between movement rate and density (Fig. 2-4, $r = -0.32, p = 0.03$). Density and home range size were also significantly negatively correlated (Fig. 2-5, $r = -0.60, p < 0.0001$). Furthermore, there was a significant positive relationship between movement rate and home range size (Fig. 2-6, $r = 0.92, p = 0.012$). Effect sizes were significantly heterogeneous across studies for all three comparisons: movement rate vs density (Fig. 2-4, $Q_6 = 277.99, p < 0.0001$), home range size vs density (Fig. 2-5, $Q_{16} = 172.82, p < 0.0001$), and movement rate vs home range size (Fig. 2-6, $Q_9 = 2185.67, p < 0.0001$).

Animal Simulations:

Under the fast, large home range scenario (realized speed 180m/h, steady-state home range 100 km^2), the mean detection rate changed linearly, such that a change in density was associated with a proportional change in detection rate. For instance, the mean detection rate produced by 100 individuals/1000km^2 (Fig 2-7. mean = 0.086detections/d, sd = 0.072) was approximately double the mean detection rate produced by 50 individuals/1000km^2 (Fig 2-7. mean = 0.043detections/d, sd = 0.053).

In contrast, the slow, small home range scenario (realized speed 57m/h, steady-state home range 1 km^2), produced a non-linear trend in detection rate, where detections increased at a diminishing rate as density increased (Fig 2-7.). Assuming the fast, large home range scenario characterizes space use in populations at lower densities and the slow, small home range scenario characterizes movement in populations at higher densities, a difference in density of at least 50 individuals/1000 km^{2}was necessary to produce a significant change in detection rate (Table 2-1).

Comparisons between movement scenarios also inaccurately represented the true change in density. For example, the slower, smaller home range scenario at 100 individuals/1000km^2 (Fig 2-7. mean = 0.074detections/d, sd = 0.42) was approximately 1.7 times greater than the faster, larger home range scenario with 50 individuals/1000km^2 (Fig 2-7. mean = 0.043detections/d, sd = 0.053).

Discussion:

As predicted, an increase in population density was associated with a significant decline in movement rate and home range size across multiple species. This relationship directly violates the assumption that changes in detection rates reflect only changes in relative abundance and not changes in movement, and has important implications for wildlife monitoring programs that rely on unvalidated detection rate indices from camera trap sampling. Because a population in decline would produce more detections per individual through increased movement, one may falsely conclude that the population is stable (or at best declining less rapidly).

Despite overall significant negative relationships between density and both movement rate and home range size, there were some exceptions. These cases exhibited a positive change in movement rate or home range size across a positive change in density. Such a relationship is also problematic for detection rate indices, as it would lead to overestimates of changes in relative abundance. At least one of these cases was explained by greater landscape patchiness in resource-rich areas (e.g. Brambilla *et al.* 2006). Delayed density-dependence may also be the cause, as when a decrease in resources has a delayed effect on population density (e.g. Quirici *et al.* 2010).

While the predicted trends were indeed common, the degree to which these relationships affect camera data depends on their magnitude. Significant heterogeneity between effect sizes indicates that no singular magnitude of effect can be expected across different taxa or different systems. Movement rate and home range size may change dramatically with density, or very little. The greatest change was seen in coyotes (Wilson and Shivik 2011), where a 2.4 fold higher density was associated with movement rates less than half as fast and home ranges less than a tenth in size.

While coyotes exhibited the most dramatic differences in movement rate and home range size, it is difficult to generalize the magnitude of these effects across similar taxa. More groundwork needs to be done to assess movement rates of populations at different densities. Because of the variation in effect sizes, species or populations that have not been extensively studied should be treated with caution when making inferences about abundance based on camera trap detection rates.

The relationships observed in this analysis are concerning and could have a significant impact on the outcome of management or conservation decisions. Consider a hypothetical example involving a species of concern which is the target of a novel conservation strategy. Cameras are used to monitor the population response after the implementation of the strategy, with detection rate used as an index of relative abundance. Unfortunately, the conservation strategy fails and the population declines to an even lower density. At this low density, individuals move at faster movement rates and over larger home ranges – perhaps due to reduced habitat quality and greater difficulty finding patches of good forage. This increases the average encounter rate between individuals and camera traps, thus masking the effect of a reduction in the number of individuals on detection rate. If this were a species where the change in home range size and movement rate were strong in magnitude, the increased number of encounters per individual may overcompensate for the abundance change and produce more detections overall than before. An analysis of the camera data would reveal a greater detection rate after implementation of the strategy. Using detections as a relative abundance index, one would conclude that the novel strategy had worked and that the population was increasing, when in fact the opposite was true. Therefore, determining the magnitude by which detection rates are affected by movement is a critical step in evaluating the reliability of these indices.

To investigate the magnitude of space use as a confound on detections, I used simulated data representing changes in animal population movement and density. When the assumption of constant space use is upheld and individuals are generally fast moving over large ranges, a detection rate index performs very well. Keeping movement rate and home range size constant under such conditions, doubling the abundance approximately doubles the mean detection rate. However, when movement patterns change with density – a relationship expected by foraging theory and confirmed via the meta-analysis – the results are less clean. Compared to the fast-moving, large home range scenario, the slower and smaller home range population exhibited far greater variation in detection rates. This is explained by the fact that that as home ranges shrink, they are less likely to overlap a camera location, inflating the number of cameras with zero detections in the dataset. Conversely, individuals that do overlap with a camera are likely to revisit it many times, as their movements are confined to a smaller area. While detection rates were significantly different between the low density and high density populations even under realistic changes in movement, the large variability indicates that detection rate indices are poorly suited to measure the magnitude of relative abundance changes. Rather, they are better reserved as an indicator of directional trends rather than absolute magnitudes. It is also important to note that these findings reflect an otherwise ideal set of conditions for camera-trapping: identical individuals moving through a homogeneous landscape with random camera placement and perfect detection. Furthermore, even if the variance in detection rate could somehow be reduced in all populations, ensuring precise estimation of the mean, the index will still be confounded. While doubling the population should result in twice the detection rate (as confirmed when the population is doubled and space use is kept constant), the mean detection rate in the larger population was only 1.7 times the detection rate of the smaller population. Thus, beyond its issues with precision, the detection rate index will also tend to underestimate changes in population abundance. Whether this degree of inaccuracy is acceptable depends on the specific goals of the monitoring programme. In general, detection rates are best used as indicators of broad directional changes, and only somewhat reliable as a measure of the true magnitude of a population change. If detection rate indices are nevertheless used to track relative abundance, scientists and managers should keep in mind that the estimated magnitude of the change could be up to 30% smaller than its true value, based on this simulation. While this is worrying if an accurate magnitude of relative abundance is desired, it is at least encouraging that a situation where changes in movement are enough to produce an opposite trend in detection rate is unlikely. By encompassing the range in space use found in the meta-analysis, this simulation likely covers the worst-case scenario as far as the strength of the confound. Users of these indices should also take note of differences in the variance of their estimates, as this may be an earlier indicator of changes in the population, even if mean detection rates are not yet significantly different.

Given that assumptions of constant movement rate and home range size are violated, scientists and managers should consider carefully how they use camera data for unmarked species. In situations where it is necessary to monitor the dynamics of an unmarked species more precisely, passive DNA sampling would be a good alternative to cameras, as it is similarly non-invasive but allows direct calculation of density through SECR (Efford *et al.* 2009), though it is acknowledged that such methods are often out of financial or logistical reach. Alternative techniques for analyzing camera trap detections of unmarked species include approaches that model the encounter process, such as the Random Encounter Model (Rowcliffe *et al.* 2008). This model assumes random movement of individuals following an "ideal-gas" model and requires knowledge of the mean movement rate and group size of the species, as gathered through focal data (Rowcliffe *et al.* 2008). Camera placement should also be as random as possible, therefore camera placement protocols must be carefully decided beforehand. Another alternative uses the spatial correlation of detections to infer individual activity centers and subsequently estimate density (Chandler & Royle 2013). These methods are made even more robust if a portion of the population can be identified; while tedious, identifying some individuals of an unmarked species can be successful by observing scarring, injuries, or presence of parasites (e.g.: Kelly *et al.* 2008). However, methods that use spatial correlation of detections are sensitive to camera spacing as it relates to home range size (Chandler & Royle 2013), something few studies explicitly choose based on their target species' movement characteristics (Burton *et al.* 2015).

This is especially problematic for studies that seek to monitor multiple species simultaneously (ironically, a major appeal of camera-trapping). Density-dependent changes in home range size and movement rate may also elicit problems for these methods, as movement rate and appropriate camera spacing may need to be regularly corrected as these parameters change. While more careful planning of study design will be necessary if future camera-trapping programs are to monitor populations reliably, skepticism over the willingness of decision-makers to adopt alternative analytical methods over simpler relative abundance indices has been raised (Sollmann *et al.* 2013a). I hope the evidence presented in this chapter will help to encourage a more careful consideration of study design as well as the analysis and interpretation of camera data.

This chapter provides quantitative evidence that across a broad range of taxa home range and movement rate are negatively density-dependent, while movement rate and home range size are positively correlated. Changes in home range size and movement rate affect the probability of animals encountering, and being detected by, camera traps. These relationships between movement rate, home range size, and density violate a core assumption of the use of camera-trap detection rates as an index of population abundance, and this study has shown that they are common across taxa. Through simulation analysis, I have shown that the confounding effect of changes in movement and density can reduce the statistical power to detect change in relative abundance from detection data, and that estimates of relative abundance changes may miss up to 30% of the true change. These results support previous calls for caution in the use of relative abundance indices from camera trap sampling (Jennelle *et al.* 2002; Harmsen *et al.* 2010; Sollmann *et al.* 2013a; Burton *et al.* 2015). While more statistically sophisticated alternatives are available (e.g. Rowcliffe *et al.* 2008; Chandler & Royle 2013), these require careful planning of study design and some *a priori* knowledge of the species' movement characteristics. These alternatives are therefore unattractive to those who chose camera-trapping for its simplicity, and alarm has been raised over the continued uncritical application of relative abundance indices (Sollmann *et al.* 2013a). It is hoped the evidence presented here will encourage a more cautious consideration of the merits of each analytical method, and more deliberate choice of study design. As relative abundance indices are frequently present at the front lines of management and conservation, I urge a more critical look at their use and interpretation.

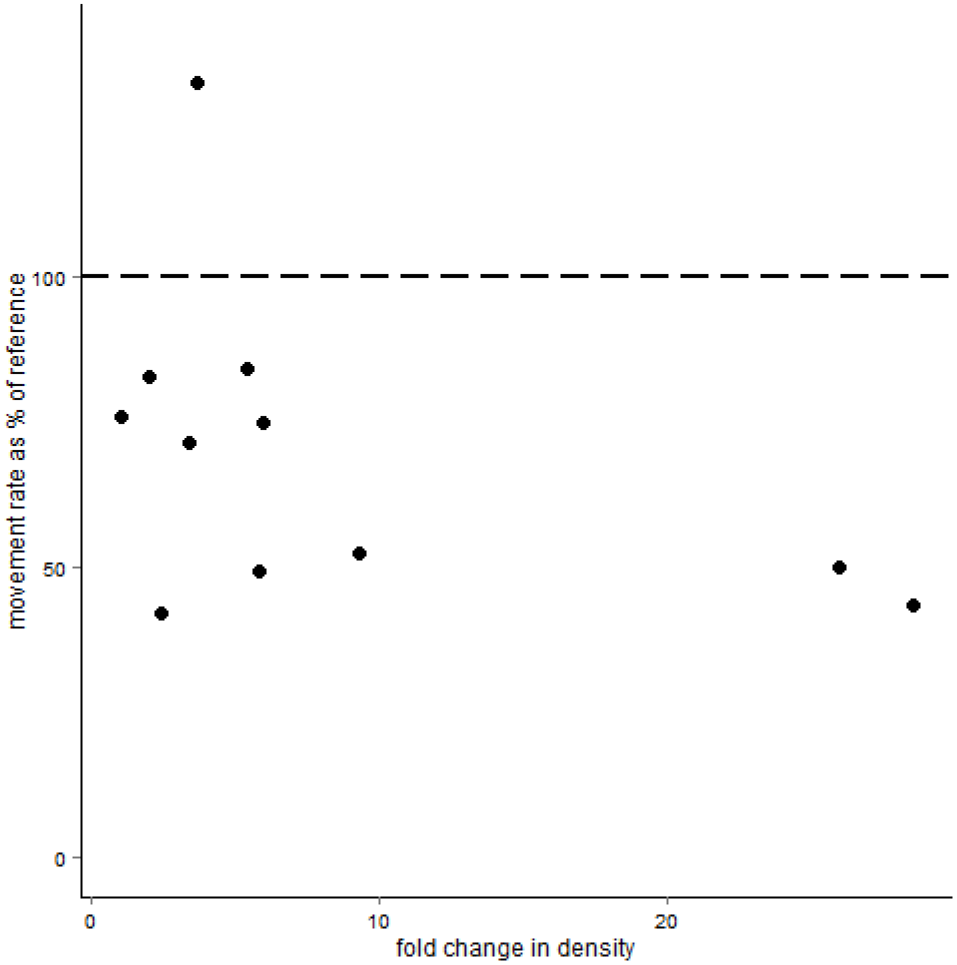


Figure 2-1: Movement rate in a higher density population expressed as a percentage of the lower density population’s movement rate (i.e. reference value). 100% represents no change in movement rate. Points that fall below the 100% line indicate a drop in movement rate over a given change in density; points that fall above the 100% line indicate an increase in movement rate over a given change in density. N=11 studies.

