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Comparing Conventional and Noninvasive Monitoring Techniques for Assessing Cougar Population Size in the Southern Greater Yellowstone Ecosystem

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COMPARING CONVENTIONAL AND NONINVASIVE MONITORING

TECHNIQUES FOR ASSESSING COUGAR POPULATION SIZE IN

THE SOUTHERN GREATER YELLOWSTONE ECOSYSTEM

by

Peter D. Alexander

A thesis submitted in partial fulfillment
of the requirements for the degree

of

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in

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ABSTRACT

Comparing Conventional and Noninvasive Monitoring Techniques for Assessing

Cougar Population Size in the Southern Greater Yellowstone Ecosystem

by

Peter D. Alexander, Master of Science

Utah State University, 2016

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Cougars (*Puma concolor*) are difficult to census due to their large home ranges, low densities, and cryptic nature. The conventional "gold-standard" method for estimating cougar abundance entails the capture and radio-tagging of individuals in a study area in an attempt to acquire a direct enumeration of animals in the population. While this method provides an accurate abundance estimate, it is logistically challenging and prohibitively expensive. Noninvasive survey techniques may offer the ability to both accurately and inexpensively monitor cougar populations. While noninvasive techniques have been used on cougar populations, there remain questions on their accuracy and comparative efficacy. We estimated the density of a cougar population in Northwest Wyoming using direct enumeration, and used this estimate as a reference with which to evaluate the accuracy and cost-effectiveness of three types of noninvasive surveys performed between 2010 and 2014. The noninvasive methods included two annual mark-

recapture sessions of: 1) remote camera trapping, 2) winter hair-collection transects, and 3) scat detection dog surveys.

We GPS tracked 13 adult cougars (males = 5, females = 8) over 3 annual periods (Sep 2010 – Sep 2013). We used proportional home range overlap to determine density in a 1,570 km^2 area. The average density was 0.82 cougars/100 km^2 ($\pm$ 0.10 SD; n = 3 years). The remote camera surveys produced a mean density of 0.60 cougars/100 km^2 (n = 2 years; relative SD = 56.5%). The scat detection dog surveys produced an average density of 2.41 cougars/100 km^2 (n = 2 years; relative SD = 12.6%). The winter transects failed to produce a sample size large enough for an abundance estimate. Due to the inclusion of non-adults in the scat sampling, and the fact that the reference estimate was essentially a minimum count of adults, we believe that the scat-based estimate was more accurate than the lower estimate produced by remote cameras. Additional analysis indicated that individual identification of cougars in photographs may not be reliable, challenging the validity of photo-based abundance estimates of cougars. On a cost-per-detection basis, scat detection dogs were the most cost effective method (scat detection dogs = $341; remote cameras = $3,241; winter transects = $7,627).

(160 pages)

PUBLIC ABSTRACT

Comparing Conventional and Noninvasive Monitoring Techniques for Assessing

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Determining the abundance or density of wildlife populations is needed for informed decision-making by wildlife biologists. Cougars (*Puma concolor*), however, are a highly secretive species occurring at very low densities across the landscape, and thus their populations are difficult for biologists to accurately assess. The conventional, and most trusted, method entails physically trapping and radio-collaring as many cougars as possible in a population, and then performing a simple count to determine a minimum population size. While accurate, this method is prohibitively expensive, logistically challenging, and behaviorally disruptive to the study animal. Many noninvasive surveying techniques, such as camera trapping, have been proposed as alternatives for cougar populations, with the goal of providing accurate estimates of population size at a lower cost and with less impact on the study animal. These methods use detections of individual cougars in a mark-recapture framework, as opposed to a simple count, and have the benefit of being true, statistically rigorous estimates with confidence intervals. However, little research has been done to empirically verify the accuracy of these methods, or to determine their comparative cost-effectiveness. We compared the accuracy and cost-effectiveness of three types of noninvasive surveys applied on a

population of cougars in Northwest Wyoming. Between 2011 and 2014, we applied two surveys each of remote camera trapping, winter snow tracking, and scat detection dogs. To evaluate these methods, we estimated the density of the same cougar population using the conventional "capture-collar-count" method, and then used that estimate as a reference. Our research indicated that: 1) on a cost-per-detection basis, scat detection dog surveys were almost an order of magnitude less expensive the other methods; and 2) remote camera trapping may not be applicable to cougars due to the difficulty of distinguishing individual cougars in photographs. Our research should be valuable to research biologists, wildlife managers, or conservation entities responsible for monitoring cougar populations.

ACKNOWLEDGMENTS

CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

Several carnivore species have undergone dramatic contractions in their historic ranges due to habitat loss or habitat fragmentation (Laliberte and Ripple 2004), and there is a call for increased effort in carnivore conservation (Gittleman et al. 2001). Both the implementation and evaluation of any conservation efforts require accurate data on presence, abundance, and population trends. However, carnivores are generally wide-ranging and secretive, and their population statuses are often difficult to assess (MacKay et al. 2008). Cougars (*Puma concolor*) are no exception: large home ranges, low densities, and a highly cryptic nature make them an especially challenging species to monitor (Beier and Cunningham 1996, Logan and Sweanor 2001, Choate et al. 2006). Conventional methods for monitoring cougar populations involve capture, tagging, and radio-collaring, followed by radio-tracking. Location data can then be used in various approaches, ranging from simple enumeration (Cougar Management Guidelines Working Group 2005) to more complex home range analyses used to estimate density (McLellan 1989, Cooley et al. 2009). These capture-based estimates are considered the "gold standard" method for accurately determining cougar abundance or density (Cougar Management Guidelines Working Group 2005). However, they are time-consuming, prohibitively expensive, and logistically challenging. Furthermore, these methods require physical capture and handling (sometimes entailing an exhaustive pursuit with trailing hounds), which can be behaviorally disruptive and potentially hazardous to the study animal. Many state wildlife management agencies instead monitor cougar populations

with a low-cost framework that uses data from hunter harvests, known mortalities, and depredation events in conjunction with empirical knowledge specific to the area of interest. Although these harvest indices may provide valuable insight into general cougar population trends, they are affected by hunting effort and reporting rates, and do not provide a true population estimate (Beier and Cunningham 1996, Anderson and Lindzey 2005, Wolfe et al. 2015).

Noninvasive surveys may offer an accurate, low-cost alternative to the conventional methods outlined above. Data such as photographs from remote camera traps or DNA extracted from cougar scat may 1) be collected relatively cheaply and without directly interfering with the behavior of the study animal, and 2) provide the information needed for an accurate population estimate using a capture-mark-recapture (CMR) framework. Cougars, like many carnivores, may be ideal for noninvasive techniques due to traits such as territorial marking behaviors, inclination to respond to baited detectors due to curiosity, and unique track morphologies (Mackay et al. 2008). While noninvasive population monitoring techniques have been applied to cougar populations, there have not been any comprehensive studies in the past decade that have attempted to assess and compare the efficacy of several methods a single population. The goal of this project was to evaluate and compare the accuracy and financial feasibility of several noninvasive cougar population monitoring techniques. We evaluated the noninvasive methods using data from a long-term cougar ecology study conducted in the Southern Greater Yellowstone Ecosystem (the Teton Cougar Project); this study provided a radio-collared cougar population with a capture-based "gold standard" estimate of abundance. In the second chapter, we examine the "gold standard"

methodology. We review the literature, and identify the various sources of bias and ambiguity in this method. We pay special attention to issues that can be problematic when comparing capture-based cougar density estimates to noninvasively conducted estimates. We then develop a novel method for estimating density from capture data, and present density estimates for three years across two neighboring areas of differing cougar density. In the third chapter, we review the various noninvasive survey methods that have been applied to cougar populations, their potential benefits and shortcomings, and the available analysis methods used to determine population density. We apply three types of noninvasive surveys to the radio-collared population: scat detection dog surveys (Beckmann 1997, Long et al. 2008), winter track transects (Sawaya et al. 2011), and remote camera surveys (Kelly et al. 2008, Negrões et al. 2010). We use multiple analyses for each type of survey to estimate cougar density in the same two areas for which we calculated capture-based density. We then perform a cost-analysis of the three methods. In the fourth chapter, we summarize our research and draw conclusions, focusing on management implications.

LITERATURE CITED

Anderson, C. R., and F. G. Lindzey. 2005. Experimental evaluation of population trend and harvest composition in a Wyoming cougar population. Wildlife Society Bulletin 33:179–188.

Beckmann, J. P. 1997. Carnivore conservation and search dogs : the value of a novel , non-invasive technique in the greater yellowstone ecosystem. Pages 28–34 *in* A. Wondrak Biel, editor. Greater Yellowstone public lands: a century of discovery,

hard lessons, and bright prospects. Proceedings of the 8th Biennial Scientific Conference on the Greater Yellowstone Ecosystem. Yellowstone Center for Resources, Yellowstone National Park, Wyoming, USA.

Beier, P., and S. Cunningham. 1996. Power of track surveys to detect changes in cougar populations. Wildlife Society Bulletin 24:540–546.

Choate, D., M. Wolfe, and D. Stoner. 2006. Evaluation of cougar population estimators in Utah. Wildlife Society Bulletin 34:782–799.

Cooley, H. S., R. B. Wielgus, G. Koehler, and B. Maletzke. 2009. Source populations in carnivore management: cougar demography and emigration in a lightly hunted population. Animal Conservation 12:321–328.

Cougar Management Guidelines Working Group. 2005. Cougar Management Guidelines. T. Beck, J. Beecham, P. Beier, T. Hofstra, M. Hornocker, F. Lindzey, K. Logan, B. Pierce, H. Quigley, I. Ross, H. Shaw, R. Sparrowe, and S. Torres, editors. WildFutures, Bainbridge Island, Washington, USA.

Gittleman, J. L., D. W. MacDonald, R. K. Wayne, and M. Gosling. 2001. Why "carnivore conservation"? Pages 1–7 *in*. J. L. Gittleman, S. M. Funk, D. W. Macdonald, and R. K. Wayne, editors. Carnivore conservation. Cambridge University Press, London, United Kingdom.

Kelly, M. J., A. J. Noss, M. S. Di Bitetti, L. Maffei, R. L. Arispe, A. Paviolo, C. D. De Angelo, and Y. E. Di Blanco. 2008. Estimating puma densities from camera trapping across three study sites: Bolivia, Argentina, and Belize. Journal of Mammalogy 89:408–418.

Laliberte, A., and W. Ripple. 2004. Range contractions of North American carnivores and ungulates. BioScience 54:123–138.

Logan, K., and L. Sweanor. 2001. Desert puma: evolutionary ecology and conservation of an enduring carnivore. Island Press, Washington, D.C., USA.

Long, R. A., P. Mackay, W. J. Zielinski, and J. C. Ray. 2008. Noninvasive survey methods for carnivores. R. A. Long, P. Mackay, W. J. Zielinski, and J. C. Ray, editors. Island Press, Washington, D.C., USA.

Mackay, P., D. A. Smith, R. A. Long, and M. Parker. 2008. Scat detection dogs. Pages 183–222 *in* P. MacKay, W. J. Zielinski, R. A. Long, and J. Ray, editors. Noninvasive survey methods for carnivores. Island Press, Washington, D.C., USA.

MacKay, P., W. J. Zielinski, R. A. Long, and J. C. Ray. 2008. Noninvasive research and carnivore conservation. Pages 1–7 *in* R. A. Long, P. Mackay, W. J. Zielinski, and J. C. Ray, editors. Noninvasive survey methods for carnivores. Island Press, Washington, D.C., USA.

McLellan, B. 1989. Dynamics of a grizzly bear population during a period of industrial resource extraction. I. density and age-sex composition. Canadian Journal of Zoology 67:1856–1860.

Negrões, N., P. Sarmento, J. Cruz, C. Eira, E. Revilla, C. Fonseca, R. Sollmann, N. M. Tôrres, M. M. Furtado, A. T. A. Jácomo, and L. Silveira. 2010. Use of camera-trapping to estimate puma density and influencing factors in central Brazil. Journal of Wildlife Management 74:1195–1203.

Sawaya, M. A., T. K. Ruth, S. Creel, J. J. Rotella, J. B. Stetz, H. B. Quigley, and S. T. Kalinowski. 2011. Evaluation of noninvasive genetic sampling methods for cougars in Yellowstone National Park. Journal of Wildlife Management 75:612–622.

Wolfe, M. L., E. M. Gese, P. Terletzky, D. C. Stoner, and L. M. Aubry. 2015. Evaluation of harvest indices for monitoring cougar survival and abundance. Journal of Wildlife Management 80:27–36.

CHAPTER 2

AN ANALYSIS OF INVASIVE TECHNIQUES USED TO DETERMINE POPULATION DENSITY OF COUGARS

ABSTRACT

Determining population size and density of large carnivores is needed for informed decision-making by many conservation groups and wildlife management agencies. Many large carnivores, including cougars (*Puma concolor*), are cryptic, occur at low density, utilize large territories, and often occupy habitat characterized by dense cover and rugged terrain, making estimates of population size a logistical and economic challenge. Consequently, in most studies in North and South America, estimates of cougar population density often do not use conventional, statistically-based population estimation techniques, but instead employ direct census methods using physical capture, radio-tracking, and, essentially, enumeration of known individuals in a defined area. In this paper, we examined the sources of bias and uncertainty associated with various telemetry-derived techniques for enumerating the number of cougars in a defined area. Using various methods to address these issues, we estimated the density of a population of cougars in northwest Wyoming. Our methods included the incorporation of remote camera data, and a novel method for delineating the spatial denominator used in the density calculation. We GPS tracked 13 adult cougars (males = 5, females = 8) over 3 annual periods (Sep 2010 – Sep 2013). We delineated two effective trapping areas within the study area to use for the spatial component of the density calculations. We used proportional home range overlap to determine the abundance within the effective

trapping areas. The average cougar densities for the two areas, and the combined area, were 0.27, 1.07, 0.82 cougars/100 km^2, respectively. Of note, the remote cameras detected uncollared cougars that would have been otherwise unaccounted for. Inclusion of these detections reduced the accuracy of our density estimates by an average of 15.3%, and highlighted the potential shortcomings of purported "saturation" trapping. Our method for delineating the area of density was particularly applicable to a study area with spatially varying cougar density that included areas of relatively low density, underscoring the importance of thoughtful design when estimating animal population density. This is especially relevant to large carnivore management, given current issues of range contraction and expansion.

INTRODUCTION

Many carnivore species have undergone dramatic contractions in their historic ranges due to habitat loss or fragmentation, and direct human persecution (Laliberte and Ripple 2004), resulting in a greater need for expanded efforts in carnivore conservation (Gittleman et al. 2001). In recent decades, however, some carnivores have recovered at local range levels; examples of such recolonizations include some populations of grizzly bears *Ursus arctos* (Pyare et al. 2004) and cougars *Puma concolor* (Thompson and Jenks 2010). Reliable abundance estimates of large carnivores are necessary for identifying areas of extirpation or recolonization, and vital for the implementation and evaluation of conservation and management efforts. However, estimating abundance of carnivores is often hampered by issues that may be less common with other animal taxa (Boitani and Powell 2012). For example, cougars, as with many other large carnivores, are a cryptic,

sparsely occurring species utilizing large territories often characterized by dense cover and rugged terrain (Pierce and Bleich 2003), and thus do not lend themselves to conventional wildlife population estimation techniques such as point counts or aerial surveys. Classic capture-mark-recapture methods (CMR) or the Lincoln-Peterson Method (Seber 1982), are not necessarily appropriate, since these models require several assumptions that are rarely met in a cougar population. For example, cougars exhibit year-round potential for breeding and dispersal, thus violating the assumption of population closure. Capture probability likely varies between individual cougars and between subsequent captures of the same cougar, violating the assumption of equal catchability (Logan and Sweanor 2001, Amstrup et al. 2005). More sophisticated CMR models relaxing assumptions for population closure (Jolly 1965, Seber 1965) may be inappropriate given the assumptions that are violated due to the extended time period required for trapping and tagging cougars. Although recent developments in CMR models and novel methods of detection (such as genetic sampling or camera trapping) may resolve these issues, the most widely accepted method for estimating cougar population size remains direct counts of known individuals (Cougar Management Guidelines Working Group 2005). Indeed, the accepted "gold standard" method for estimating cougar density is derived from long-term radio-telemetry studies that attempt to radio-collar all or most resident cougars, followed by monitoring of individuals (Cougar Management Guidelines Working Group 2005). These types of studies allow researchers to identify residents versus transients, monitor births, deaths, immigrations and emigrations, and produce an informed enumeration of known resident cougars in a given area (e.g., Seidensticker and Hornocker 1973, Ross and Jalkotzy 1992, Spreadbury

et al. 1996). Despite the straightforwardness of this method, there are issues related to capture effort, spatial scale and certain subjective assumptions that researchers must decide (e.g., assigning demographic class). In this paper, we outline the various telemetry-derived census methods used in the published literature, including techniques used to reduce bias and subjectivity. One important caveat is that almost all published density estimates for cougars were calculated for the purposes of multi-seasonal demographic analysis within a single study area, and, as most studies acknowledge, are not especially useful for direct comparisons with other studies' population estimates or other population estimation methods. After outlining the various advantages and disadvantages of the different methodologies, we present a method by which we seek to minimize the identified biases and uncertainties. Although our methodology would not necessarily aid in direct comparisons with other studies' density estimates, our goal was to allow for comparisons with results from statistically-based noninvasive population estimators surveying the same study area.

Calculating Density

Often cougar population estimates, especially from earlier cougar studies, are simple densities calculated by dividing the count of known marked resident cougars, N, by the study area size, A (e.g., Seidensticker and Hornocker 1973, Ross and Jalkotzy 1992, Spreadbury et al. 1996, Choate et al. 2006). While these measures of density appear to be inherently simple, the two variables in this ratio can nonetheless be difficult to precisely define and are susceptible to different biases related to capture effort, spatial extent, and natural spatial and temporal variation of cougar densities across a landscape. In the case of the numerator N, few cougar studies can confidently report to have

captured and counted all resident cougars in an area, and the raw count of marked

cougars is generally considered a minimum known estimate or an underestimate (e.g.,

Neal et al. 1987, Franklin et al. 1999, Logan and Sweanor 2001, Choate et al. 2006). The

denominator, *A*, can also be difficult to define objectively, and is prone to biases due to

spatial inconsistencies and extrapolation issues (Smallwood 1997, Rinehart et al. 2014).

Hereafter we refer to the spatial area used in calculating density as the "area divisor", so

as to avoid confusion in cases when it is not identical to the size of the study area.

Demographic Class

Depending on study scope, independent subadult cougars or dependent juveniles

(i.e., kittens) may or may not be included in population estimates. Choate et al. (2006)

included subadults in their estimate, under the assumption these individuals were

potentially available for hunter harvest. This is empirically true in some areas; in

Wyoming, for example, 49% of cougar harvest across the state (2010-2012) was

classified as subadult (Thompson 2013). Furthermore, subadults play an ecological role

equal or similar to resident adults (Knopff et al. 2010), and inclusion of subadults in

population estimates may be incorporated into management objectives. However,

uncertainty of residency status, such as in instances when individuals are detected but not

captured (and subsequently marked and tracked) may introduce problems (see below).

Studies may not have the capacity for, or interest in, marking and monitoring cougar

kittens. Maternal status of individual females in a population has important ecological

implications by influencing kill rate (Knopff et al. 2010) and population growth.

However, kitten survival rates are often low (Quigley and Hornocker 2010), and unless

kittens are rigorously monitored until they reach subadult or adult status, kitten counts

may not necessarily contribute to a useful population estimate.

Unmonitored Individuals

Even rigorous detection and capture efforts are unlikely to radio-collar all cougars

within a study area. Often, but not necessarily, this shortcoming is confirmed by

detecting, but failing to capture, unmarked cougars within the study area. These

unmonitored individuals could either be residents that were missed in capture efforts, or

transients moving through a study area. The difficulty thus arises on whether to

incorporate these detections into a population estimate despite the potential for

misattributing residency status or misidentifying an individual, thus resulting in double-

counting single individuals or under-counting multiple individuals. Hereafter,

"unmonitored residents" will refer to these detected, but uncollared and untracked,

cougars.

Detections of unmonitored residents can be collected from multiple sources, such

as mortalities from vehicle collisions or hunter harvest, track/spoor data, remote cameras,

or other noninvasively collected data (e.g. Choate et al. 2006, Kelly et al. 2008, Sawaya

et al. 2011). At a minimum, collecting these various types of detections is useful for

researchers' assessment of occupancy, movement patterns, and general insights into the

population. However, the inability to reconcile different detection types (e.g., comparing

a genetic sample and a camera-trap photograph) may result in a dataset that is less than

the sum of its parts, and researchers may be limited in their use of these data.

Reported mortalities are useful as there is no risk of double counting a single

individual, although transient status cannot necessarily be verified. In order to prevent

double counting, some studies (e.g., Robinson et al. 2008; Cooley et al. 2009*a*, *b*) limited inclusion of unmonitored residents strictly to reported mortalities. Other studies have accepted more ambiguous detections such as snow track detections: Choate et al. (2006), for example, assumed that same-sexed tracks repeatedly encountered in a watershed were from a single resident individual. While accurately attributing tracks to individuals is possible with rigorous field techniques and discriminant analysis (Lewison et al. 2001), we found no studies that used these methods and the accuracy of such data remains uncertain. This issue may be exacerbated in certain study areas where relatively localized "hot spots" of cougar presence occur, and detections of multiple individuals of the same sex or age is highly probable.

Finally, unmonitored residents (as well as completely undetected resident cougars) that are missed by initial capture efforts are sometimes "backlogged" if captured in subsequent seasons. Once a cougar was captured and the sex and age was determined, the previous enumerations would be adjusted under the assumption that a male likely immigrated at a certain age (usually 21 months) and a female cougar was likely a native to the area (Neal et al. 1987, Logan and Sweanor 2001, Choate et al. 2006, Cooley et al. 2009*a*).

Inclusion of unmonitored individuals in a census creates potential for errors and the possibility of generating a minimum density estimate that is greater than the true density. Despite being prone to error, inclusion of these data sources may nonetheless be preferable to the alternative of simply ignoring these individuals, as long as the issues outlined above are carefully considered.

Proportional Residency

One technique used for animals with large home ranges is to calculate the proportional residency within the boundary of a defined area (i.e., the area divisor), with the intent of reducing biases associated with large, unevenly monitored populations and increase the precision of the population estimate. This has been done with other large carnivores such as grizzly bears (e.g. McLellan 1989) and leopards (*Panthera pardus*) (e.g. Balme et al. 2009), as well as cougars (e.g. Neal et al. 1987; Hopkins and Barrett 1991; Cooley et al. 2009*a*, *b*; Elbroch and Wittmer 2012; Allen 2014). Under this method, radio-collared animals contribute the proportion of their home range falling within the area divisor to the total count. For example, an animal with 45% of its home range overlapping the area divisor would contribute 0.45 individuals to the total count, and only animals with their entire home range contained within the area would count as a "whole" animal (Fig. 2.1). One benefit of this method is that it allows for the inclusion of individuals with home ranges extending beyond the study area or into areas with less frequent monitoring, without making any assumptions about the population density in those distal areas. Generally, this method assumes that all individuals occurring within the area divisor are captured. If unmonitored cougars in the area divisor are detected and assumed to be resident, researchers must either ignore this information or assign an unmeasured proportional residency. Cooley et al. (2009*b*) assigned the mean proportional residency of all radio-collared cougars to these unmonitored individuals.

In recent decades, home range analysis has improved markedly in precision and sophistication (Cagnacci et al. 2010, Kie et al. 2010). With modern GPS collars, the underlying location data for home range delineation has increased in accuracy and

collection rate. Besides allowing for a greater number of more accurate relocations, GPS collars can reduce bias in home range estimates for wide-ranging animals such as cougars (Kie et al. 2010). For example, older studies that triangulated VHF locations from the ground may have overestimated home range sizes for animals distal from human access points due to telemetry error (Withey et al. 2001). This bias in home range shape would potentially translate to a biased measure of proportional residency, depending on the location of VHF triangulation points in relation to the area divisor. Improved location data have in turn improved the precision of home range delineation with more sophisticated home range estimators such as kernel density estimation (KDE; Worton 1989) or Brownian Bridge movement models (BBMM; Bullard 1991). Ostensibly, measures of proportional residency would not be greatly affected by the precision of a home range estimator, since the proportionality of spatial overlap on the area divisor should remain constant between different home range estimators (provided that relocation data are spatially unbiased). However, the modern estimators listed above are likely more appropriate than traditional minimum convex polygons, since they tend to better exclude space unused by animals and reduce the potential for mis-delineating a home range inside or outside the area divisor (Walter et al. 2009). See Figure 2.2 for a comparison of various home range delineations and corresponding proportional overlap values for a hypothetical area divisor.

Delineating the Area Divisor

Objectively delineating the spatial area over which animal density is calculated can be complicated by several factors. The predefined study area can be used to determine the area divisor, but a study area is often defined wholly or partially by

political boundaries or other subjectively defined boundaries, and may not be biologically appropriate to the study animal or well-suited to animal detection and capture efforts. Except in rare cases such as "island" populations of cougars (e.g., Logan and Sweanor 2001, Bacon 2010), most cougar study areas only encompass a fragment of the spatial extent of the population being studied. Calculating the proportional residency may help reduce bias related to uneven monitoring across expansive home ranges, but may not address issues related to extrapolating density estimates across the greater landscape. For example, researchers may "go for the low hanging fruit" by focusing detection and capture efforts in areas with high quality cougar habitat relative to the surrounding landscape. Consequently, in extrapolating the estimated density to the larger landscape, there is a potential for overestimating density (i.e., sampling frame error; Smallwood and Schonewald 1996, Rinehart et al. 2014). Conversely, if areas with low detection effort are included in the area divisor, there is the potential to underestimate density due to the failure to detect resident cougars.