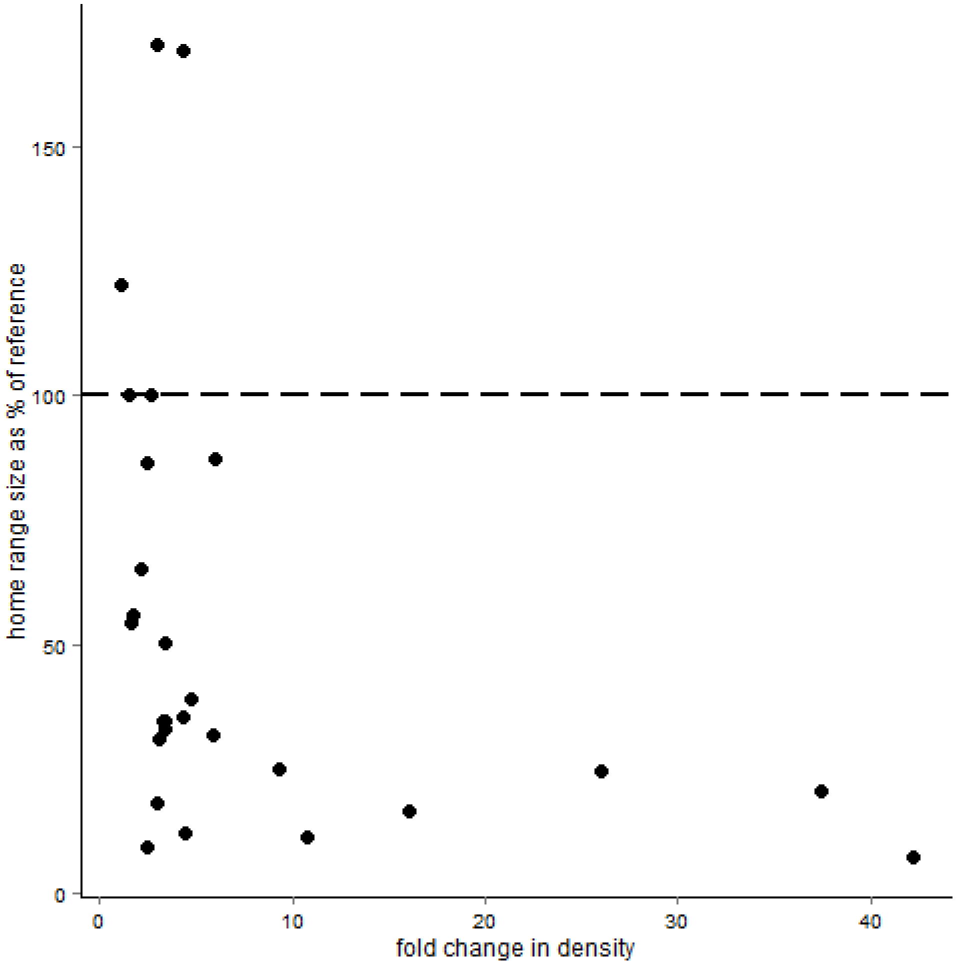


Figure 2-2: Home range size in a higher density population expressed as a percentage of the lower density population's home range (i.e. reference value). 100% represents no change in home range size. Points that fall below the 100% line indicate a drop in home range size over a given change in density; points that fall above the 100% line indicate an increase in home range size over a given change in density. N=26 studies.

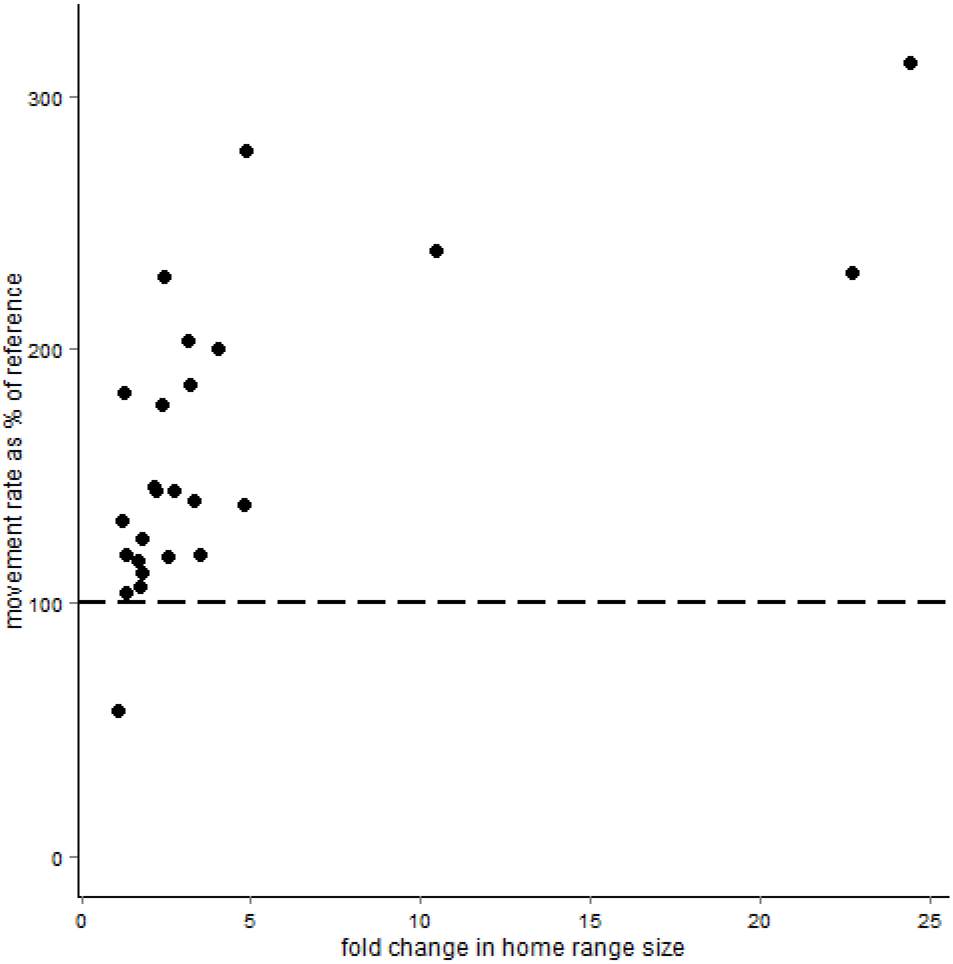


Figure 2-3: Movement rate in a population with larger home ranges expressed as a percentage of the smaller home range population's movement rate (i.e. reference value). 100% represents no change in movement rate. Points that fall below the 100% line indicate a drop in movement rate over a given change in home range size; points that fall above the 100% line indicate an increase in movement rate over a given change in home range size. N=25 studies.

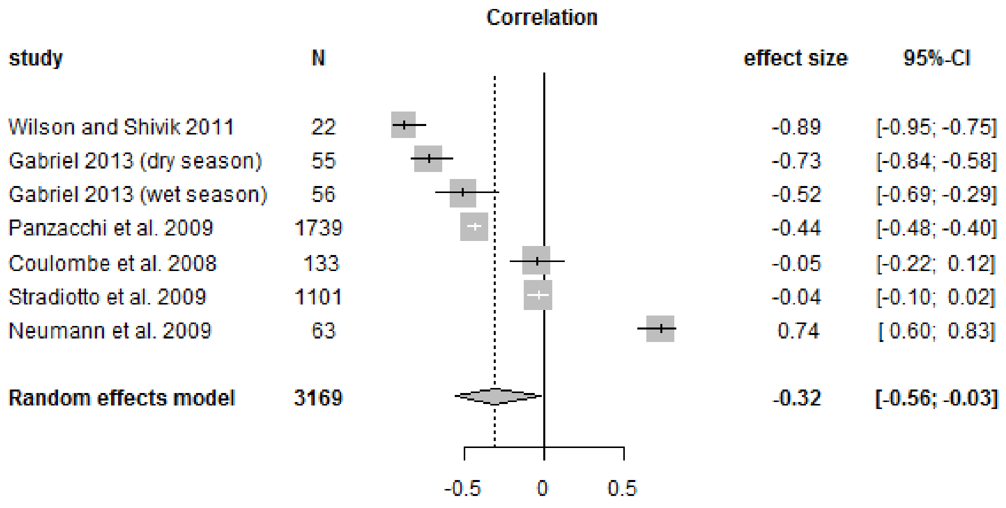


Figure 2-4: Forest plot indicating the mean effect size (correlation coefficient) of studies that reported movement rates across different densities. The effect size is significant if its 95% confidence interval (the black bar) does not overlap zero. Negative correlation coefficients indicate that movement rates are slower at higher densities. The diamond indicates the overall effect size as determined by a random effects model.

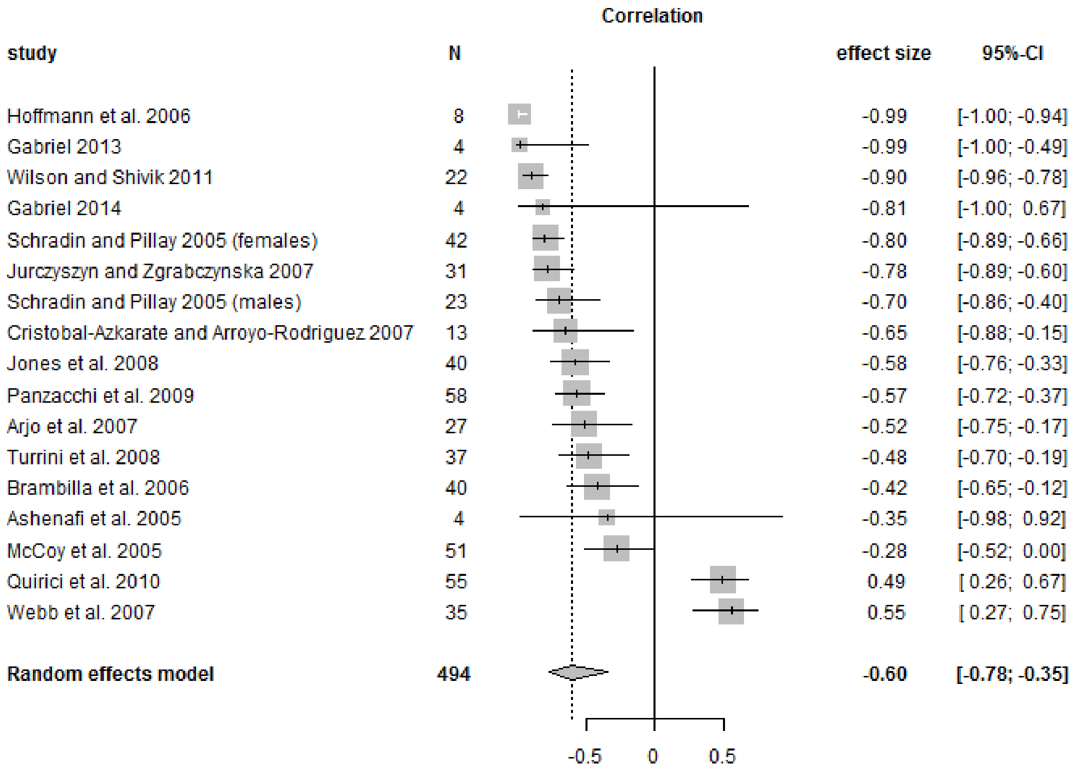
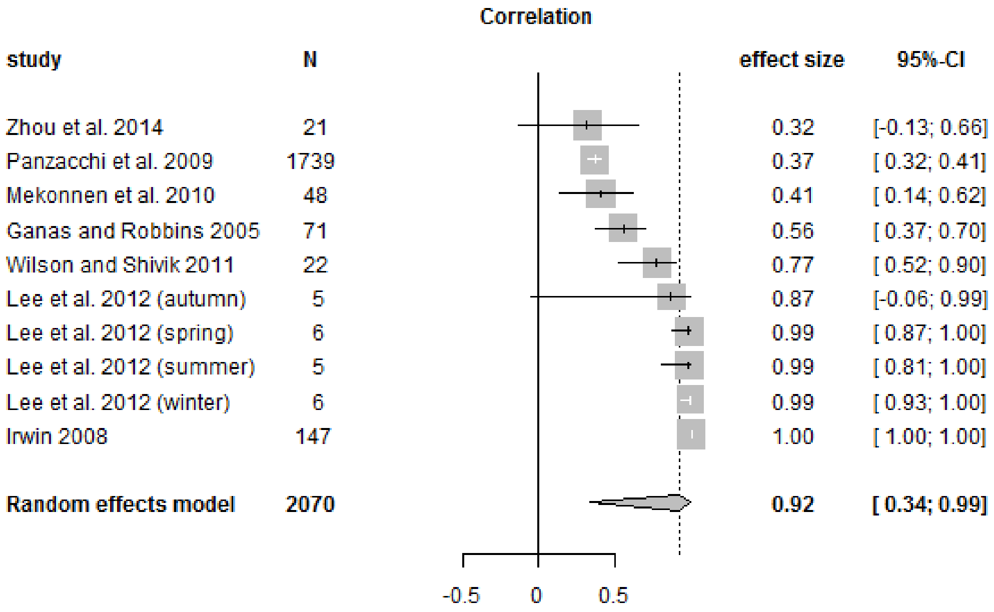


Figure 2-5: Forest plot indicating the mean effect size (correlation coefficient) of studies that reported home range sizes across different densities. The effect size is significant if its 95% confidence interval (the black bar) does not overlap zero. Negative correlation coefficients indicate that home ranges are smaller at higher densities. The diamond indicates the overall effect size as determined by a random effects model.



study	N	effect size	95%-CI
Zhou et al. 2014	21	0.32	[-0.13; 0.66]
Panzacchi et al. 2009	1739	0.37	[0.32; 0.41]
Mekonnen et al. 2010	48	0.41	[0.14; 0.62]
Ganas and Robbins 2005	71	0.56	[0.37; 0.70]
Wilson and Shivik 2011	22	0.77	[0.52; 0.90]
Lee et al. 2012 (autumn)	5	0.87	[-0.06; 0.99]
Lee et al. 2012 (spring)	6	0.99	[0.87; 1.00]
Lee et al. 2012 (summer)	5	0.99	[0.81; 1.00]
Lee et al. 2012 (winter)	6	0.99	[0.93; 1.00]
Irwin 2008	147	1.00	[1.00; 1.00]
Random effects model	**2070**	**0.92**	**[0.34; 0.99]**

Figure 2-6: Forest plot indicating the mean effect size (correlation coefficient) of studies that reported movement rates across populations with different home range sizes. The effect size is significant if its 95% confidence interval (the black bar) does not overlap zero. Positive correlation coefficients indicate that movement rates are slower at when home ranges are smaller. The diamond indicates the overall effect size as determined by a random effects model.

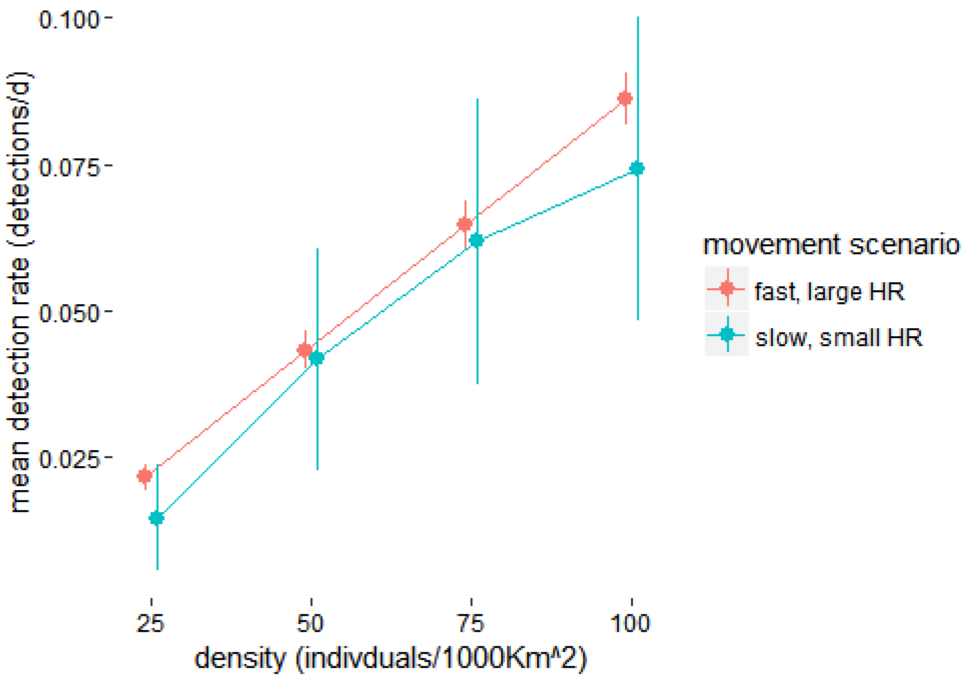


Figure 2-7: Mean detection rate under different densities and movement scenarios. Movement scenarios represent home range sizes and movement rates that co-vary and encompass the possible range in behaviour as seen in the meta-analysis. Populations of 25, 50, 75, and 100 individuals were simulated in a 1000 km^{2}domain. The fast movement, large home range scenario is indicated in red (realized speed 180m/h, steady-state home range 100 km^2) while the slow movement, small home range scenario is indicated in blue (realized speed 57m/h, steady-state home range 1 km^2). Detection rates represent the mean detection rate across 1000 randomly-placed cameras over a time span of six months. Error bars represent 95% confidence intervals.

Table 2-1: Pairwise comparisons of simulated detection rates.

treatment 1	treatment 2	difference	lower limit	upper limit	p-value	
fast_large:25	fast_large:50	0.0217	-0.0109	0.0542	0.4681	
fast_large:25	**fast_large:75**	0.0431	0.0106	0.0757	**0.0015**	*
fast_large:25	**fast_large:100**	0.0646	0.0321	0.0972	**<0.0001**	*
fast_large:25	slow_small:25	-0.0070	-0.0395	0.0256	0.9981	
fast_large:25	slow_small:50	0.0202	-0.0124	0.0527	0.5660	
fast_large:25	**slow_small:75**	0.0402	0.0077	0.0728	**0.0045**	*
fast_large:25	**slow_small:100**	0.0526	0.0200	0.0851	**<0.0001**	*
fast_large:50	fast_large:75	0.0215	-0.0111	0.0540	0.4824	
fast_large:50	**fast_large:100**	0.0430	0.0104	0.0755	**0.0016**	*
fast_large:50	slow_small:50	-0.0015	-0.0341	0.0310	1.0000	
fast_large:50	slow_small:75	0.0185	-0.0140	0.0511	0.6698	
fast_large:50	slow_small:100	0.0309	-0.0016	0.0634	0.0769	
fast_large:75	fast_large:100	0.0215	-0.0110	0.0540	0.4799	
fast_large:75	slow_small:75	-0.0029	-0.0355	0.0296	1.0000	
fast_large:75	slow_small:100	0.0094	-0.0231	0.0420	0.9878	
fast_large:100	slow_small:100	-0.0120	-0.0446	0.0205	0.9521	
slow_small:25	fast_large:50	0.0287	-0.0039	0.0612	0.1316	
slow_small:25	**fast_large:75**	0.0501	0.0176	0.0827	**0.0001**	*
slow_small:25	**fast_large:100**	0.0716	0.0391	0.1042	**<0.0001**	*
slow_small:25	slow_small:50	0.0271	-0.0054	0.0597	0.1832	
slow_small:25	**slow_small:75**	0.0472	0.0147	0.0797	**0.0003**	*
slow_small:25	**slow_small:100**	0.0596	0.0270	0.0921	**<0.0001**	*
slow_small:50	fast_large:75	0.0230	-0.0096	0.0555	0.3883	
slow_small:50	**fast_large:100**	0.0445	0.0119	0.0770	**0.0009**	*
slow_small:50	slow_small:100	0.0324	-0.0001	0.0650	0.0515	
slow_small:50	slow_small:75	0.0201	-0.0125	0.0526	0.5728	
slow_small:75	fast_large:100	0.0244	-0.0081	0.0570	0.3073	
slow_small:75	slow_small:100	0.0124	-0.0202	0.0449	0.9449	

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CHAPTER III: Variation in Space Use Within Populations

Introduction:

Assumptions of Emerging Analytical Techniques for Camera Traps

In Chapter II, the relationship between movement rate and home range size at an inter-population level was quantified. As expected, movement rate and home range size were positively correlated. However, the range of space use within populations is also an important subject worthy of investigation. While individual variation is often ignored in favor of population-level trends (Bolnick *et al.* 2003; Dall *et al.* 2012), individual variation in behavior is likely to result in fitness consequences and is an important factor in resource ecology and population dynamics (Dall *et al.* 2012).

Furthermore, individual variation in space use is an important consideration for camera trap study design. A variety of analytical techniques are available for tracking population dynamics from camera trap data, and these techniques differ with respect to their assumptions about the relationship between camera spacing and movement. For simplicity, they can be divided into several broad categories. First are techniques like spatially explicit capture-recapture (SECR) (Efford 2004) and similar spatially explicit density models for unmarked species (Chandler & Royle 2013). Because these methods use the spatial correlation of detections amongst sites to estimate the locations of animal activity centers, individuals *must* be detected at more than one location. Thus, to use such models, cameras must not be spaced apart farther than the species' home range size. In contrast, N-mixture models (Royle & Nichols 2003) and occupancy models (Mackenzie *et al.* 2005) assume sites are independent, where no individual is detected at more than one site. For these methods, cameras should be spaced out at least as far as the species' home range size lest the model assumption be violated. Finally, the random encounter model described by Rowcliffe *et al.* (2008) (which uses detection rates along *with a priori* estimates of animal speed and camera trapping area to estimate density) requires random spacing of cameras. While it has the advantage of being insensitive to animal home range size, accurate estimates of the target species' movement rate must be determined for input into the model.

Few camera trap studies explicitly incorporate *a priori* information about the target species' space use into the study design process (Burton *et al.* 2015). However, even if a practitioner decides to follow best practices and use known information of their species' space use to decide on camera trap spacing, doing so is not straightforward. As camera traps are often used as an alternative to more invasive methods like radio-telemetry, detailed data on the movement of the study population is most likely unavailable. Practitioners may turn to the literature for this information, but a mean home range size or movement rate for the species may not be representative of the target population. Even if the practitioner is fortunate enough to find, say, a mean home range size that is accurate for their own population, individual variation will result in some individuals having larger ranges and some individuals having smaller ranges. If this variation is large, cameras may not be spaced close enough or far apart enough to completely meet the assumptions of the chosen analytical model. It is therefore important to understand the degree to which space use varies between individuals within a population.