There are two techniques commonly cited by cougar studies for delineating the area divisor beyond simply using the predefined study area. One method reduces capture effort bias through the use of a "trapping area" (McLellan 1989). McLellan (1989) estimated grizzly bear density using proportional residency within an area defined by the trapping effort (i.e., where the majority of trapping sites were located), as opposed to the extent of the entire study area. A second technique attempts to reduce the subjectivity of delineating the area divisor by defining boundaries *a posteriori* around aggregate cougar locations. For example, Hopkins and Barrett (1991) proposed an area divisor based on an average of a weekly minimum convex polygon enclosing all radio-collared cougars'

locations. More recently, studies have used a composite of cougar home ranges (defined by KDEs) to delineate the area (e.g., Cooley et al. 2009*a*, *b*; Elbroch and Wittmer 2012). These latter methods could be described as "letting the study animal decide", which presumably reduces the bias from subjectively defining the area divisor boundaries. However, unless detection and trapping efforts are equivalent across the aggregate home ranges, there is the probability of telemetered cougar home ranges extending into areas that were not as thoroughly trapped, and where there is a greater chance of undetected cougars occurring (Fig. 2.3). Elbroch and Wittmer (2012) essentially combined the two techniques by first identifying an area where they believed they had captured all resident cougars (analogous to a trapping area), then aggregated the cougar KDE home ranges that fell completely within that area. While this method may reduce bias associated with uneven detection and capture effort, telemetered cougar home ranges, as a matter of course, would exclude areas where cougars were not detected despite equal effort (Fig. 2.3). Limiting the density estimate exclusively to areas occupied by the study animal may not generate a realistic pattern of abundance in the study area as a whole (Smallwood 1999). For example, certain parts of a study area may have lower cougar abundance despite apparent habitat quality. This could be due to factors such as differing hunting pressure, human disturbance, prey abundance, or interspecific competition with other large carnivores such as wolves (Kortello et al. 2007, Bartnick et al. 2013, Lendrum et al. 2014).

STUDY AREA

The greater study area encompassed 5,120 km^2, including much of the Jackson

Hole basin and adjacent lands in northwest Wyoming. The area was delineated by the

Teton Range in Grand Teton National Park (GTNP) on the west, the Gros Ventre Range

on the east, the Teton Wilderness Area on the north, and on the south by Wyoming state

highway 22 and the Cache Creek drainage. Most lands within the study area were

administered by the U.S. Forest Service (Bridger-Teton National Forest), the National

Park Service (Grand Teton National Park), and U. S. Fish and Wildlife Service (National

Elk Refuge). A small percentage (~ 5%) was comprised of privately owned ranches or

residential areas (Fig. 2.4). Elevations in the study area ranged from ~1,800 m in the

Jackson Hole basin to >3,600 m in the mountains. The area was characterized by short,

cool summers and long winters with frequent snowstorms. Average monthly temperature

minimums and maximums ranged from -17.3°C and -3.4°C in January, to 5.3°C and

26.9°C in July. Precipitation occurred mostly as snow, and mean maximum snow depths

ranged from 100 cm at lower elevations to >245 cm at intermediate elevations of 2,000 –

2,400 m (Grand Teton National Park 2015).

Plant communities included cottonwood (*Populus angustifolia*) riparian zones

interspersed by sagebrush (*Artemisia spp.)* uplands at lower elevations. At intermediate

elevations, aspen (*P. tremuloides*), Douglas-fir (*Pseudotsuga menziesii*), and lodgepole

pine (*Pinus contorta*) were the dominant species. Spruce (*Picea engelmannii*) and fir

(*Abies lasiocarpa*) were the primary tree species at the higher elevations (Marston and

Anderson 1991, Knight 1996).

Primary prey species available included mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), white-tailed deer (*O. virginianus*), moose (*Alces alces*), bighorn sheep (*Ovis canadensis*), and various small to medium sized mammal and avian species. The study area also included all historically occurring large carnivores: grizzly bears (*Ursus arctos*), black bears (*U. americanus*), and gray wolves (*Canis lupus*), as well as several mesocarnivores, including coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*), and possibly two other sympatric felids: bobcats (*Lynx rufus*) and lynx (*Lynx canadensis*).

METHODS

Cougar Capture and Radio-collaring

Cougar capture efforts were focused in two areas within the greater study area: the Gros Ventre River and Buffalo Valley drainages (Fig. 2.5); capture efforts in these areas were used to define the area divisors in order to improve the precision of our density estimates, as described above. We captured and radio-collared cougars primarily during winter months (November to April) when snow cover facilitated tracking and enabled researchers to identify cougar presence. Density estimates were derived from radio-collars deployed between 2010 and 2014, although some additional analysis utilized telemetry data from as early as 2004. After snowfall events, predetermined transects were surveyed on foot, truck or snowmobile to search for cougar tracks. Transects were selected based on topographic features characteristic of cougar habitat or travel routes, and ease of access for trackers. Once we located tracks and determined them to be from an unknown adult cougar without very young kittens (≤4 months old), we typically used trailing hounds to pursue the cougar into a tree or rocky outcrops where

we could safely approach and immobilize the cougar following procedures outlined by

Sikes and Gannon (2011), Quigley (2000), and the Jackson Institutional Animal Care and

Use Committee (Protocol 027-10EGDBS-060210). Occasionally circumstances allowed

for a walk-in type of cage trap to be used (Tru-Catch Traps, Belle Fourche, South Dakota,

USA), wherein bait such as road-killed deer was used to lure the cougar. We initially

administered ketamine at 4.0 mg/kg, followed by medetomidine at 0.07 mg/kg. In the

case of "treed" cougars, we initially administered the ketamine dose via a CO_2 powered

dart-gun (Dan Inject North America, Fort Collins, Colorado, USA). We then climbed the

tree and used rope to hobble and lower the semi-immobilized cougar to the ground,

where upon the medetomidine dose was hand-injected. Once fully immobilized, the

cougar's heart rate, temperature, and respiratory rate were monitored every 5 minutes.

We collected genetic samples (hair and tissue), body measurements, and estimated age

using tooth condition (Heffelfinger 2010) and a gum line recession metric (Laundre et al.

2000). We fitted cougars with GPS collars (Lotek, Newmarket, Ontario, Canada;

Northstar, King George, Virginia, USA; Televilt, Bandygatan, Sweden; Telonics, Mesa,

Arizona, USA; Vectronics, Berlin, Germany), programmed to collect locations between 4

and 10 times per day. After animal processing was completed, and sufficient time had

elapsed to allow for the metabolism of the ketamine (~60 minutes), we administered

Atipamezole at 0.375 mg/kg to reverse the effects of the medetomidine. We monitored

cougars during recovery until they were able to safely depart the area on their own,

typically 5 – 15 minutes after the reversal drug was administered.

Density Estimate

We used GPS collar data and proportional residency to estimate the minimum density of cougars in the area divisor as defined by trapping efforts (McLellan 1989), and amended that minimum density with other sources of cougar detections, including remote camera detections from a static camera trapping array and remote video detections from cameras placed at cougar prey-sites. Although data was available for dependent kittens, we limited our enumeration to independent, non-transient adults and subadults, as this was more comparable to other density estimates. We chose to use proportional residency in an area divisor defined by trapping effort in order to reduce bias created by uneven capture effort across the greater study area. We did not delineate sampling area with aggregate home ranges (Cooley et al. 2009*a*, *b*), as we believed the areas of trapping effort better represented the study area as a whole, including areas of apparently suitable cougar habitat that had low or zero cougar density, based on the very low detection rates of cougars during capture efforts, remote camera surveys, and scat detection dog surveys (Chapter 3).

We delineated the area divisor based on where the majority of detection and capture effort occurred, with the exception of replacing radio-collars or opportunistic captures that occasionally occurred outside of this area. We based this boundary around the winter transects used by capture teams, and which were rarely or never crossed by unknown cougars by the conclusion of a capture season. While McLellan (1989) used a minimum convex polygon around point locations of bear trapping stations, our "trapping stations" were defined by the 2-dimensional snow transects. To represent the effective trapping area of the transects, we buffered the transects by the average female home

range radius (analogous to the commonly used mean-maximum-distance-moved metric)

during winter trapping months, calculated from all GPS collar data spanning the history

of the study (Fig.2.2). Home ranges were defined by 95% KDE using the plug-in

bandwidth (see below). We defined the resulting polygon as a space in which any or

almost any resident cougar would be detected, captured, and radio-collared. This method

allowed for a more systematic area divisor than the composite home range method (e.g.,

Cooley et al. 2009*a*, *b*; Elbroch and Wittmer 2012; Allen et al. 2015), which gave a less

biased density estimate across the whole study area (including areas with very low

density); this method also allowed for the comparison of results from alternative density

estimators with spatially corresponding extents (i.e., noninvasive sampling and

population estimators; Chapter 3).

Cougar densities were calculated separately and together for the Buffalo Valley

and the Gros Ventre drainages, for the years 2011 through 2013 (years were defined as

September 1 to August 30th of the following year). All spatial analysis was done in R (R

Version 3.0, www.r-project.org, accessed 10 Oct 2013) and Geospatial Modeling

Environment (Geospatial Modeling Environment Version 0.7.2.0,

http://www.spatialecology.com/gme, accessed 31 Aug 2012), with visualization of

processes implemented in ArcMap 10.2 (Environmental Systems Resource Institute

2013). We delineated home ranges in R with 95% KDEs using the plug-in method for

bandwidth selection (Jones et al. 1996). This was performed using the adehabitat package

(Calenge 2011) and the ks package (Duong 2014), as outlined by Walter and Fischer

(2015). We also used the R packages maptools (Bivand and Lewin-Koh 2014), rgeos

(Bivand and Rundel 2011), and shapefiles (Stabler 2014) to build trapping buffers and

calculate proportional overlap of the resulting polygons. Densities were scaled to cougars/100 km^2.

 Appropriateness of trapping buffer.— One critical assumption behind our selection of the winter trapping buffer as the area divisor was that most or all cougars that used the space within the buffer could be detected and captured from the winter trapping transects. However, a hypothetical cougar home range could have potentially overlapped the trapping buffer, while failing to intersect the transect line (thus preventing the cougar from being detected and captured), resulting in an underestimation of cougar density. We tested our assumption that the winter trapping transects were adequate in transecting the home ranges of cougars that were resident in the area divisor with a resource selection function (RSF; Manly et al. 2002). We constructed the RSF under a use-availability framework using the R package ResourceSelection (Lele et al. 2013) to compare available locations to radio-collared cougar winter locations within the winter trapping buffer. We note that these models were not intended to test any underlying ecological process, but only to test if there was evidence of cougars avoiding the designated transects.

Unmonitored Individuals

 We followed protocols by Neal et al. (1987), Logan and Sweanor (2001), Choate et al. (2006), and Cooley et al. (2009*a*) to incorporate detections of unmonitored cougars into the yearly enumerations when ≥2 detections could be confidently attributed to a single non-transient individual. These protocols also allowed for "backlogging" the enumerations in cases when individuals were captured in subsequent years and, depending on age and sex, were likely present in previous years. Detections were

primarily collected from remote cameras placed within or adjacent to the trapping area.

Remote camera detections were collected from two sources: remote video cameras placed

at cougar prey-sites, and remote camera stations setup with scent-lure. The video data

was generated by a concurrent study within our study area examining cougar foraging

behavior using remote video cameras (Bushnell Trophy Cam HD Max, Bushnell Outdoor

Products, Overland Park, Kansas, USA) placed at cougar prey-sites identified by GPS

clusters (Anderson and Lindzey 2003). GPS collar data was transmitted via satellite 2 to

6 times per day, allowing researchers to identify and visit prey-sites to install cameras.

Generally this could be done within the first 48 hours after a kill, often before the cougar

had consumed or abandoned a kill. The video data indicated that prey-sites were

occasionally visited by cougars other than the individual from which the prey-site was

detected, including uncollared individuals. Uncollared cougars were also detected by

means of an array of 55 remote camera stations, split between the Gros Ventre and

Buffalo Valley drainages. Stations were operational from June to September of 2012 and

2013. The majority of camera stations (n = 43) used a non-reward scent lure comprised of

aged cattle blood; the additional sites (n = 12) used a cologne based "curiosity" lure and

were placed along high-use trails where we were restricted from using the blood-based

lure (see Chapter 3 for more information on the remote camera station study design). We

identified and distinguished individual cougars in photographs and videos based on

artificial tags, physical features (i.e., kinked tails, facial features, or size), and

spatial/temporal distance between detections. Unmonitored cougars were only included in

the enumeration when multiple detections could be confidently attributed to the same

individual, indicating non-transient status. We also included detections from hunter

harvest and other known mortalities of unmonitored adult cougars. However, we note that hunting pressure was relatively low in the study area. The mean harvest rate for the 6,434 km^2 management area (Hunt Area 2) in which the study area was located was 2.0 cougars per year between 2009 and 2013 (Thompson 2010, 2013; Clapp 2014). Detections only included hunter harvest mortalities that occurred within the Buffalo Valley and Gros Ventre drainages, and did not include subadults since non-transient status could not be verified (except in cases when residency could be backed up by other sources of detection).