Individual Movement Rate and Home Range Size

Given that general space use at the population level is driven by individual-level processes, I expect to see similar broad relationships at the individual level as at the population level. The more an animal stops to forage, the slower it moves, therefore more productive areas should be associated with less movement (Owen-Smith *et al.* 2010). This response is observed in a number of species (e.g. Novellie 1978; Owen-Smith 1979; Fryxell *et al.* 2008). A home range represents the area in which an animal lives (Burt 1943; Brown and Orians 1970), and therefore its size is a response to the distribution of resources necessary for survival (Harestad & Bunnel 1979). On this basis, one would expect individuals with large home ranges to have higher movement rates – similar to the trend seen between populations in Chapter II. However, the way animals with larger ranges spread out their movements through space may depend on the spatial distribution of resources and competitors that necessitated the large home range in the first place. Whereas an environment with fewer but relatively dispersed resources may cause an individual to spread its activity over a large area, a poor but heterogeneous environment may cause a pattern of focused activity within relatively small areas despite a large overall home range. The larger a home range, the more likely it is to overlap poor quality patches (Harestad & Bunnel 1979), and focused activity in resource-rich patches punctuated by long directed movements between patches has been observed in elk (Fryxell *et al.* 2008).

Seasonality is another source of variation as some species alter their space use in the winter (e.g. Ager *et al.* 2003; Ferguson & Elkie 2004). While resources generally become more scarce in winter, animals may switch to different feeding strategies (Halfpenny & Ozanne 1989) and be impeded by snow (Luccarini *et al.* 2006). Finally, trophic level may cause differences in space use patterns. It is already well-established that carnivores have larger home ranges than herbivores of the same body size (Harestad & Bunnel 1979). Whether they also exhibit different movement – home range relationships or a different degree of heterogeneity is yet to be seen.

Chapter Objectives

This chapter aims to characterize heterogeneity in space use within populations by examining telemetry data for two herbivores and a carnivore. Using this combined dataset, I will describe how individual movement rate varies with home range, how seasonality affects overall variation in space use, how carnivores and herbivores differ in their degree of individual heterogeneity, and how within-population differences compare to between-population differences. This will provide a detailed description of spatial behavior at the individual level, of which the implications for camera trap study design will also be addressed.

Methods:

Datasets

Telemetry location data were used from a number of existing datasets. Dispersing individuals identified by unusually long excursions to a new home range were excluded from analysis if present.

Manitoba white-tailed deer (MB deer): This white-tailed deer (*Odocoileus virginianus*) dataset was collected from southwestern Manitoba in 2006 and 2007 (see Laforge *et al.* 2015). Adult white-tailed deer were fitted with GPS collars programmed to record their location every four hours. Movement rate was calculated using four-hour long steps between telemetry relocations. The number of available four-hour steps per deer ranged from 49 to 2051 steps in summer (14 deer) and from 197 to 1296 steps in winter (13 deer). An individual's mean movement rate was then calculated as the average distance travelled during a step converted into km/d.

Alberta white-tailed deer (AB deer): This white-tailed deer dataset was collected in Northeastern Alberta from 2012-2015 as part of the Alberta Boreal Deer Project, conducted by Alberta Innovates Technology Futures (AITF; Fisher et al. 2016). GPS collars were programmed to record locations every two hours. The number of recorded two-hour steps per deer ranged from 893 to 7020 steps in summer (15 deer) and from 133 to 5216 steps in winter (33 deer).

Alberta moose (AB moose): These data from the Athabasca oilsands region of Alberta were collected as part of the Wildlife Habitat Effectiveness and Connectivity Research Program (WHEC) from 2010 to 2012. Twenty-five Moose (*Alces alces*) were fitted with GPS collars programmed to record locations every three hours. Movement rate was calculated for each individual as the average distance of their three-hour steps. The number of such steps recorded per moose ranged from 280 to 4389 steps in summer and from 208 to 3343 steps in winter.

Alberta wolves 1 (AB wolves (1)): This dataset was collected as part of a Regional Industry Caribou Collaboration (RICC) project in northeastern Alberta in 2013 and 2014. The dataset reflects wolves (*Canis lupus*) from six different packs within the Devon Energy lease rights (21 individuals during summer and 13 during winter). Wolves were fitted with GPS collars programmed to record locations on a cycle of every five minutes for two days and every hour for four days during spring/summer, and every five minutes during the winter. Movement rate was calculated using only steps with a five-minute interval. The number of available five-minute steps per wolf ranged from 5176 to 9090 steps in summer and from 2395 to 19020 steps in winter.

Alberta wolves 2 (AB wolves (2)): This wolf dataset was collected from the Athabasca oilsands region of Alberta as part of the Wildlife Habitat Effectiveness and Connectivity Research Program (WHEC) from 2012 to 2014. Wolves were captured from 11 packs and GPS collars recorded locations at a variety of intervals (from 15 minutes up to 12 hours apart). Only the 15-minute long steps were used to calculate movement rate, and the number of such steps recorded for each wolf ranged from 1419 to 7713 steps in the summer (23 wolves) and from 541 to 14880 steps in the winter (23 wolves).

British Columbia wolves (BC wolves): This dataset was collected in Northeastern British Columbia near Fort Nelson in 2013 and 2014. Wolves were fitted with GPS collars programmed to record locations every 15 minutes. These data were collected as part of the caribou project: "Assessing Spatial Factors Affecting Predation Risk to Boreal Caribou Calves: Implications for Management." For this reason, detailed GPS data (15 minute fixes) were only collected for the caribou calving season: May-June. The number of 15-minute steps recorded for each wolf ranged from 794 to 11465 steps (12 wolves).

Data Analysis

Small numbers of relocations tend to underestimate home range sizes when using the minimum convex polygon method (MCP), and inflate home range sizes when using kernel density estimation (KDE). A minimum of 30 locations is recommended (Samuel and Garton 1985), therefore individuals with fewer than 30 relocations were excluded. Most individuals had well above 30 locations - an average of 3252 locations were used to calculate an individual's home range.

Home range was estimated using the 95% minimum convex polygon (MCP) for each individual. Movement rate was calculated as the mean kilometers travelled per day. This was calculated using the step intervals detailed above; the lengths of all available steps for an individual were averaged to determine the mean straight-line distance travelled during that time interval, and then converted into km/d. For each dataset, summer (April-Sept) and winter (Oct-Mar) were analyzed separately in order to reveal seasonal differences in space use. Because movement rate cannot increase past a threshold determined by a species' physiological limits, a logarithmic function may better describe the relationship between movement rate and home range size. To determine the best fit, two linear models were fit using either the original or log-transformed home range size as the predictor variable and movement rate as the response variable for each comparison. The two models were ranked using corrected Akaike's information criterion (AICc) to determine whether a linear or logarithmic function best described the relationship.

To determine how movements were distributed within home ranges, core range areas were estimated using a 50% kernel density estimate (KDE) for each individual and compared to the overall home range using a 95% kernel density estimate.

To test for seasonal differences in behavior, mean home range sizes and mean movement rates across the two seasons were compared using Welch's unequal variances t-test (except for the BC wolves dataset which only includes summer data).

These analyses were performed in R 3.3.1 using the packages "adehabitatHR," "adehabitatLT," and "AICcmodavg."

Results:

A logarithmic curve was found to be a better fit for all comparisons except for the Manitoba deer in summer and Alberta deer in winter (see Appendix B for evidence ratios). In 7 out of the 11 populations examined, there was a significant positive relationship between individual movement rate and home range size (Fig 3-1, 3-2; see Appendix D for more detailed breakdown by population and season). The BC wolf population in summer was the only case in which there was a significant negative relationship (Fig 3-2.)

In nearly all cases, individual variation in movement rate and home range size between individuals was an order of magnitude greater than the variation in average movement between populations. For example, mean summer movement rates of the Alberta wolf populations differed by 4.29 km/day, while individuals with the highest and lowest movement rates differed by 13.64km/d and 23.59km/d in the respective populations. Similarly, mean summer home range sizes differed between populations by 133.7 km^2, whereas individuals with the largest and smallest home ranges within those populations differed by 1151.2 km^2 and 815.1 km^2 respectively.

Wolf populations in general exhibited greater variability than the ungulate populations. When comparing the smallest home range to the largest home range within a population, individual deer differed by at most 20.9 km^2 (MB deer in summer: min 0.2 km^2, max 28.4 km^2) while individual moose differed by at most 137.4 km^2 (AB moose in winter: min 0.10 km^2, max 137.5 km^2). In contrast, wolf home ranges differed by as much as 1205.2 km^2 (AB wolves (2) in winter: min 42.8 km^2, max 1248 km^2). Even the least variable wolf population, AB wolves (1) in winter, still had a range of home range sizes of 500.4 km^2 (min 156.8 km^2, max 657.2 km^2). Similarly, the slowest and fastest deer and moose movement rates differed by at most 2.7km/d (AB deer in winter: min 0.5km/d, max 3.1km/d) and 1.3km/d (AB moose in winter: min

0.3km/d, max 1.6km/d) respectively, while wolf movement rates differed by as much as 25.2km/d (BC wolves: min 17.6km/d, max 42.8km/d).

The sizes of core (50% kernel) home ranges for individuals in all ungulate and wolf populations exhibited a significant positive relationship with total home range (95% kernel) in summer and in winter, but the slopes of the relationships were weak (Fig 3-3, 3-4). In other words, the time an individual spends in given parts of its home range is more uneven when the home range is large.

In the ungulate populations, there was no significant difference in home range size between summer and winter, but movement rates were always slower in winter (Fig 3-5). The same trend was seen in wolves, where home range sizes did not differ significantly between summer and winter, but movement rates were significantly slower in winter (Fig 3-6).

Discussion:

In Chapter II, I found that populations with greater mean home ranges had greater mean movement rates. In this chapter, home range – movement rate relationships between individuals mirrored those found at the population level: home range size and movement rate were usually positively correlated. One possible explanation is that individuals located in better-quality patches do not need to move as much to find resources as individuals that place their home ranges in poorer patches. The BC wolf population was an interesting exception, as it displayed the opposite relationship, where individuals with smaller home ranges tended to move more. This may be a result of territoriality where the best (and smallest) territories must be marked/defended more often. Nevertheless, the overall positive relationship between movement rate and home range size suggests that when individuals must search for resources over a larger area, they compensate by moving more. This more or less maintains a similar rate of nutrient intake over time so that metabolic needs are met.

While the relationship between core range (i.e. the area where an individual spends 50% of its time) and total home range size were positively correlated, the slope of this relationship is small, meaning the core area does not increase proportionally for individuals with a large overall home range. This indicates that far-ranging individuals do not simply replicate the movements of smaller-ranging individuals over a larger area. Rather, their activities are concentrated on relatively small patches which are dispersed through space. This spatial distribution of movement reflects the pattern of convoluted movements punctuated by long directed movements between patches observed in other systems (Fryxell *et al.* 2008). Large home ranges are likely to contain unproductive patches (Harestad & Bunnel 1979), and unproductive patches are associated with more directed movement as the animal doesn't stop to feed as often (Owen-Smith *et al.* 2010).

Analysis of the telemetry data also revealed common seasonal differences. For both wolves and ungulates, home ranges did not change significantly between seasons, while winter movement rates decreased to approximately 55-85% of the summer movement rates. Given reduced habitat productivity in winter, one might expect home ranges and movement rates to increase to compensate. However, many species switch foraging strategies during winter. Ungulates shift to lower ranges and switch from grazing to browsing shrubs (Halfpenny and Ozanne 1989). Animals may also spend more time resting to reduce energy expenditures and conserve heat (Halfpenny and Ozanne 1989). Fat reserves may reduce the need of large ungulates to range widely, and poorer quality forage may necessitate more time ruminating

(Mysterud, Perez-Barberia & Gordon 2001). Also, snow cover may account for reduced mobility in winter (Luccarini *et al.* 2006).

Despite the overall correlation between home range size and movement rate, there was considerable variation around the trend in most cases. In fact, individual variation within populations was much greater than the variation in mean movement rate or home range size between populations. Numerous individuals defied overall trends; some smaller ranging individuals exhibited relatively fast movement rates, while some far ranging individuals moved relatively slowly. This variation suggests that the factors that drive space use are complex and go beyond simplistic responses to habitat quality.

One source of this complexity could be due to sex or age differences. It is well established that home range size often differs between sexes and age classes (Harestad & Bunnel 1979). While such differences are largely explained by differences in individual body weight, other factors like breeding status can play a role. For example, an adult female with high resource requirements may have her home range constrained by her offspring, meaning she must acquire the resources she needs without leaving a relatively small area (Harestad & Bunnel 1979). Resource distribution may also interact with factors like mating status in predicting home range size, where individuals working to acquire mates do not respond to other resources as expected (Brambilla *et al.* 2006).

Space use may also be a characteristic of personality. It is known that personality traits like boldness can affect large-scale movement processes like migration (Chapman *et al.* 2011) and dispersal (Cote *et al.* 2010). Differences in individual space use may in fact reflect different strategies for balancing risk vs resource acquisition. Bolder individuals tend to take more foraging risks; they are faster to begin foraging and spend less time vigilant (Dammhahn &

Almeling 2012). Greater tendency towards exploration of novel environments is also associated with greater space use (Boyer *et al.* 2010). Boon, Réale and Boutin (2008) found that personality-dependent space use ultimately leads to fitness consequences, where bolder individuals exhibit reduced life span. Thus, heterogeneity in space use may represent a range of strategies where different individuals are making different life history trade-offs.

While all species exhibited broad variation in home range size and movement rate, wolves exhibited much greater variation compared to the ungulate species. This difference between carnivores and herbivores may have a number of explanations. Prey biomass is much more sparsely distributed than forage biomass, so a carnivore requires a much greater home range to meet its metabolic requirements compared to an herbivore of similar size (Harestad & Bunnel 1979). It is possible that at this larger scale, there is more heterogeneity in resource richness (i.e. prey quality) and distribution. Individual carnivores may also differ in hunting behavior and preferences for certain prey (Dickman & Newsome 2015). For example, individual specialization for different prey species has been documented in cougars, persisting even when the preferred prey is less abundant (Ross & Jalkotzy 1996; Elbroch & Wittmer 2013). Great differences in prey biomass and distribution could contribute to the broad heterogeneity observed in the carnivore populations, especially if individuals exhibit preferences for different prey.

The potential factors causing variation in home range size and movement rate are numerous, and how they interact is a worthy topic of future research. Regardless of the source of this heterogeneity, individual variation in space use has important implications for camera trap study design. Because different analytical methods make different assumptions regarding the scale of animal movement relative to the spacing of camera sampling sites, it is recommended that *a priori* knowledge of the target species' spatial ecology be incorporated into the camera study design (Burton *et al.* 2015). Knowing the home range size of the species in question, cameras can be spaced either close enough to ensure repeat detections at multiple locations (as required by SECR or similar methods for unmarked animals) or far enough to ensure site independence (as required by occupancy or N-mixture models). However, intra-population variability in space use may complicate the choosing of an appropriate study design.

Suppose a manager wishes to monitor white-tailed deer and intends on applying N-mixture models to camera detection data. Detailed space-use information on the target population is likely not available, since cameras are often favored as a way of avoiding the collection of costly and invasive telemetry data (Kucera & Barrett 2011). Careful study planning would call for the manager to use *a priori* information on the target species' spatial ecology when deciding on camera spacing (Burton *et al.* 2015). Without information specific to the target population in question, the manager would likely base the spacing on the species' home range size as reported in the literature – e.g. 1.96 km^2 (Harestad & Bunnel 1979). Based on this reported home range size, cameras spaced 2-3 km apart should meet the N-mixture model assumption of site independence (i.e. no home ranges overlap more than one camera). However, looking at both the white-tailed deer populations examined in this chapter, most individuals have ranges far larger than 1.96 km^2. Even if cameras were spaced very conservatively at 10 km apart, some individuals could still violate the assumption of site independence. In fact, during summer, almost half of the MB deer population had a home range size greater than 10 km^2.

The consequences of violated model assumptions for these relatively new analytical techniques are still not fully understood. While Efford and Mowat (2014) suggested that SECR could underestimate density if individual heterogeneity is not included in the model, they found that SECR is reasonably robust to variation in spatial behavior. This is because variation in the scale of movement (i.e. home range size) tends to be compensated for by changes in the probability of detection at the home range center (a function of movement rate) (Efford & Mowat 2014). This finding is supported by the overall trends found here between movement rate and home range size, though some caution is called for as not all populations exhibit a significant correlation. Of course, those monitoring unmarked species must consider alternatives to SECR. The more recent spatially explicit density model developed by Chandler and Royle (2013) operates similarly by using the spatial autocorrelation of counts to estimate animal home range centers. While this method represents a promising advance, low encounter rates and small scale of movement (i.e. slower speeds and smaller home ranges) tend to produce biased estimates (Chandler & Royle 2013). Partially marking the population greatly improved model performance in simulations (Chandler & Royle 2013), and natural marks can sometimes be used to identify some individuals from camera data (Kelly *et al.* 2008). However, consideration should be made as to whether the presence of natural markings is independent of space use. Individuals with identifiable scars, wounds, or parasites may differ in health or boldness from the general population, and exhibit correspondingly different movement patterns. For instance, Boyer *et al.* (2010) found that parasite load was related to personality-dependent space use.

Occupancy and N-mixture models present different challenges. When using occupancy models, fast movement over large ranges necessitate that repeat surveys be conducted over a short time span lest the assumption of site independence be violated (Mackenzie & Royle 2005). To truly meet the model assumption, the interval between surveys must be short enough that the fastest/furthest ranging individuals in the population do not have enough time to reach more than one camera site. It is also recommended that heterogeneity in detection probability between sites be minimized as much as possible(Mackenzie & Royle 2005), however, heterogeneity in detections due to different behavior of individuals located at different sites is difficult to account for. N-mixture models work similarly to occupancy models but instead estimate abundance from counts (Royle & Nichols 2003). Differences in detection probability are essentially modeled as a random effect, where it is assumed that local abundance drives site-specific detections (Royle & Nichols 2003). While this method helps account for heterogeneity in detection probability, it is assumed that this heterogeneity is driven solely by abundance, and that all individuals detected at a given site are otherwise the same (Royle 2004). Given the wide variability in individual movement rates and home range sizes, this assumption is rarely true. Such problems only add to the difficulties caused by density-dependent space use. As Efford and Dawson (2012) noted, the proportion of area occupied is affected by both density and home range size, making occupancy poorly suited for tracking population dynamics when these are correlated.

The random encounter model developed by Rowcliffe *et al.* (2008), which combines detection rate with sampling area and animal movement rate to estimate density, has the advantage of being insensitive to home range size. However, the model produces inaccurate estimates when camera placement is biased compared to the population distribution (Rowcliffe *et al.* 2008). Thus, cameras must be placed in random locations across the study area for the method to be appropriate. The model also requires independent estimation of the species' movement rate, however wide range in movement rate amongst individuals may make precise estimation of this parameter difficult. Rowcliffe *et al.* (2008) note that estimation of movement rate is best conducted at the same time as the camera trapping (rather than derived from the literature), though biased sampling of individuals is difficult to avoid. If, for instance, focal watches are used to observe movement rates, sampling should be extensive enough to ensure slow moving individuals with small home ranges do not go undetected.

The comparative performance of these emerging methods remains largely untested in the field (Dénes, Silveira & Beissinger 2015). As the robustness of analytical techniques for unmarked populations continue to be investigated, even more statistical methods are likely to emerge (Dénes *et al.* 2015). Individual heterogeneity in space use adds a layer of complexity to the study design process, and those employing camera traps should carefully consider which analytical method they will ultimately use, the assumptions it makes regarding animal behavior, and the appropriate spacing of cameras needed to ensure assumptions are met. Given that individuals within a population differ widely in home range size, camera spacing must be quite conservative relative to home ranges as reported in the literature if assumptions are to be met. If using methods like SECR or the spatially explicit density model for unmarked species, cameras should be spaced much closer than what might be considered necessary given *a priori* estimates of the species' home range size. If using methods like occupancy or N-mixture models, cameras should be spaced much farther apart than what might be considered necessary. If using the random encounter model, cameras should have truly random placement and movement rate should be estimated from thorough observation of the target population in question. The magnitude of individual variation described in this chapter underscores the importance of testing the performance of these techniques when assumptions are violated, as well as the ongoing need for new statistical methods that can estimate population density of unmarked species that are not confounded by movement.

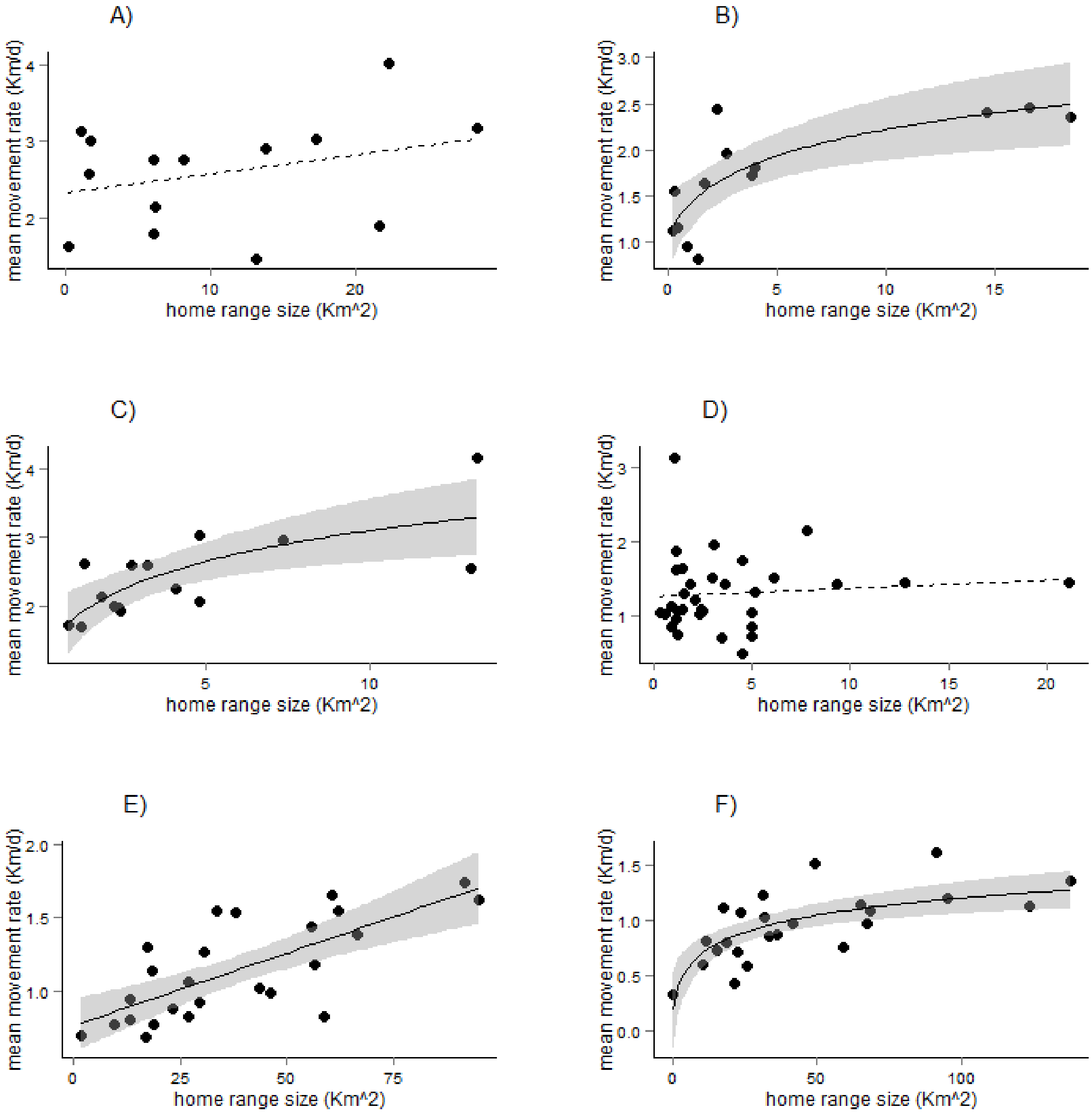

Figure 3-1: Individual movement rates (km/d) and home range sizes of three ungulate populations. MB deer in A) summer (N=14) and B) winter (N=13), AB deer in C) summer (N=15) and D) winter (N=33), and AB moose in E) summer (N=25) and F) winter (N=25). Regression line is depicted in black (dashed when not significant) while the grey shaded area represents the 95% confidence interval.