We backlogged newly radio-collared or detected cougars to previous seasons following protocols of Logan and Sweanor (2001), Robinson et al. (2008), and Cooley et al. (2009a), which assumed that males immigrated at 21 months and females were native to the study area. Proportional residency was unknown; we therefore assigned either the mean proportion of all radio-collared cougars of the same sex, or, if the cougar was captured in subsequent seasons, back-logged that individual's proportional residency or mean proportional residency (if tracked for multiple years).

Percent accuracy.— We estimated capture success using the percent accuracy metric developed by Logan and Sweanor (2001):

$$PA=[1-BL_{year\ i}/(BL_{year\ i}+C_{year\ i})]x100$$

where BL is the number of backlogged individuals for year i, and C is the number actually tracked and enumerated. We also calculated a modified version of this equation that used the proportional residency values instead of the whole number enumerations used in the original equation.

RESULTS

Capture, Tracking and Home Range Delineation

We GPS tracked 13 individual adult cougars over the course of the study from September 2011 to August 2014. The trapping events in which these individuals were captured and radio-collared occurred between the winters of 2007 and 2014. Trapping effort (as expressed in km transected) was only quantified in 2012 and 2013; mean effort was 684.5 km ($\pm$ 197.9 SD, n = 2). We note that all years were similar in capture effort, and used the same trapping transects (Table 2.1). The GPS tracked individuals included 5 males and 8 females; dependent kittens were also marked but not included in this analysis. Excluding recaptures or captures of juveniles that were aided by radio-telemetry, we performed 12 "blind captures" for 11 of the individuals which were initiated by track detection along the snow transects. All but one of these were detected on the trapping transects. The GPS location data was collected and divided into 3 annual time periods covering September 1 – August 30. We calculated annual home ranges for 7, 8, and 8 individual cougars for each year (2011-2013), respectively.

Mean annual home range size for male cougars (weighted by individual) ranged from 223.9 km^2 to 538.6 km^2 (n = 5, $\bar{x}$ = 369.43 $\pm$ 134.9 SD). Mean annual home range size for female cougars ranged from 67.3 km^2 to 219.4 km^2 (n = 8, $\bar{x}$ = 148.1 $\pm$ 67.7 SD). One newly independent female (F097) collected 19 locations in 2012, and was excluded for that year. One male (M029) was fitted with an advanced radio-collar which collected 6,270 locations in 2013. Excluding these outliers, quantity of yearly GPS relocations per individual ranged from 276 to 1,896 ($\bar{x}$ = 894.5 $\pm$ 445.0 SD). One additional individual (M085) was captured in the subsequent 2014 season and was determined to have been a

resident cougar in previous seasons based on age and remote camera data. When accounting for backlogged home ranges, there were 11, 10, and 9 calculated individual home ranges included in each year (2011-2013), respectively.

Area Divisor Delineation

To construct the area divisors, we first determined the average home range size during winter for females by examining all GPS-based winter home ranges collected as early as 2004. Home ranges were only included if the individual's seasonal home range was comprised of a minimum of 50 relocations, as recommended by Seaman et al. (1999), and incorporated a minimum of 100 days. The mean female home range size, weighted by individual, during winter capture seasons (defined as November 15 to April 15, based on average monthly snow coverage; Grand Teton National Park 2015) was 102.4 km^2 ($\pm$ 86.8 SD, n = 9). The resulting geometric radius was 5.7 km, creating area divisors of 843.7 km^2, 783.1 km^2, and 1,570.3 km^2 for the Gros Ventre, Buffalo Valley, and combined areas, respectively. There was a 5.6% overlap between the two areas.

Unmonitored Cougars

We enumerated an additional three unmonitored cougars into the density estimate. One female was captured but not tracked due to a failed radio-collar; this individual was first captured in early 2010 and visually sighted as late as early 2013. Using photo and video data from remote cameras, we identified a minimum of two additional unmonitored females that we determined to be adult residents. Outside of these unmonitored residents, the remote camera stations collected 17 and 20 detections of uncollared cougars in 2012 and 2013, respectively. These detections were either determined to be individuals which

were captured in subsequent years (and were accordingly backlogged), or could not be

confidently identified as resident individuals. The three unmonitored residents were

assigned the average proportional residency value for the sex and area divisor in which

they were detected. From 2011 through 2014, the Wyoming Game and Fish Department

reported 10 cougar mortalities in the local management area (Hunt Area 2) due to hunter

harvest (Thompson 2013, Clapp 2014, Wyoming Game and Fish Department 2015).

Seven harvests were reported outside of the watersheds in which the area divisor was

drawn. The remaining three were radio-collared cougars that were already included in

the enumeration.

Density Estimates

The mean unadjusted density estimates covering all three years were 0.13, 0.85

and 0.50 cougars/100 km^2 for the Buffalo Valley, Gros Ventre, and combined areas,

respectively. When adjusting for uncollared residents, the estimates averaged 0.27, 1.07,

0.82 cougars/100 km^2 (Table 2.2). To examine the sensitivity of density estimates to

buffer size, we also calculated density estimates using area divisors based on one

standard deviation above and below the mean female winter home range (Table 2.3).

Percent Accuracy.— We estimated capture success using Logan and Sweanor's

(2001) percent accuracy method. Before accounting for unmonitored residents (and only

using radio-collared individuals for backlogging), percent accuracy averaged 74.2%

across the trapping areas and years. When including uncollared individuals detected from

video detections, accuracy averaged 58.9%. Similar numbers are reported when using

proportional residency, averaged with and without the inclusion of unmonitored

individuals (Table 2.4).

Appropriateness of trapping buffer.— Radio-collared cougars selected for lower elevations within the trapping buffer (β = -2.979, P < 0.001). Transects were generally located along drainage bottoms and lower elevations, suggesting that cougars, if present within the trapping buffer, would not avoid the lower elevations and therefore should be detectible along transects. We ran a second RSPF using distance-to-transect as an attribute, and found that radio-collared cougars selected against areas distal to the winter transects themselves (β = -1.364, P < 0.001), suggesting that cougars present within the winter trapping buffer should be detected at the transect.

DISCUSSION

Our density estimates for the Gros Ventre area were within the range of published estimates from other cougar studies in North America (Smallwood 1997, Quigley and Hornocker 2010). Our estimates for the Buffalo Valley area were below the lowest reported estimates that we found in the literature. The differences in density estimates between the Buffalo Valley and Gros Ventre areas were not especially surprising, given the former's lower capture success, as well as the lower detection rates from other noninvasive sources of detection (i.e., remote camera and scat detection dog surveys; Chapter 3). Possibly, the differences in densities were due to intra-guild competition with recently recolonized wolves (Bartnick et al. 2013, Lendrum et al. 2014, Elbroch et al. 2015) or grizzly bears in the Buffalo Valley area. However, given these carnivores' large home ranges, low densities, and cryptic natures, research on their interactions is notoriously difficult (Kortello et al. 2007), and conclusive interpretation may remain dubious.

Our criteria for including unmonitored residents in the enumeration was more conservative than those used by Choate et al. (2006) and Robinson et al. (2008). For example, we ignored several remote camera detections that could not be verified as resident cougars. This was in part due to the difficulty in identifying individual cougars (see Chapter 3), and it was highly possible that some of these detected individual cougars were indeed residents. Thus, our estimates were much more likely to have been underestimates than overestimates of the true density. Using the Logan and Sweanor (2001) method, our mean percent accuracy metric (before adjusting for unmonitored residents) was 74.2%. Logan and Sweanor (2001) reported an average percent accuracy of 87.4%, and Sawaya et al. (2011) reported an average of 90.5% accuracy. Critically, our average percent accuracy measure dropped 15.3% to 58.9% when including the unmonitored resident cougars detected by remote camera. This reduction in accuracy likely would not have been realized without the aid of remote cameras and remote video surveys, and highlights the difficulties and limitations of purported saturation trapping.

While this thesis addresses certain biases in cougar trapping and telemetry-based density estimation, other biases in trapping effort and capture success likely remain, despite our methodology. Cougar trapping was a relatively protracted process with low capture rates. It was often dependent on several intangible and interactive factors including weather conditions, physical and political accessibility, and the experience and behavior of both researchers and trailing hounds. To some degree, it was an inherently opportunistic and haphazard process, and precisely quantifying effort was difficult. Nonetheless, we recommend careful recording of capture effort to minimize the uncertainties and subjectivity that could otherwise bias density estimates.

In this paper, we argue that an area divisor was best defined by the effective trapping area, as opposed to the composite home range method used by Robinson et al. (2008), Cooley et al. (2009*a*, *b*), Elbroch and Wittmer (2012), and Allen et al. (2015). Our method reduces bias by 1) preserving the sampling frame near the trapping effort, whereas a composite home range could include areas distal from the sampling effort, especially given the large home ranges of cougars, and 2) including sampled areas with low or no cougar density, which would otherwise be excluded by a composite home range. We note the studies by Elbroch and Wittmer (2012) and Allen et al. (2015) specifically addressed the issue of uneven sampling effort by restricting the composite home range to an area of high trapping effort. However, the area divisors used by Elbroch and Wittmer (2012) and Allen et al. (2015) were 450 km^2 and 402 km^2, respectively. These spatial extents were on the lower range of Smallwood's (1997) review of published estimates of cougar density, which found a negative correlation between density estimates and study area (i.e., area divisor) size. Our combined area divisor was ~8% smaller than the mean size of 1,700 km^2 as reported by Smallwood (1997).

Furthermore, the composite home range method may be biased towards "hot spot" areas of cougar presence, and may not accurately reflect the natural variations in cougar density across a landscape. Indeed, Smallwood (1997) found that almost all published density estimates were likely focused at cougar aggregations (i.e., "hot spots"), and called for future studies to increase their spatial extent to areas beyond these aggregations. Our area divisors included such areas that had very low cougar density. Management or conservation efforts may choose to monitor such areas, especially when evaluating possible scenarios of recolonization or extirpation, and the methods used by the studies

listed above would not necessarily be appropriate. Furthermore, cougar populations at a regional scale likely exhibit spatially shifting aggregations over the course of several years (Smallwood 1997). As many carnivore populations are currently undergoing varying degrees of range contraction and expansion (Laliberte and Ripple 2004), regional population densities may be affected by poorly understood inter-specific interactions with other newly or formerly sympatric carnivore species (Kortello et al. 2007). Due to these issues, cougar density estimates that are spatially limited to high density areas (either due to purposely focusing research at population aggregations, or through the use of a composite home range based area divisor), may not be representative of the regional cougar population on a whole or its long-term trend. Researchers should carefully consider the spatial extent of detection or capture efforts and the potential biases related to variations in animal density across a landscape.

LITERATURE CITED

Allen, M. L. 2014. The ecology and behaviour of pumas (*Puma concolor*) in northern California, USA. Dissertation, Victoria University of Wellington, Wellington, New Zealand.

Allen, M. L., L. M. Elbroch, D. S. Casady, and H. U. Wittmer. 2015. Feeding and spatial ecology of mountain lions in the Mendocino National Forest , California. California Fish and Game 101:51–65.

Amstrup, S., T. McDonald, and B. Manly. 2005. Handbook of capture-recapture analysis. Princeton University Press, Princeton, New Jersey, USA.

Anderson, C. R., and F. G. Lindzey. 2003. Estimating cougar predation rates from GPS location clusters. Journal of Wildlife Management 67:307–316.

Bacon, M. 2010. The ecology of a re-established cougar (*Puma concolor*) population in southeastern Alberta and southwestern Saskatchewan. Thesis, University of Alberta, Edmonton, Canada.

Balme, G. A., L. T. B. Hunter, and R. Slotow. 2009. Evaluating methods for counting cryptic carnivores. Journal of Wildlife Management 73:433–441.

Bartnick, T., T. R. Ven Deelen, H. B. Quigley, and D. Craighead. 2013. Variation in cougar (*Puma concolor*) predation habits during wolf (*Canis lupus*) recovery in the southern Greater Yellowstone Ecosystem. Canadian Journal of Zoology 93:82–93.

Bivand, R., N. Lewin-Koh. 2014. maptools. R package version 0.8-30. <https://cran.r-project.org/web/packages/maptools/maptools.pdf>. Accessed 8 Mar 2014.

Bivand, R., and C. Rundel. 2011. rgeos. R package version 0.1-8. <http://cran.r-project.org/web/packages/rgeos/rgeos.pdf >. Accessed 25 April 2014.

Boitani, L., and R. A. Powell. 2012. Carnivore ecology and conservation: a handbook of techniques. Oxford University Press, New York, New York, USA.

Bullard, F. 1991. Estimating the home range of an animal: a Brownian bridge approach. Johns Hopkins University, Chapel Hill, North Carolina, USA.

Cagnacci, F., L. Boitani, R. A. Powell, and M. S. Boyce. 2010. Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. Philosophical Transactions of the Royal Society B: Biological Sciences 365:2157–2162.

Calenge, C. 2011. Home range estimation in R: the adehabitatHR package. <https://cran.r-project.org/web/packages/adehabitatHR/adehabitatHR.pdf>. Accessed 8 Mar 2014.

Choate, D., M. Wolfe, and D. Stoner. 2006. Evaluation of cougar population estimators in Utah. Wildlife Society Bulletin 34:782–799.

Clapp, J. 2014. Wyoming mountain lion mortality report harvest year 2013. Wyoming Game and Fish Department, Laramie, Wyoming, USA.

Cooley, H. S., R. B. Wielgus, G. Koehler, and B. Maletzke. 2009*a*. Source populations in carnivore management: cougar demography and emigration in a lightly hunted population. Animal Conservation 12:321–328.

Cooley, H. S., R. Wielgus, G. M. Koehler, H. S. Robinson, and B. T. Maletzke. 2009*b*. Does hunting regulate cougar populations? A test of the compensatory mortality hypothesis. Ecology 90:2913–2921.

Cougar Management Guidelines Working Group. 2005. Cougar Management Guidelines. T. Beck, J. Beecham, P. Beier, T. Hofstra, M. Hornocker, F. Lindzey, K. Logan, B. Pierce, H. Quigley, I. Ross, H. Shaw, R. Sparrowe, and S. Torres, editors. WildFutures, Bainbridge Island, Washington, USA.

Duong, T. 2014. ks: Kernel smoothing. R package version 1.9.3. <https://cran.r-project.org/web/packages/ks/ks.pdf>. Accessed 8 Mar 2014.

Elbroch, L. M., P. E. Lendrum, J. Newby, H. Quigley, and D. J. Thompson. 2015. Recolonizing wolves influence the realized niche of resident cougars. Zoological Studies 54:2-11.

Elbroch, L. M., and H. U. Wittmer. 2012. Puma spatial ecology in open habitats with aggregate prey. Mammalian Biology 77:377–384.

Franklin, W., W. Johnson, R. Sarno, and J. Iriarte. 1999. Ecology of the Patagonia puma *Felis concolor patagonica* in southern Chile. Biological Conservation 90:33–40.

Gittleman, J. L., D. W. MacDonald, R. K. Wayne, and M. Gosling. 2001. Why "carnivore conservation"? Pages 1–7 *in*. J. L. Gittleman, S. M. Funk, D. W. Macdonald, and R. K. Wayne, editors. Carnivore conservation. Cambridge University Press, London, United Kingdom.

Grand Teton National Park. 2015. <http://www.nps.gov/grte/naturescience/weather.htm>. Accessed 10 Apr 2014.

Heffelfinger, J. 2010. Age criteria for southwestern game animals. Special Report #19. Arizona Game and Fish Department, Phoenix, Arizona, USA.

Hopkins, R. A., and R. H. Barrett. 1991. Population characteristics of the mountain lion in the Diablo Range, California. Pages 21–22 *in*. Mountain lion-human interaction symposium and workshop. Colorado Division of Wildlife, Denver, Colorado, USA.

Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. Biometrika 52:225–247.

Jones, M. C., J. S. Marron, and S. J. Sheather. 1996. A brief survey of bandwidth selection for density estimation. Journal of the American Statistical Association 91:401–407.

Kelly, M. J., A. J. Noss, M. S. Di Bitetti, L. Maffei, R. L. Arispe, A. Paviolo, C. D. De Angelo, and Y. E. Di Blanco. 2008. Estimating puma densities from camera

trapping across three study sites: Bolivia, Argentina, and Belize. Journal of Mammalogy 89:408–418.

Kie, J. G., J. Matthiopoulos, J. Fieberg, R. A. Powell, F. Cagnacci, M. S. Mitchell, J. M. Gaillard, and P. R. Moorcroft. 2010. The home-range concept: are traditional estimators still relevant with modern telemetry technology? Philosophical transactions of the Royal Society of London. Series B, Biological sciences 365:2221–2231.

Knight, D. H. 1996. Mountains and plains: The ecology of Wyoming landscapes. Yale University Press, New Haven, Connecticut, USA.

Knopff, K. H., A. A. Knopff, A. Kortello, and M. S. Boyce. 2010. Cougar kill rate and prey composition in a multiprey system. Journal of Wildlife Management 74:1435–1447.

Kortello, A., T. Hurd, and D. Murray. 2007. Interactions between cougars (*Puma concolor*) and gray wolves (*Canis lupus*) in Banff National Park, Alberta. Ecoscience 14:214–222.

Laliberte, A., and W. Ripple. 2004. Range contractions of North American carnivores and ungulates. BioScience 54:123–138.

Laundre, J. W., L. Hernandez, D. Streubel, K. Altendorf, and C. Lopez Gonzalez. 2000. Aging mountain lions using gum-line recession. Wildlife Society Bulletin 28:963–966.

Lele, S., J. Keim, P. Solymos, and M. Solymos. 2013. ResourceSelection. R package version 0.2-4.

<https://cran.r-project.org/web/packages/ResourceSelection/ResourceSelection.pdf>. Accessed 6 Oct 2014.

Lendrum, P. E., L. M. Elbroch, H. Quigley, D. J. Thompson, M. Jimenez, and D. Craighead. 2014. Home range characteristics of a subordinate predator: selection for refugia or hunt opportunity? Journal of Zoology 294:59–67.

Lewison, R., E. Fitzhugh, and S. Galentine. 2001. Validation of a rigorous track classification technique : identifying individual mountain lions. Biological Conservation 99:313–321.

Logan, K., and L. Sweanor. 2001. Desert puma: evolutionary ecology and conservation of an enduring carnivore. Island Press, Washington, D.C., USA.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. 2nd edition. Kluwer Academic Publishers, Boston, Massachusetts, USA.

Marston, R. A., and J. E. Anderson. 1991. Watersheds and vegetation of the Greater Yellowstone Ecosystem. Conservation Biology 5:338–346.

McLellan, B. 1989. Dynamics of a grizzly bear population during a period of industrial resource extraction. I. density and age-sex composition. Canadian Journal of Zoology 67:1856–1860.

Neal, D. L., G. N. Steger, and R. C. Bertram. 1987. Mountain lions: preliminary findings on home-range use and density in the central Sierra Nevada. USDA PSW-392. Pacific Southwest Forest and Range Experiment Station, Berkeley, California, USA.

Pierce, B. M., and V. C. Bleich. 2003. Mountain lion (*Puma concolor*). Pages 744–757 *in*

    G. A. Feldhammer, B. Thompson, and J. Chapman, editors. Wild mammals of

    North America. 2nd edition. Johns Hopkins University Press, Baltimore,

    Maryland, USA.

Pyare, S., S. Cain, D. Moody, C. Schwartz, and J. Berger. 2004. Carnivore re-

    colonisation: reality, possibility and a non-equilibrium century for grizzly bears in

    the southern Yellowstone ecosystem. Animal Conservation 7:71–77.

Quigley, H. B., and M. G. Hornocker. 2010. Cougar population dynamics. Pages 59–75

    in M. G. Hornocker and S. Negri, editors. Cougar: ecology and conservation.

    University of Chicago Press, Chicago, Illinois, USA.

Quigley, K. 2000. Immobilization and biological sampling protocols. Hornocker Wildlife

    Institute/Wildlife Conservation Society, Bozeman, Montana, USA.

Rinehart, K. A., L. M. Elbroch, and H. U. Wittmer. 2014. Common biases in density

    estimation based on home range overlap with reference to pumas in Patagonia.

    Wildlife Biology 20:19–26.

Robinson, H. S., R. B. Wielgus, H. S. Cooley, and S. W. Cooley. 2008. Sink populations

    in carnivore management : cougar demography and immigration in a hunted

    population. Ecological Applications 18:1028–1037.

Ross, P. I., and M. G. Jalkotzy. 1992. Characteristics of a hunted population of cougars in

    southwestern Alberta. Journal of Wildlife Management 56:417–426.

Sawaya, M. A., T. K. Ruth, S. Creel, J. J. Rotella, J. B. Stetz, H. B. Quigley, and S. T.

    Kalinowski. 2011. Evaluation of noninvasive genetic sampling methods for

cougars in Yellowstone National Park. Journal of Wildlife Management 75:612–622.

Seaman, D. E., J. J. Millspaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke, and R. A. Gitzen. 1999. Effects of sample size on kernel home range estimates. Journal of Wildlife Management 63:739–747.

Seber, G. A. F. 1965. A note on the multiple-recapture census. Biometrika 52:249–259.

Seber, G. A. F. 1982. The estimation of animal abundance and related parameters. Second edition. Volume 2. Charles Griffith and Company, Ltd, London, United Kingdom.

Seidensticker, J., and M. Hornocker. 1973. Mountain lion social organization in the Idaho Primitive Area. Wildlife Monographs 35:3–60.

Sikes, R. S., and W. L. Gannon. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 92:235–253.

Smallwood, K. S., and C. Schonewald. 1996. Scaling population density and spatial pattern for terrestrial, mammalian carnivores. Oecologia 105:329–335.

Smallwood, K. S. 1997. Interpreting puma (*Puma concolor*) population estimates for theory and management. Environmental Conservation 24:283–289.

Smallwood, K. S. 1999. Suggested study attributes for making useful population density estimates. Transactions of the Western Section of The Wildlife Society 35:76–82.

Spreadbury, B., R. Musil, and J. Musil. 1996. Cougar population characteristics in southeastern British Columbia. Journal of Wildlife Management 60:962–969.

Stabler, B. 2014. shapefiles. R package version 0.7.

<https://cran.r-project.org/web/packages/shapefiles/shapefiles.pdf>. Accessed 10
Feb 2014.

Thompson, D. J. 2010. Wyoming mountain lion mortality report harvest year 2009.
Wyoming Game and Fish Department, Laramie, Wyoming, USA.

Thompson, D. J. 2013. Wyoming mountain lion mortality report harvest years : 2010-
2012. Wyoming Game and Fish Department, Laramie, Wyoming, USA.

Thompson, D. J., and J. A. Jenks. 2010. Dispersal movements of subadult cougars from
the Black Hills: the notions of range expansion and recolonization. Ecosphere
1:1–11.

Walter, W. D., J. W. Fischer, S. Baruch-Mordo, and K. C. Vercauteren. 2009. What is the
proper method to delineate home range of an animal using today's advanced GPS
telemetry systems: the initial step. Pages 249–268 *in* O. Krejcar, editor. Modern
Telemetry. InTech Open Access Publisher.
<http://www.intechopen.com/books/show/title/modern-telemetry>. Accessed 16
Apr 2014.

Walter, W. D., and J. W. Fischer. 2015. Manual of Applied Spatial Ecology. Walter
Applied Spatial Ecology Lab, Pennsylvania State University. University Park,
Pennsylvania, USA.

Withey, J. C., T. D. Bloxton, and J. M. Marzluff. 2001. Effects of tagging and location
error in wildlife radiotelemetry studies. Pages 43–75 *in* J. Millspaugh and J. M.
Marzluff, editors. Radio tracking and animal populations. Academic Press, San
Diego, California, USA.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164–168.

Wyoming Game and Fish Department. 2015. Wyoming Game and Fish Department Mountain Lion Harvest Quota. <https://wgfd.wyo.gov/web2011/HUNTING-1000743.aspx>. Accessed 1 Jan 2015.

Table 2.1.Winter snow transects for the detection and capture of cougars, listed by mode

of transect and trapping area, northwest Wyoming, 2011-2013.

	Distance (km)	% of total
Mode of Transect		
Foot	42.91	18.97%
Snowmobile	136.77	60.48%
Truck	46.46	20.55%
Total	226.14	100.00%
Trapping area		
Buffalo Valley	123.10	54.44%
Gros Ventre	103.04	45.56%
Total	226.14	100.00%

Table 2.2. Density estimates (cougars/100 km^2) for a population of cougars in northwest Wyoming, 2011-2013, using enumeration and proportional residency.

		Enumeration	Adjusted enumeration	Density	Adjusted density
2011	Buffalo Valley	1.60	2.72	0.20	0.34
	Gros Ventre	7.91	9.77	0.94	1.16
	Combined areas	9.26	11.90	0.59	0.91
2012	Buffalo Valley	0.50	1.62	0.06	0.20
	Gros Ventre	7.91	9.77	0.94	1.16
	Combined areas	8.22	10.86	0.52	0.84
2013	Buffalo Valley	0.90	2.02	0.11	0.25
	Gros Ventre	5.68	7.55	0.67	0.90
	Combined areas	6.25	8.89	0.40	0.72

Table 2.3. Enumerations and density estimates of cougars in Northwest Wyoming, using area divisors based on one standard deviation above and below the mean female home range size. Area divisors were drawn by buffering capture transects with the geometric radius of the mean female home range.

| | | Adjusted enumeration | | Adjusted density | |
		buffer -1 σ	buffer +1 σ	buffer -1 σ	buffer +1 σ
2011	Buffalo Valley	1.59	3.13	0.40	0.30
	Gros Ventre	6.99	10.68	1.80	0.94
	Combined areas	8.47	12.77	1.30	0.75
2012	Buffalo Valley	0.90	1.97	0.22	0.19
	Gros Ventre	6.47	10.71	1.67	0.95
	Combined areas	7.26	11.74	1.14	0.70
2013	Buffalo Valley	1.10	2.41	0.27	0.23
	Gros Ventre	5.14	8.34	1.33	0.74
	Combined areas	6.13	9.68	1.00	0.60

Table 2.4. Percent accuracy of density estimates of a cougar population in northwest Wyoming, 2011-2013 using the method described by Logan and Sweanor (2001), as well as a modified method using proportional residency. The "adjusted" values include residents that were detected, but not radio-collared and tracked.