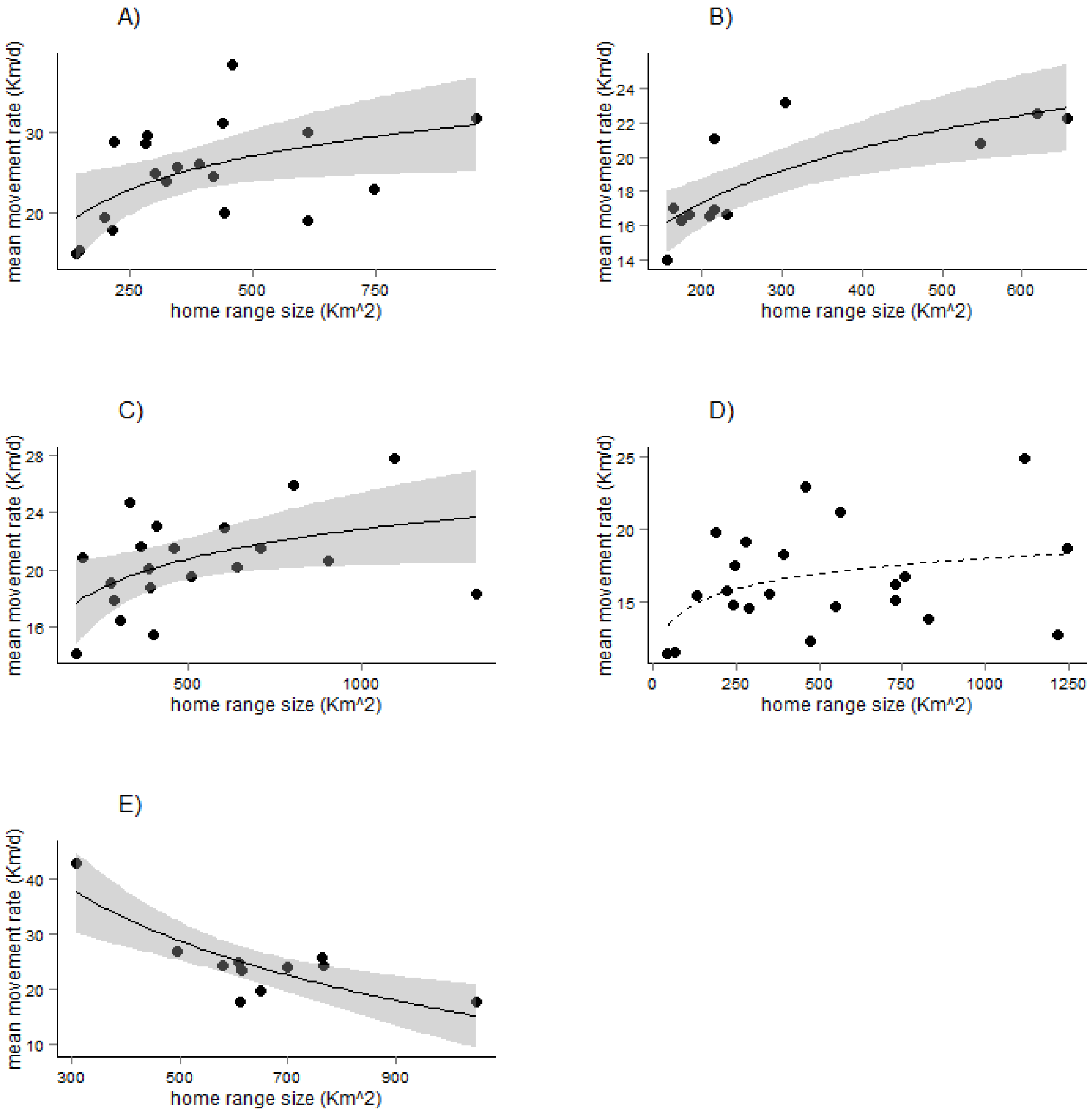

Figure 3-2: Individual movement rates (km/d) and home range sizes of three wolf populations. . AB wolves (1) in A) summer (N=19) and B) winter (N=12), AB wolves (2) in C) summer (N=20) and D) winter (N=22), and BC wolves in E) summer (N=11).Regression line is depicted in black (dashed when not significant) while the grey shaded area represents the 95% confidence interval.

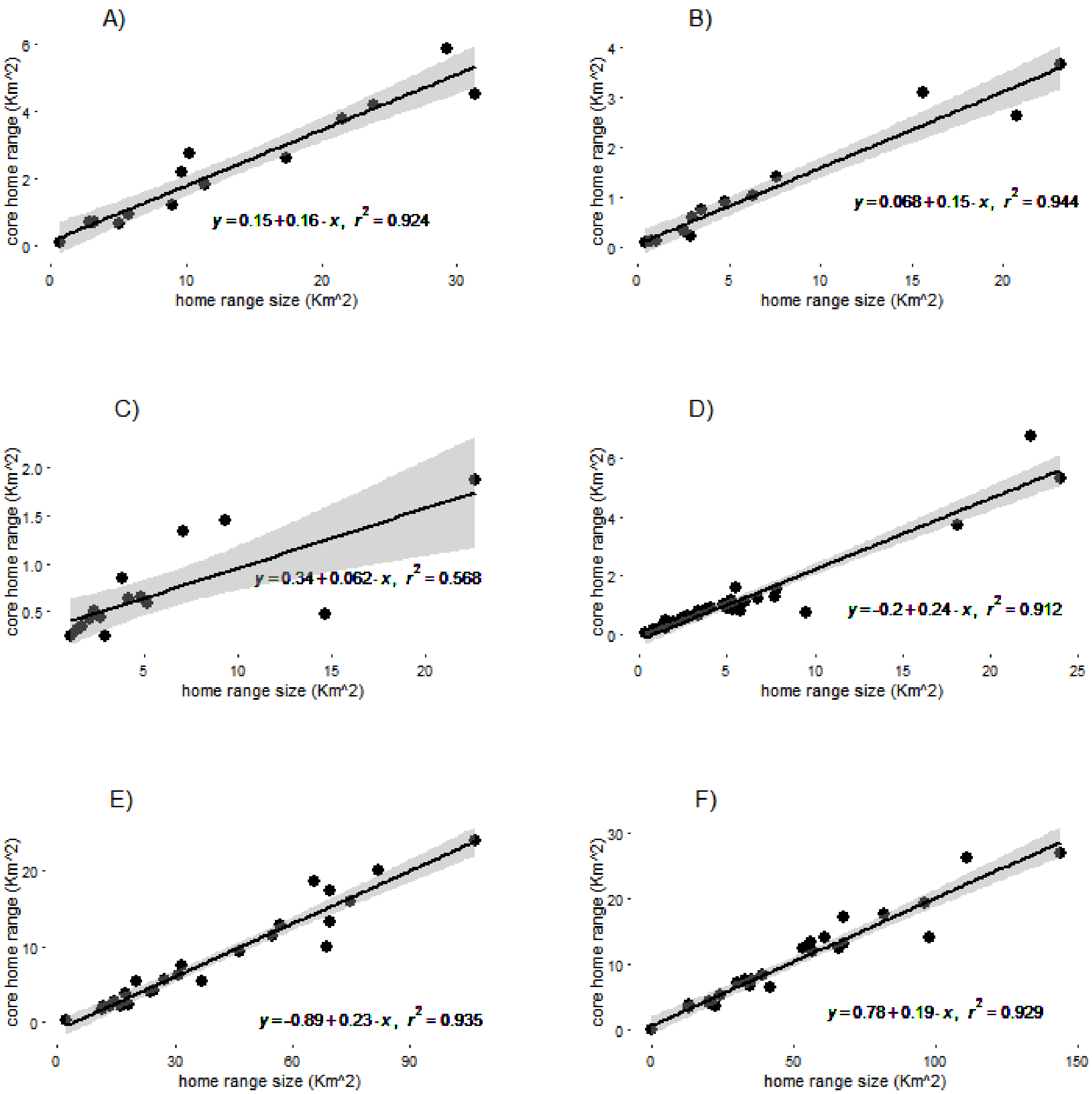

Figure 3-3: Individual core home ranges (50% KDE) and total home ranges (95% KDE) of three ungulate populations. MB deer in A) summer (N=14) and B) winter (N=13), AB deer in C) summer (N=15) and D) winter (N=33), and AB moose in E) summer (N=25) and F) winter (N=25). Regression line is depicted in black while the grey shaded area represents the 95% confidence interval.

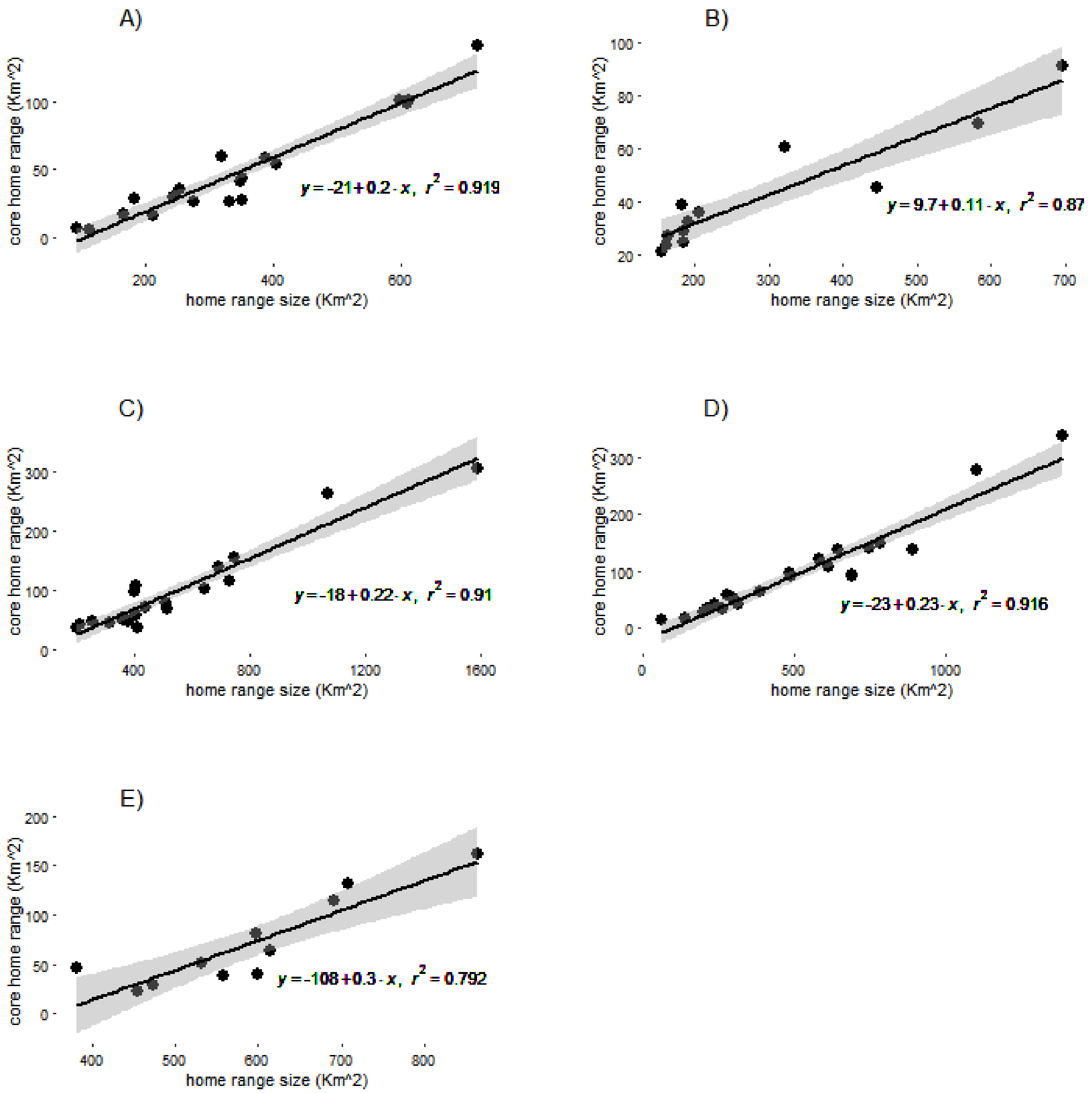

Figure 3-4: Individual core home ranges (50% KDE) and total home range sizes (95% KDE) of three wolf populations. . AB wolves (1) in A) summer (N=19) and B) winter (N=12), AB wolves (2) in C) summer (N=20) and D) winter (N=22), and BC wolves in E) summer (N=11).Regression line is depicted in black while the grey shaded area represents the 95% confidence interval.