	Percent accuracy	Adjusted percent accuracy	Difference
Logan-Sweanor method			
2011	63.6%	50.0%	13.6%
2012	70.0%	53.8%	16.2%
2013	88.9%	72.7%	16.2%
Proportional residency method			
2011	69.5%	54.1%	15.4%
2012	77.8%	58.9%	18.9%
2013	89.9%	70.2%	19.7%
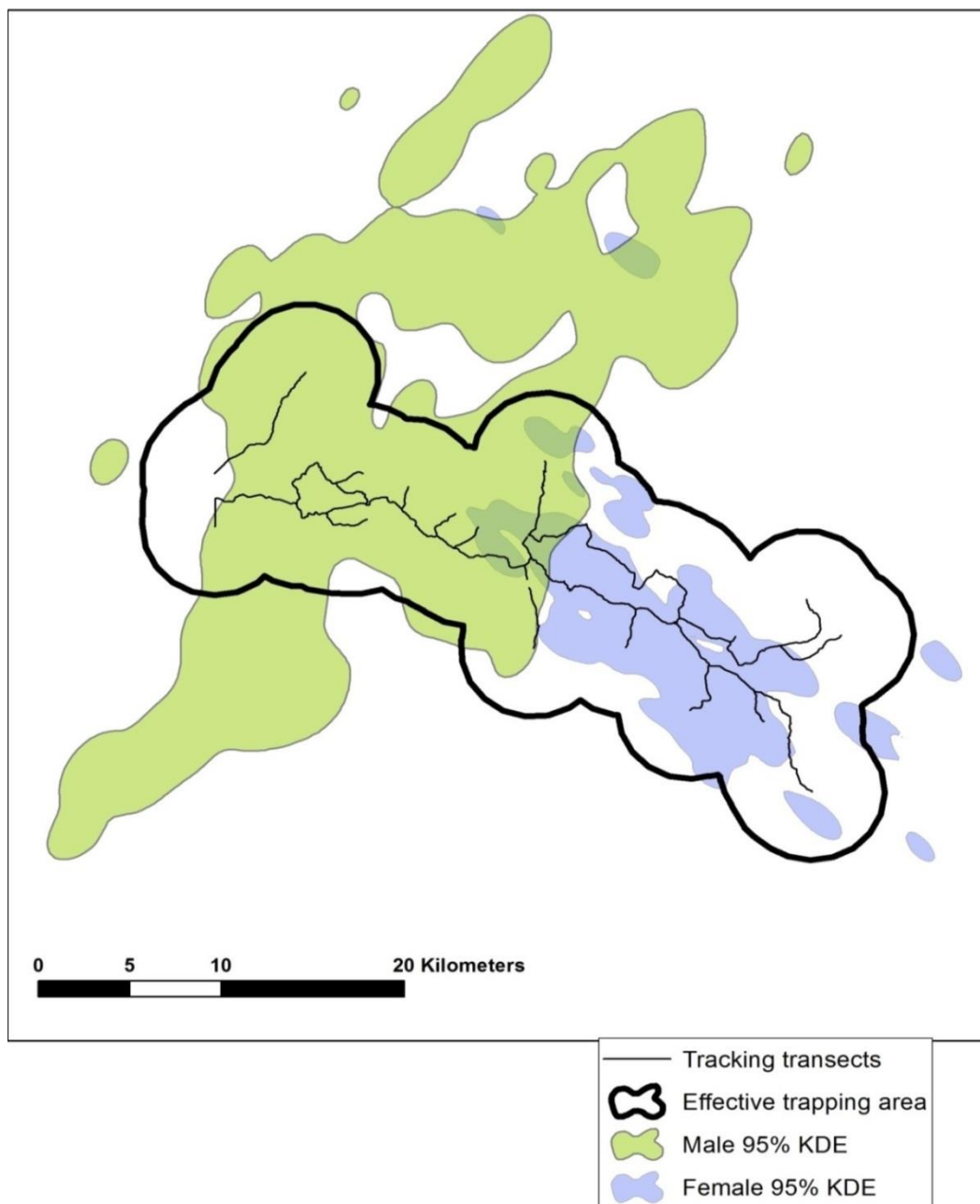
Figure 2.1. Example of population density estimation using enumeration of proportional residency. This example represents 39% of a male home range (green), and 91% of a female home range (blue) intersecting an effective trapping area. In this scenario, the total density would be 1.3 animals in the trapping area.
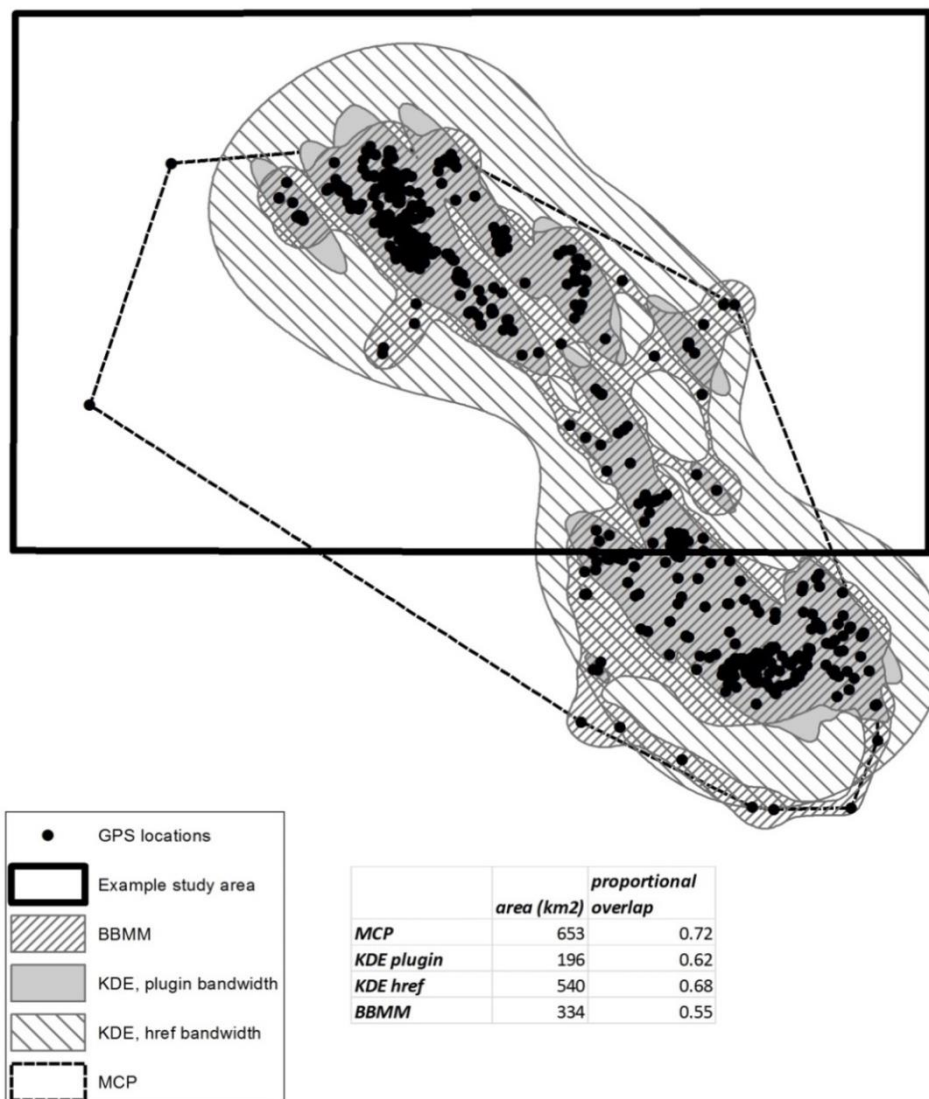
Figure 2.2. Several home range delineations using location data from one female cougar, including Brownian Bridge Movement Model (BBMM), minimum convex polygon (MCP), and Kernel Density Estimation (KDE) using both "plugin" and "href" bandwidths. Home range delineations are overlaid on a hypothetical study area in which proportional residency values are calculated.
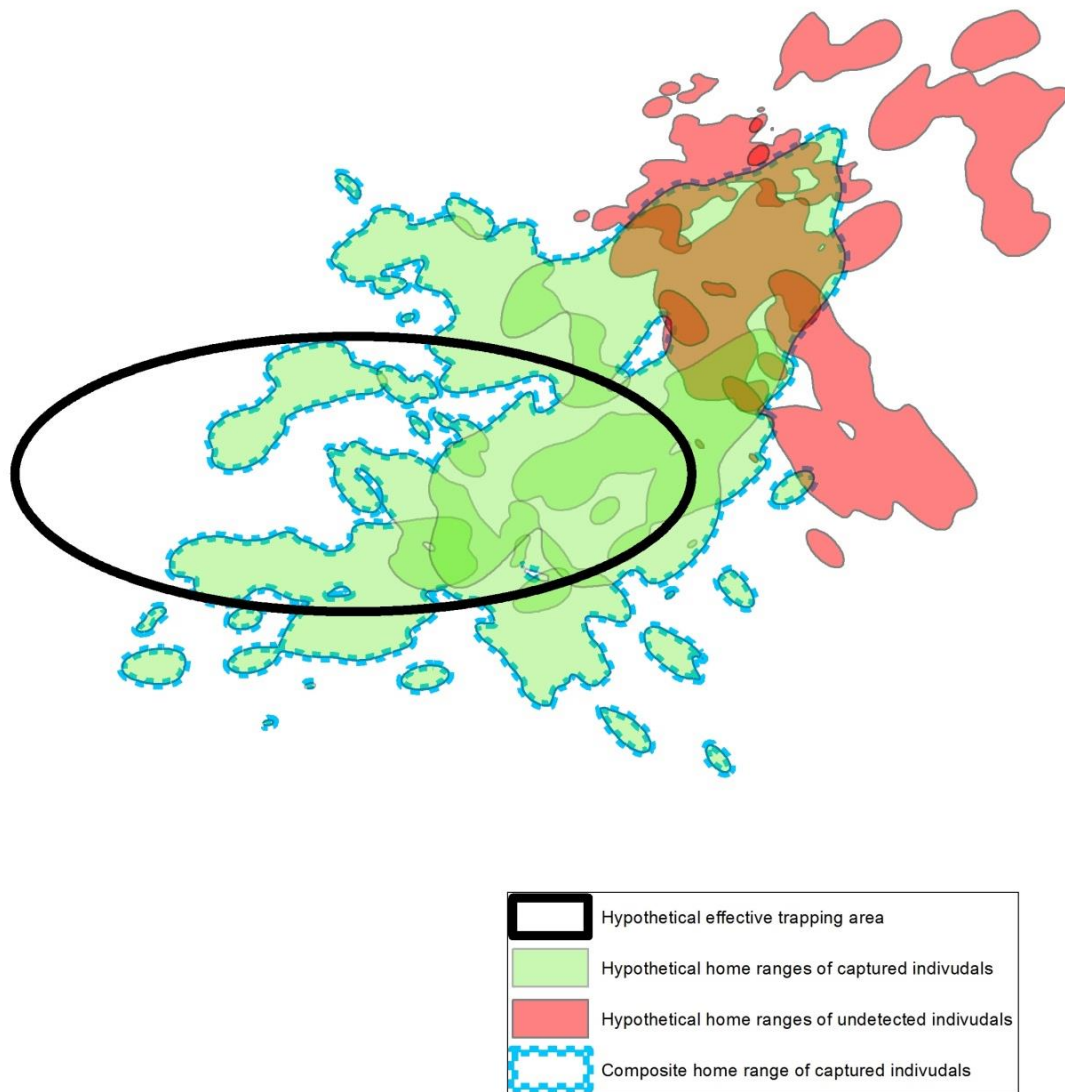
Figure 2.3. Hypothetical home ranges of telemetered cougars (green) and undetected cougars (red), demonstrating the potential to underestimate density when using a composite of telemetered home ranges as the area over which to calculate proportional residency and density.
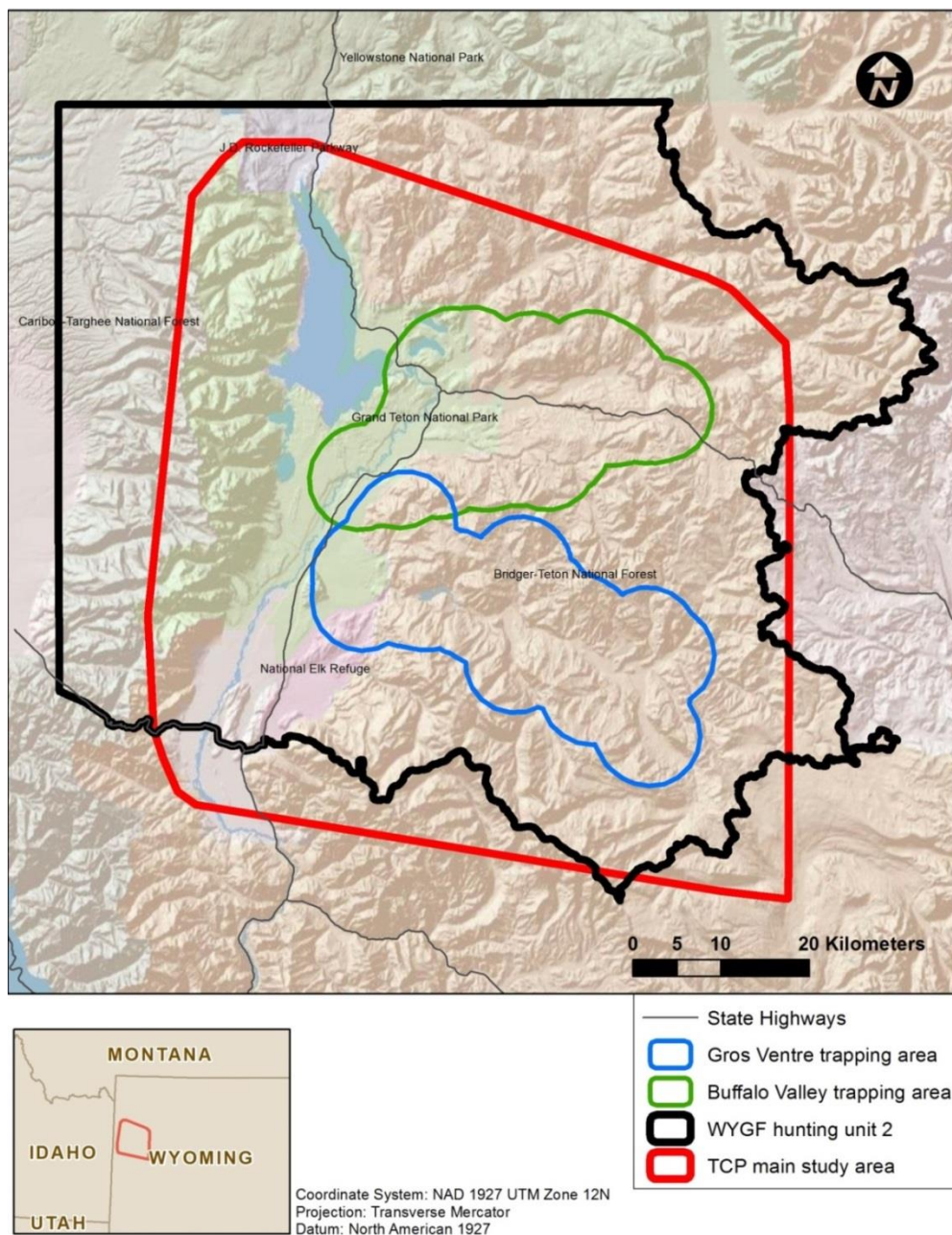
Figure 2.4. The greater study area in northwest Wyoming, represented by a minimum convex polygon of all resident cougar locations over the history of the study. Also shown is the Wyoming Game and Fish regional cougar hunting area (Hunt Area 2), and the effective trapping areas created by buffering winter track transects by the mean female home range radius.
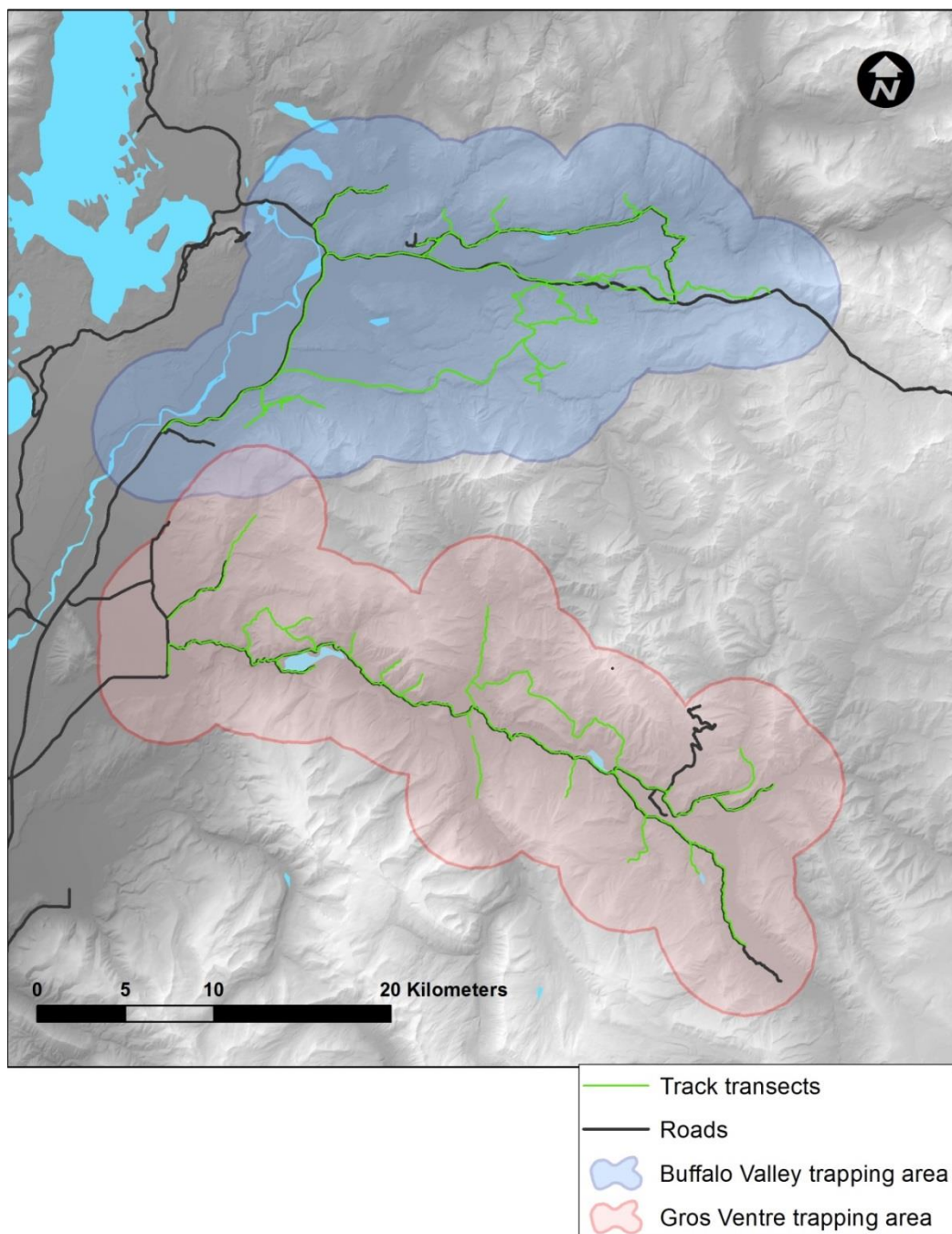
Figure 2.5. Effective cougar trapping areas around snow tracking transects in northwest Wyoming. These areas were delineated by buffering transects by average female home range radius, and used to define the area divisor, or area over which cougar density was calculated.

CHAPTER 3

A COMPARISON OF NONINVASIVE TECHNIQUES USED TO DETERMINE POPULATION DENSITY OF COUGARS

ABSTRACT

Determining the size and trend of an animal population is fundamentally needed for making informed management decisions. Most carnivores, such as cougars (*Puma concolor*), occur at low densities, utilize large territories, and are behaviorally and morphologically cryptic making counting and estimation of population size extremely difficult. Consequently, most carnivores are unsuitable for conventional sight-based surveys. In addition, direct census methods involving physical capture and radio-collaring of the species are costly, invasive, and logistically challenging. Recent advances in noninvasive survey methods may offer solutions to these difficulties, but questions remain on their effectiveness and reliability. Our study objectives were to determine the density of a cougar population in northwest Wyoming using conventional capture and radio-collar methodologies, and then apply three noninvasive survey methods to the same population to evaluate and compare their accuracy and efficacy in determining population density. The noninvasive field methods included two annual sessions of 1) genetic mark-recapture using cougar hair collected from snow transects, 2) photographic mark-recapture using remote camera trapping, and 3) genetic mark-recapture using cougar scat collected with detection dogs. We used multiple types of analyses for each method, including conventional capture-mark-recapture (CMR) models, spatially explicit capture-recapture (SECR) models, and capture with replacement (CAPWIRE) models. The

reference density estimate was based on the mean count of known resident adult cougars in the study area over multiple years ($\bar{x}$ = 0.82 cougars/100 km^2 ± 0.10 SD; n = 3 years). We found scat detection dogs produced more plausible density estimates, were less prone to violating mark—recapture assumptions, and were more cost-effective than the other survey methods examined. The hair collection transects failed to produce a sample size large enough for a CMR abundance estimate due to poor success in field collection and genotyping. Using a SECR framework, the remote camera surveys produced a mean density estimate of 0.60 cougars/100 km^2 (n = 2 years; relative SD = 56.5%), and were on average 29.2% lower than the reference estimate. Only one of the two annual camera surveys produced results with confidence intervals encompassing the reference estimate. Additional analysis indicated that individual identification of cougars in photographs may not be reliable, essentially violating assumptions of tag loss and challenging the validity of photo-based population estimates of cougars. Surveys using a detection dog along transects followed by SECR analysis produced an average density of 2.41 cougars/100 km^2 (n = 2 years; relative SD = 12.6%). Both of the detection dog surveys produced confidence intervals encompassing the reference estimate, but density results were on average 71.8% greater than the reference estimate. Given the reference estimate was, in effect, a minimum count of known individuals, the detection dog estimates were more plausible than the underestimates produced by the remote camera surveys. The overestimation using scats found with detection dogs may be in part due to the detection of transient individuals which resulted in a high number of single detections; adjusting the timing of surveys may lessen this bias. The scat collection survey using detection dogs was also the most cost effective, with a cost-per-detection of $341. Remote camera

surveys and hair collection transects had cost-per-detection estimates of $3,241 and $7,627, respectively. Our results indicate that scat detection dog surveys are more cost effective and reliable than the other methods we examined, and we recommend this method for monitoring cougar populations. Furthermore, our findings suggest that scat detection dog surveys likewise may be the most feasible method for other wide ranging carnivores with a uniform pelage.

INTRODUCTION

Throughout the world, many carnivore populations are declining with several species becoming threatened or endangered due to a variety of reasons (Ripple et al. 2014). Accurate data on animal presence, abundance and population trends are essential for informed and effective decisions in management and conservation. In North America, cougars (*Puma concolor*) can be particularly difficult to census due to their large home range sizes, low densities, and cryptic nature (Beier and Cunningham 1996, Logan and Sweanor 2001, Choate et al. 2006). The conventional invasive method for monitoring cougar populations involve capture and radio-collaring, followed by radio-tracking to verify residency (e.g. Logan and Sweanor 2001; Cooley et al. 2009*a*, *b*). The resulting data can then be used in various enumerative approaches, ranging from a simple count of known individuals to determine abundance, to more precise methods using home range analyses to determine proportional residency and density (McLellan 1989, Cooley et al. 2009*a*; see Chapter 2). Although these methods have been regarded as the "gold standard" in cougar population estimation (Cougar Management Guidelines Working Group 2005), these methods are time-consuming, prohibitively expensive, and

logistically challenging. Furthermore, the process of live-capturing cougars requires direct physical contact, and can be potentially compromising to the natural behavior and health of the study animal (Proulx et al. 2012). A low-cost approach commonly used by wildlife managers is to monitor populations through data collected from hunter harvest reports and other known mortalities (Wolfe et al. 2016). While these data may provide general insights into population trends (Wolfe et al. 2016), they are affected by factors such as hunting effort and reporting rate, both of which may vary spatially and temporally in and between areas of interest (Beier and Cunningham 1996, Anderson and Lindzey 2005). Noninvasive survey techniques may offer opportunities to accurately monitor cougar population trends at a lower cost and with less impact on the study animal than conventional capture-based methods. Many carnivores are ideal for noninvasive methods due to traits such as territorial marking behaviors, inclination to respond to baited detectors due to curiosity, and scat or track morphologies unique to a species or individual (e.g. MacKay et al. 2008, Dempsey et al. 2014). The cougar's large distribution and their role as an umbrella species (Beier 2009) make them an especially attractive candidate for a cost effective method of population monitoring.