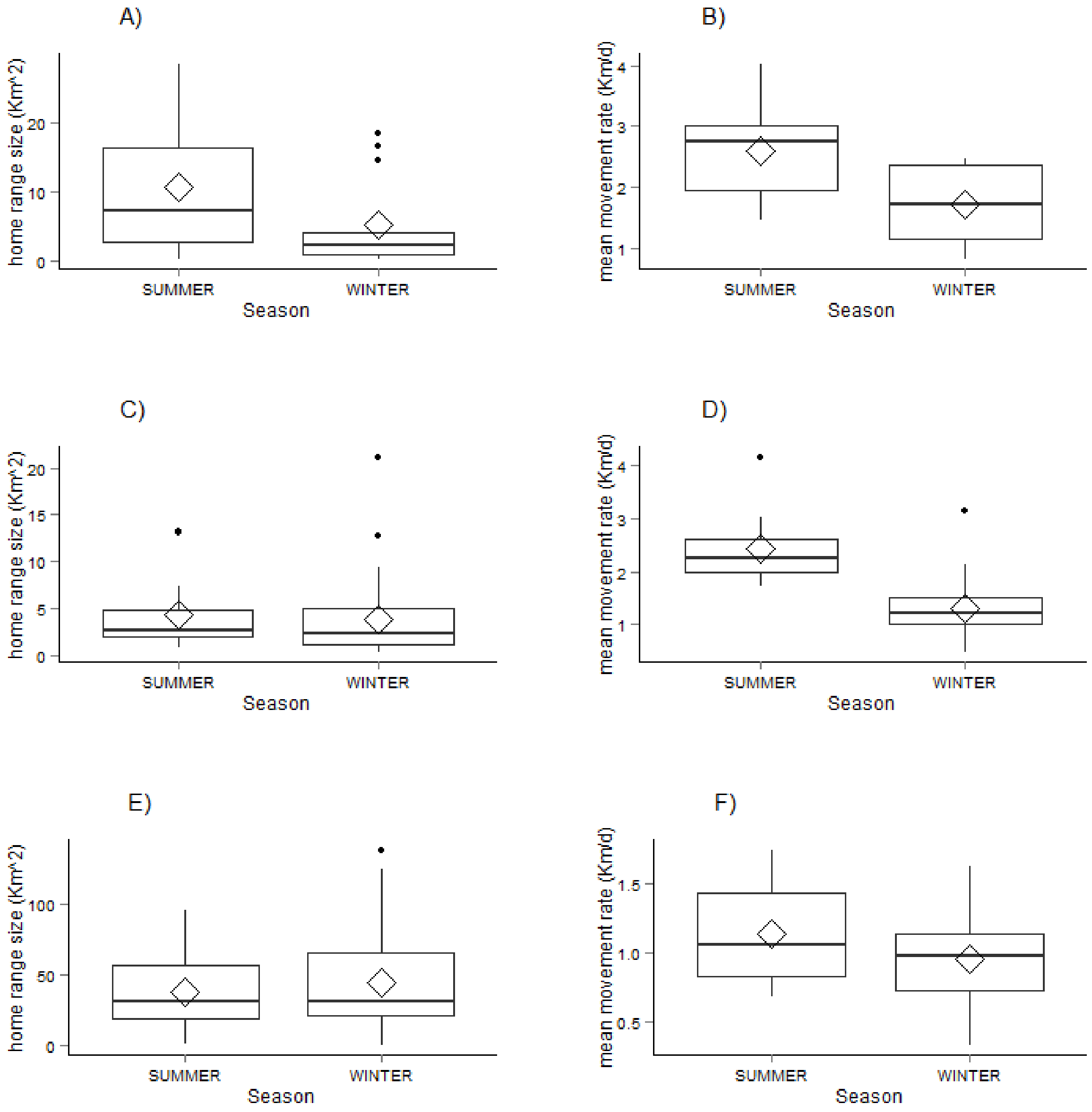

Figure 3-5: Seasonal comparisons of mean movement rates and home range sizes in three ungulate populations. MB deer home range sizes (A) and movement rates (B) across seasons, AB deer home range sizes (C) and movement rates (D) across seasons, and AB moose home range sizes (E) and movement rates (F) across seasons. Box plots depict mean (open diamond), median (horizontal line), 25th and 75th percentiles (boundary of box), 1.5 times interquartile range (vertical bars), and outliers (solid points).

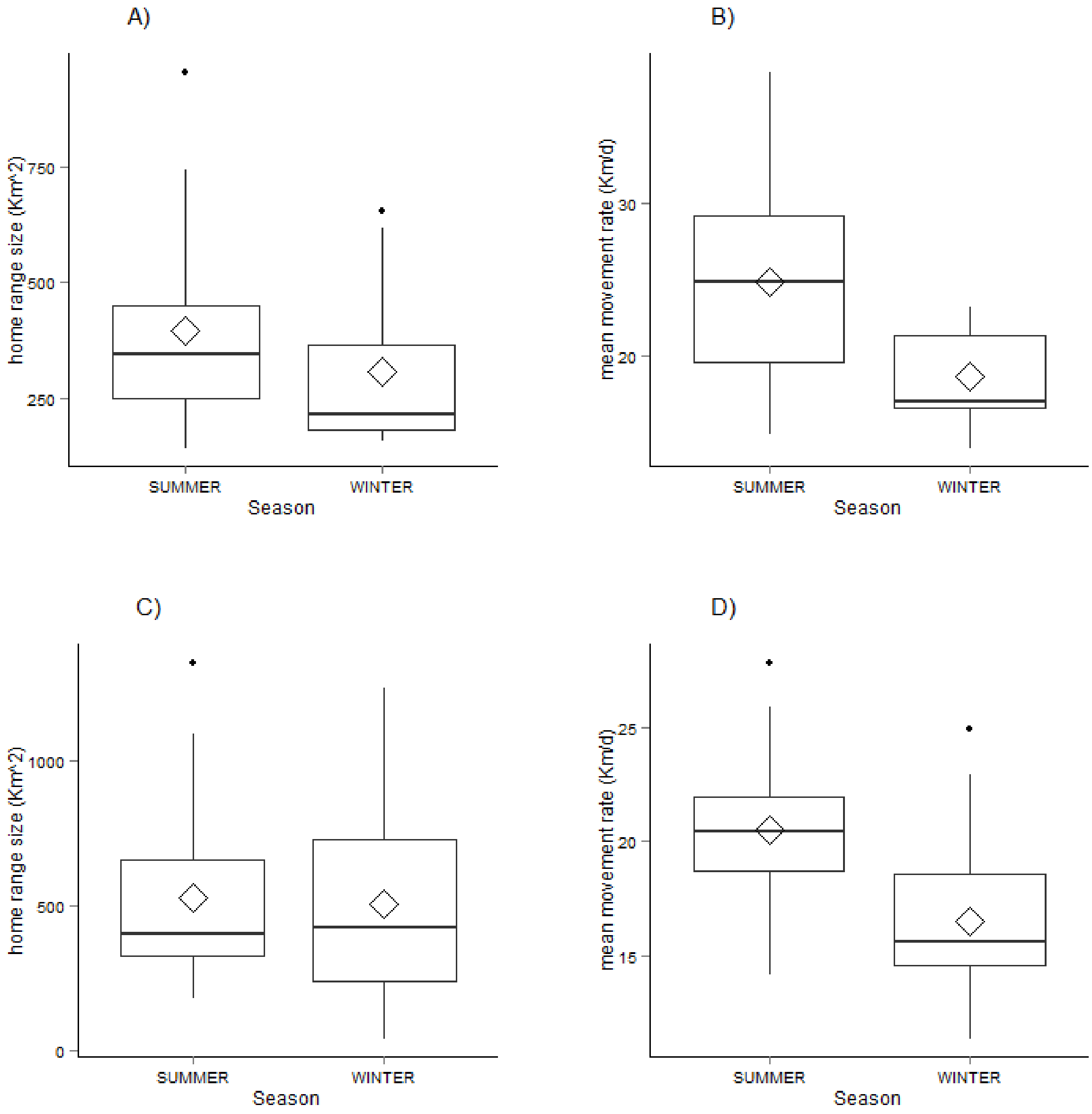

Figure 3-6: Seasonal comparisons of mean movement rates and home range sizes in two wolf populations. AB wolves (1) home range sizes (A) and movement rates (B) across seasons, and AB wolves (2) home range sizes (C) and movement rates (D) across seasons. Box plots depict mean (open diamond), median (horizontal line), 25th and 75th percentiles (boundary of box), 1.5 times interquartile range (vertical bars), and outliers (solid points).

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CHAPTER IV: General Conclusions

This thesis has investigated patterns of space use at multiple levels. I found that movement rate and home range size both exhibit a significant negative correlation with density. These relationships are common across a broad range of mammalian taxa. Through simulated data, I determined that density-dependent changes in space use can obscure trends in relative abundance and will tend to underestimate the magnitude of abundance changes. In particular, changes in space use can greatly affect the precision of such relative abundance estimates. Given this, practitioners should be cautious when using detection rate indices to monitor wildlife populations. These indices are best reserved for indicating directional changes in populations, rather than seen as a reliable way to track the actual magnitude of changes in relative abundance.

Practitioners could consider using more sophisticated analytical techniques, however these are not without their own challenges. I found that movement rate and home range size vary widely amongst individuals. While the same overall relationship between movement rate and home range size exists when comparing individuals as when comparing populations (i.e. movement rate and home range size are significantly positively correlated), the degree of heterogeneity around this trend is considerable. Individual variation was found to be an order of magnitude greater than variation between the studied populations. Variability in movement rate and home range size within a population makes choosing an appropriate study design difficult. Cameras spaced according to average home range sizes reported in the literature can easily be spaced such that some individuals are able to visit more than one camera (a violation of occupancy and N-mixture model assumptions), while others can only reach a single camera site at most (violating assumptions of SECR and spatially explicit density models for unmarked species). Considering that individual variation can be an order of magnitude greater than variation between populations, practitioners must be very conservative with their camera spacing if they are to ensure assumptions are not violated. This should especially be of concern when monitoring carnivores, which exhibit much greater individual variation than herbivores.

The specific ways in which space use affects camera detections is an ongoing subject of investigation. Next steps for research in this area include conducting more complex movement simulations – for example modeling the effects of environmental heterogeneity, territoriality, individual variation, etc. Emerging analytical techniques for camera trap data must continue to be tested against violated assumptions, ideally with increasingly realistic movement simulations. While this thesis has described individual variability within populations, more investigation is needed to reveal which mechanisms are the primary drivers behind individual heterogeneity in space use. Finally, researchers should continue to develop new techniques for analyzing camera data that are less sensitive to the target animal's space use.

In conclusion, while camera traps are an exciting tool for wildlife monitoring, they are not a silver bullet. Practitioners must carefully consider the objectives of their monitoring programme and whether the potential for confounded estimates illustrated here presents too great of a risk. Consideration for the target species' space use should be given due credit when designing the camera trapping protocol, and practitioners can safely assume that some portion of the population is likely violating one or more of their model assumptions. I hope that this thesis serves to encourage a more cautious and critical analysis of camera trap data in the future.

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APPENDIX A

Table A1: Shortlisted literature from systematic review

author names	year	order/superorder	common name	species name	density/abundance estimation method	tracking method	home range estimation method	movement fix rate
Le Mar and McArthur	2005	australidelphian	brushtail possum	*Trichosurus vulpecula fuliginosus*	secondary	N/A	secondary	N/A
Ashenafi et al.	2005	carnivore	Ethiopian wolf	*Canis simensis*	line transect, secondary	VHF	MCP	N/A
Di Bitetti et al.	2006	carnivore	ocelot	*Leopardus pardalis*	mark-recapture	N/A	secondary	N/A
Stoen et al.	2006	carnivore	brown bear	*Ursus arctos*	survey	VHF	MCP	N/A
St-Pierre et al.	2006	carnivore	ermine	*Mustela erminea*	N/A	VHF	MCP	12h-24h
St-Pierre et al.	2006	carnivore	long-tailed weasel	*Mustela frenata*	N/A	VHF	MCP	12h-24h
Astete et al.	2008	carnivore	jaguar	*Panthera onca*	secondary	N/A	secondary	N/A
Jones et al.	2008	carnivore	Western spotted skunk	*Spilogale gracilis amphiala*	MNA	VHF	KDE	N/A
Schmidt	2008	carnivore	Eurasian lynx	*Lynx lynx*	N/A	VHF	MCP	24h
Wilson and Shivik	2011	carnivore	coyote	*Canis latrans*	secondary	GPS	LoCoH	15min

Elizalde-Arellano et al.	2012	carnivore	bobcat	*Lynx rufus*	N/A	GPS	MCP, secondary	1h, secondary
Pereira et al.	2012	carnivore	Geoffroy's cat	*Leopardus geoffroyi*	N/A	VHF	MCP	30min
Leuchtenberger et al.	2013	carnivore	giant otter	*Pteronura brasiliensis*	secondary	VHF	MCP, KDE, LoCoH	30min
Allen et al.	2014	carnivore	grey wolf (dingo)	*Canis lupus dingo*	qualitative	GPS	MCP	30min - 2h
Devillard et al.	2008	lagomorph	European rabbit	*Oryctolagus cuniculus*	unknown	VHF	MCP	N/A
Ganas and Robbins	2005	primate	eastern gorilla	*Gorilla beringei beringei*	N/A	follow	MCP, quadrat	continuous
Merker et al.	2005	primate	Dian's tarsier	*Tarsius dianae*	survey	VHF	MCP	15min
Stevenson	2006	primate	woolly monkey	*Lagothrix lagothricha*	secondary	follow	MCP	30min
Cristobal-Azkarate and Arroyo-Rodriguez	2007	primate	mantled howler monkey	*alouatta palliata*	secondary	N/A	secondary	N/A
Irwin	2008	primate	diademed sifaka	*Propithecus diadema*	N/A	follow	MCP, KDE	unknown
Mekonnen et al.	2010	primate	bale monkey	*Chlorocebus djamdjamensis*	N/A	follow	MCP	15min
Amaral Nascimento et al.	2011	primate	golden lion tamarin	*Leontopithecus rosalia*	secondary	N/A	secondary	secondary
Amaral Nascimento et al.	2011	primate	black-faced lion tamarin	*Leontopithecus caissara*	secondary	follow	MCP, KDE, DMP	20min

Amaral Nascimento et al.	2011	primate	golden-headed lion tamarin	*Leontopithecus chrysomelas*	secondary	N/A	secondary	secondary
Cristina Palma et al.	2011	primate	red howler monkey	*Alouatta seniculus*	secondary	follow	quadrants, secondary	15min, secondary
Kim et al.	2011	primate	Javan gibbon	*Hylobates moloch*	N/A	follow	MCP	30min
Gabriel	2013	primate	ring-tailed lemur	*Lemur catta*	secondary	follow	KDE	continuous
Zhou et al.	2014	primate	Assamese macaque	*Macaca assamensis*	N/A	follow	quadrat	30min
Schradin and Pillay	2005	rodent	striped mouse	*Rhabdomys pumilio*	mark-recapture	VHF	MCP	N/A
Hoffmann et al.	2006	rodent	African grass rat	*Arvicanthis niloticus*	unknown	VHF	MCP	N/A
Jurczyszyn	2006	rodent	edible dormouse	*Glis glis*	N/A	VHF	MCP	1h
Arjo et al.	2007	rodent	mountain beaver	*Aplodontia rufa*	MNA	VHF	KDE	N/A
Jurczyszyn and Zgrabczynska	2007	rodent	edible dormouse	*Glis glis*	index	VHF	MCP	1h
Turrini et al.	2008	rodent	European ground squirrel	*Spermophilus citellus*	MNA	VHF	MCP	N/A
Stradiotto et al.	2009	rodent	yellow-necked mouse	*Apodemus flavicollis*	mark-recapture	VHF	KDE	>=50min
Quirici et al.	2010	rodent	degu	*Octodon degus*	mark-recapture	VHF	MCP, KDE	N/A
Sommaro et al.	2010	rodent	corn mouse	*Calomys*	known	trapping	MCP	N/A

				musculinus				
Lee et al.	2012	rodent	Korean field mouse	*Apodemus peninsulae*	N/A	VHF	MCP	4.25h
King and Gurnell	2005	ungulate	takhi	*Equus ferus przewalskii*	known	follow	KDE	N/A
McCoy et al.	2005	ungulate	white-tailed deer	*Odocoileus virginianus*	secondary	VHF	KDE	N/A
Brambilla et al.	2006	ungulate	chamois	*Rupicapra rupicapra*	unknown	VHF	MCP	N/A
Webb et al.	2007	ungulate	white-tailed deer	*Odocoileus virginianus*	secondary	VHF	MCP, KDE	N/A
Coulombe et al.	2008	ungulate	white-tailed deer	*Odocoileus virginianus*	known	VHF	N/A	>3h
Neumann et al.	2009	ungulate	moose	*Alces alces*	unknown	GPS	N/A	30min-1h
Panzacchi et al.	2009	ungulate	roe deer	*Capreolus capreolus*	secondary	VHF	MCP	24h

APPENDIX B

Shortlisted Literature for Meta-analysis:

Allen, B.L. & Leung, L.K.-P. (2014) The (Non)Effects of Lethal Population Control on the Diet of Australian Dingoes. *Plos One*, **9**, e108251–e108251.

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APPENDIX C

Table B1: Models chosen for best fit using AICc. Evidence ratios indicate support for either a model using untransformed home ranges to describe movement rate, or log transformed home ranges.

dataset	season	log/linear model	evidence ratio	R^2	p
AB wolves (1)	summer	log	3.02	0.2575	0.02657
AB wolves (1)	winter	log	3.18	0.6392	0.001803
AB wolves (2)	summer	log	2.3	0.2283	0.03311
AB wolves (2)	winter	log	2.47	0.1417	0.08422
BC wolves	summer	log	8.56	0.6721	0.002005
MB deer	summer	lm	1.31	0.0968	0.2789
MB deer	winter	log	5.02	0.6351	0.001108
AB deer	summer	log	1.07	0.5284	0.00214
AB deer	winter	lm	1.07	0.0080	0.6218
AB moose	summer	log	3.89	0.5342	3.33E-05
AB moose	winter	log	5.77	0.5026	7.29E-05

APPENDIX D

The following are more detailed statistical summaries of the telemetry datasets.

Movement Rate vs Home Range

MB deer
During summer, there was no significant relationship between movement rate and home range size (Fig. 3-1A, $\mathrm{r}^2 = 0.10, \mathrm{p} = 0.279$). In winter, however, there was a significant positive relationship (Fig. 3-1B, $\mathrm{r}^2 = 0.64, \mathrm{p} = 0.001$).

AB deer
There was a significant positive relationship between movement rate and home range size in summer (Fig. 3-1C, $\mathrm{r}^2 = 0.53, \mathrm{p} = 0.002$), but no relationship in winter (Fig. 3-1D, $\mathrm{r}^2 = 0.01, \mathrm{p} = 0.622$).

AB Moose
There was a significant positive relationship between movement rate and home range size both in summer (Fig. 3-1E, $\mathrm{r}^2 = 0.53, \mathrm{p} < 0.0001$) and in winter (Fig. 3-1F, $\mathrm{r}^2 = 0.50, \mathrm{p} < 0.0001$)

AB wolves (1)
There was a significant positive relationship between movement rate and home range size in summer (Fig. 3-2A, $\mathrm{r}^2 = 0.26, \mathrm{p} = 0.027$) as well as in winter (Fig. 3-2B, $\mathrm{r}^2 = 0.64, \mathrm{p} = 0.002$)

AB wolves (2)
There was a significant positive relationship between movement rate and home range size in summer (Fig. 3-2C, $\mathrm{r}^2 = 0.23, \mathrm{p} = 0.033$) but not in winter (Fig. 3-2D, $\mathrm{r}^2 = 0.14, \mathrm{p} = 0.084$).

BC wolves
In summer, there was a significant negative relationship between movement rate and home range size (Fig. 3-2E, $\mathrm{r}^2 = 0.67, \mathrm{p} = 0.002$)

Core vs Total Home Range

Ungulate core ranges exhibited a significant positive relationship with total home range in summer (MB deer: Fig. 3-3A, $\beta = 0.16, \mathrm{r}^2 = 0.924, \mathrm{p} < 0.0001$; AB deer: Fig. 3-3C, $\beta = 0.062, \mathrm{r}^2 = 0.568, \mathrm{p} = 0.001172$; AB moose: Fig. 3-3E, $\beta = 0.23, \mathrm{r}^2 = 0.936, \mathrm{p} < 0.0001$) and in winter (MB deer: Fig. 3-3B, $\beta = 0.15, \mathrm{r}^2 = 0.944, \mathrm{p} < 0.0001$; AB deer: Fig. 3-3D, $\beta = 0.24, \mathrm{r}^2 = 0.912, \mathrm{p} < 0.0001$; AB moose: Fig. 3-3F, $\beta = 0.19, \mathrm{r}^2 = 0.929, \mathrm{p} < 0.0001$), but the slopes of the relationships were weak.

Wolves showed a similar pattern also in summer (AB wolves (1): Fig. 3-4A, $\beta = 0.2, \mathrm{r}^2 = 0.919, \mathrm{p} < 0.0001$; AB wolves (2): Fig. 3-4C, $\beta = 0.22, \mathrm{r}^2 = 0.910, \mathrm{p} < 0.0001$, BC wolves:

Fig. 3-4E, $\beta = 0.3, r^2 = 0.792, p < 0.001$) and in winter (AB wolves (1): Fig. 3-4A, $\beta = 0.11, r^2 = 0.876, p < 0.0001$; AB wolves (2): Fig. 3-4C, $\beta = 0.23, r^2 = 0.916, p < 0.0001$).

Seasonal Differences

In the ungulates, there was no significant difference in home range size between summer and winter (MB deer: Fig. 3-5A, $t_{23.79} = 1.77$, $p = 0.087$; AB deer: Fig. 3-5C, $t_{28.38} = 0.47$, $p = 0.642$; AB moose: Fig. 3-5E, $t_{42.78} = -0.75$, $p = 0.458$), but movement rates were always slower in winter (MB deer: Fig. 3-5B, $\text{Mean}_a = 2.6 \pm 0.7\text{km}^2$, $\text{Mean}_b = 1.7 \pm 0.6\text{km}^2$, $t_{24.59} = 3.44$, $p < 0.001$; AB deer: Fig. 3-5D, $\text{Mean}_a = 2.4 \pm 0.6\text{Kkm}^2$, $\text{Mean}_b = 1.3 \pm 0.5\text{km}^2$, $t_{22.59} = 6.12$, $p < 0.0001$; AB moose: Fig. 3-5F, $\text{Mean}_a = 1.1 \pm 0.3\text{km}^2$, $\text{Mean}_b = 1.0 \pm 0.3\text{km}^2$, $t_{47.80} = 2.06$, $p = 0.045$)

The same trend was seen in wolves, where home range sizes did not differ significantly between summer and winter (AB wolves (1): Fig. 3-6A, $t_{25.74} = 1.22$, $p = 0.233$; AB wolves (2): Fig. 3-6C, $t_{39.83} = 0.24$, $p = 0.815$), but movement rates were significantly slower in winter (AB wolves (1): Fig. 3-6B, $\text{Mean}_a = 24.8 \pm 6.2\text{km}^2$, $\text{Mean}_b = 18.7 \pm 3.1\text{km}^2$, $t_{27.81} = 3.68$, $p < 0.001$; AB wolves (2): Fig. 3-6D, $\text{Mean}_a = 20.5 \pm 3.4\text{km}^2$, $\text{Mean}_b = 16.5 \pm 3.6\text{km}^2$, $t_{39.95} = 3.78$, $p < 0.001$)