Published cougar abundance estimates using or attempting to use noninvasive methods include remote camera trapping surveys (Kelly et al. 2008, Negrões et al. 2010), DNA collection using winter track transects (Sawaya et al. 2011), hair-snares (Sawaya et al. 2011) or scat collection (Ernest et al. 2000, Davidson et al. 2014), and aerial winter track surveys (VanSickle and Lindzey 1991, Choate et al. 2006). Other methods include population indices using scent-lured track plates and ground-based winter tracking surveys (Choate et al. 2006). In our review of the literature, only the studies by Sawaya et

al. (2011) and Choate et al. (2006) were applied to marked and enumerated populations which allowed for a comparative evaluation of the noninvasive method; only the Choate et al. (2006) study attempted a comprehensive comparison of several noninvasive techniques. Based on our literature review, certain noninvasive detection techniques appeared impractical for cougars. For example, there has been little success in attracting cougars to noninvasive detectors using scent–based lures: Sawaya et al. (2011) and Choate et al. (2006) were unable to attract cougars to detectors (hair snares, and track plates, respectively) using various curiosity scents such as skunk or catnip oil. Long et al. (2003) also had little success attracting cougars to remote camera traps using similar lures; however, other studies using passive (i.e., non-baited) remote camera arrays reported practical detection rates (Kelly et al. 2008, Negrões et al. 2010). Similarly, passive genetic sampling also appeared feasible based on studies by Davidson et al. (2014) and Russell et al. (2012). Based on the studies above, we focused our research on capture-mark-recapture (CMR) analyses as opposed to population indices (Choate et al. 2006).

Noninvasive estimates of animal abundance or density are typically achieved using capture-mark-recapture based methods (also known as capture-recapture or mark-recapture; hereafter referred to as capture-mark-recapture or CMR; Otis et al. 1978, Seber 1982). There exists a wide variety of CMR-based models with different classes of statistics and various assumptions of the modeled population and trapping method, and relatively recent models have incorporated spatially-explicit data (e.g., Efford 2004, Royle et al. 2013). However, all CMR-based models are, in essence, based on refinements of the Lincoln-Peterson estimator (Kays and Slauson 2008). Traditionally,

CMR analyses require physically capturing animals, affixing a unique mark or tag before releasing them, and then carrying out subsequent captures to determine the probability of recapturing those individuals. Under a true noninvasive framework, individuals are not physically captured; they are instead effectively captured by some type of noninvasive encounter or remote detection, allowing for an already-existing and naturally-occurring mark to be recorded (hereafter we will use the terms "capture", "encounter", and "detect" interchangeably). These natural marks can be any physical or genotypic trait, as long as that trait is unique to the individual and reliably recognizable with whatever subsequent detection method is used. The resulting capture history of noninvasive captures and recaptures is recorded and analyzed similarly to traditional CMR methods (e.g., Karanth 1995, Wasser et al. 2004).

Among other model assumptions (Williams et al. 2002), conventional CMR analyses generally require population closure (i.e., the demographics of a surveyed population are assumed to remain constant during a sampling period with no births, deaths, immigration or emigration). Cougars, consequently, are particularly problematic due to their year-round potential for breeding and dispersal. Ostensibly, the observed increase in denning and dispersal during summer months (Logan and Sweanor 2010, Ruth et al. 2011), would aid in reducing closure issues when surveys are timed accordingly. However, this is somewhat negated since cougars often exhibit a semi-independent stage before full independence and dispersal (Quigley and Hornocker 2010). Population closure issues are further exasperated in areas with high hunting mortality (e.g., Cooley et al. 2009*a*, *b*). Due to these uncertainties, survey methods using

temporally short sampling periods are generally recommended to reduce closure issues (Harihar et al. 2009).

Further underpinning the uncertainties of closure is the problem of spatial scale. Spatial scale is a frequently cited issue for estimates of population density (Efford 2004). As with traditional trap arrays, the area that is effectively trapped around noninvasive detectors (i.e., remote cameras or sampling transects) is difficult to quantify (Wilson and Anderson 1985, Efford 2004, Royle et al. 2013). This can be considered an issue of population closure since individuals residing on the edge of a trapping grid are, effectively, temporary immigrants and emigrants (Kendall et al. 1997). This may be especially applicable to cougars due to their large home ranges. A commonly used method for determining the effective trapping area is to spatially buffer the trap array by some distance, under the assumption the buffer would include any animals that could be captured by the trapping array. Often, one half of the average home range diameter of the study animal was used to determine the buffer distance (Dice 1938, Karanth and Nichols 1998). Radio-telemetry data may not be available for determining average home range size; it was instead determined by proxy using an individuals' detection locations on the detector array to measure the mean maximum distance moved (MMDM; Wilson and Anderson 1985, Karanth and Nichols 1998). Jaguar research by Soisalo and Cavalcanti (2006) compared the MMDM derived from camera detections to home ranges determined from GPS telemetry, and reported the MMDM method significantly underestimated the distances actually moved by jaguars on the trapping array. Using the incorrect measure of MMDM created an underestimated effective trapping area, and thus inflated density

estimates (Soisalo and Cavalcanti 2006). This error in spatial extent could likely affect density estimates for other animals with large home ranges, including cougars.

A relatively recent solution to the issue of spatial uncertainty in CMR models is spatially explicit capture-recapture models (SECR; Efford 2004, Royle et al. 2013). These models incorporate the locations of detections into the capture history, resulting in a spatially-explicit abundance estimate by which density is directly parameterized. In general, SECR models use a hierarchical framework to calculate the probability of detection as a function of the distance of an individual's home range center to a detector (Efford 2004, Royle et al. 2013). SECR models have been employed for cougar density estimates in scat detection dog surveys (Davidson et al. 2014) and winter hair collection surveys (Russell et al. 2012). SECR is advantageous since it eliminates the ad hoc spatiality, thereby eliminating the need for a trap buffer and somewhat relaxes the assumption of population closure (Gardner et al. 2009). However, this relaxed assumption is likely more applicable to the temporary emigrant/immigrant scenario outlined above, as opposed to completely transient individuals that do not have a home range to be modeled. Therefore, a survey method with a brief sampling period is likely still prudent.

Photographic Mark Recapture

Automatically triggered cameras have been used in wildlife research since as early as the 1920s when biologists used them to document species presence and richness. However, their use was somewhat limited until the 1980s when relatively inexpensive camera units using motion sensor technology became available (Kays and Slauson 2008). In the 1990s, studies began using large arrays of motion sensor cameras to estimate

population size for difficult-to-observe species such as grizzlies (*Ursus arctos*; Mace et

al. 1994) and tigers (*Panthera tigris*; Karanth 1995). Tigers, having a unique pelage for

each individual, were ideal for modern CMR methods since individuals could be

confidently identified in photographs without the need for artificial tags (Karanth 1995).

An important assumption of CMR models is that once captured and tagged, individual

animals are dependably recognized in subsequent captures (Seber 1982). Since tigers are

naturally "marked", photographic captures and subsequent re-captures of the same

individual can be identified (Karanth 1995). However, there has been some debate as to

whether species without obvious markings, such as cougars, can be reliably identified at

the individual level in photographs, thereby respecting the identifiable marks assumption

(Kays and Slauson 2008, Kelly et al. 2008). Some studies have estimated cougar

population size using remote camera trapping without artificial marks (e.g., Kelly et al.

2008, Negrões et al. 2010, Soria-Díaz et al. 2010). These studies argued that individual

cougars could indeed be reliably identified by natural pelage markings, scarring, or

morphology, and therefore qualified to perform CMR analysis. The work by Kelly et al.

(2008) specifically examined the extent to which independent investigators agreed with

one another when identifying individual cougars in remote camera images, and found

72.9% average agreement between three independent investigator teams. However,

research on individual identifiability of other animals with a uniform pelage (Yoshizaki et

al. 2009, Oliveira-Santos et al. 2010) suggested that even small discrepancies in

encounter histories created large variances in the resulting abundance estimate, and

stressed caution if relying on this type of identifying mark. Furthermore, investigators

may identify cougars using physical traits that, while distinctive, may not be unique (e.g.,

a kinked tail or missing ear). Consequently, as a sample size increases, the likelihood of multiple cougars with the same trait would also increase (Harmsen 2006), thereby increasing the potential for misidentification.

Genetic Mark Recapture

Genetic CMR uses DNA as a captured individual's identifying mark. In recent decades, technological advances in molecular biology and genetics have given researchers access to these methods at relatively low cost (Parker et al. 1998). Noninvasive sampling techniques typically focus on scat or hair that has been deposited by an animal, either naturally or at a predetermined sampling site using an attractant. Examples include using trained dogs to locate and collect grizzly bear scat (Wasser et al. 2004), or setting up hair snares for black bears (*U. americanus*) and grizzly bears (Woods et al. 1999). Samples are then genotyped to determine the individual identity using polymerase chain reaction (PCR) and microsatellite analysis (Schwartz and Monfort 2008), which are then incorporated in the capture history and subsequent CMR analysis. An important drawback to these methods is that DNA analysis cannot currently provide information on a detected individual's age (Schwartz and Monfort 2008) or known fate (i.e., death or dispersal). Uncertainty in age is problematic for genetic surveys of cougar populations, since cougar offspring may remain dependent members of a family group as late as two years old (Quigley and Hornocker 2010). Consequently, a noninvasive genetic survey would not be able to differentiate members of a single family group from multiple independent adults. Depending on research focus and scope, distinguishing these age classes may not be important to management decisions, since female kill rate increases when caring for dependent young (Knopff et al. 2010), and thereby kittens can play an

influential ecological role. However, this uncertainty in age class likely biases CMR analyses due to heterogeneity in detection probability between dependent kittens and adults: since mother cougars will typically spend part of their time hunting or traveling without their kittens, kittens likely have a lower probability of detection than adults (Logan and Sweanor 2001, Davidson et al. 2014). Since age class is unknown in a capture history, this heterogeneity cannot be explicitly modeled as a covariate into a CMR abundance estimate. Furthermore, as kittens grow older, this heterogeneity likely changes over a relatively short amount of time, potentially within the temporal sample period of a multi-sample genetic survey. It is worth noting that this issue may soon be resolved due to research on chromosomal telomere shortening as a function of aging (Nakagawa et al. 2004), which may allow for the age of an individual to be reliably determined from a genetic sample.

Genetic CMR via snow tracking for hair samples.— Hair collection has likely been used to identify species presence for millennia (Kendall and McKelvey 2008), but only with relatively recent technological advances in molecular biology have researchers been able to discern individual identity from hair, thus allowing for genetic CMR analysis. Kendall and McKelvey (2008) divided hair collection methods into two basic categories: baited and passive. Whereas baited methodology involves an attractant and usually some type of collector (i.e., a hair snare), passive hair collection attempts to locate hair naturally shed by the study animal. Both categories have advantages and disadvantages depending on the traits of the study animal and accepted level of invasiveness. In cougar research, however, researchers have had little success with baited hair snares (Choate et al. 2006, Sawaya et al. 2011). Sawaya et al. (2011) and Russell et

al. (2012) used a passive method of following cougar tracks in snow to find and collect

hair naturally deposited at bedsites and natural vegetative snags. Kendall and McKelvey

(2008) stressed caution, as extracting DNA from hair at the quality sufficient for

determining individual identity was difficult, and different species likely shed DNA at

different rates (Goossens et al. 1998). Felids, in particular, shed low amounts of DNA

with hair as compared to other carnivores (Kendall and McKelvey 2008). Since there was

little to no genetic material in a hair shaft, extraction success was dependent on follicles

being present in the sample (Goossens et al. 1998). Cougars may not regularly shed hair

that includes follicles, and follicle presence in a sample may not be easily discerned by

investigators in the field. Russell et al. (2012) and Sawaya et al. (2011) reported between

13% and 39% success rate for successful DNA extraction from hair to the individual

level, suggesting that a relatively large sample was required for successful abundance

estimates.

 Genetic CMR via scat detection dogs.— Scat is probably the most abundant

animal byproduct collected noninvasively and used for genetic analysis (Wasser et al.

2004). Genetic analysis of scat is dependent on sloughed epithelial cells from the

digestive tract, which remain on scat after being defecated. Careful collection and

extraction of scats can produce high quality DNA markers usable for individual

identification (Schwartz and Monfort 2008). However, locating scat from cryptic and

sparsely occurring species such as cougars is often difficult (Harmsen et al. 2010). A

common solution is the use of scat detection dogs (also known as scat dogs or

conservation dogs). Domestic dogs (*Canis familiaris*) have highly sensitive olfactory

systems relative to that of humans. Combined with their trainability, these traits have

long been exploited by humans. Since as early as the 1800s, wildlife biologists have used

dogs for the detection of wildlife or wildlife sign (Mackay et al. 2008). In recent years,

researchers have been able to incorporate detection dogs with genetic analysis (e.g.,

Smith et al. 2003, 2005). Davidson et al. (2014) estimated the density of a cougar

population in Oregon using this method, and found comparable density estimates using

several CMR-based models. Davidson et al. (2014) was not able to evaluate their result

with a direct enumerative estimate. One disadvantage to scat surveys relates to the

uncertainty of the temporal sampling window. Typically, trapping surveys (including

remote camera surveys) have distinct timeframes of capture. Likewise, genetic surveys

collecting samples from a target species' tracks in snow or a baited hair-snare will have a

temporal window within which the individual was known to be present. However, there

may not be information about the length of time a scat on a passive transect is detectible,

creating uncertainty in the sampling window, and potentially violating assumptions of

population closure. One solution is to initially "clean" (i.e., collect and discard) scats

along transects before subsequent transects. However, financial cost may prohibit

multiple transect visits. An upper limit to the sampling window is likely determinable by

genotyping success: Lonsinger et al. (2015) found PCR success for scat samples collected

from coyotes (*Canis latrans*) and kit foxes (*Vulpes macrotis*) was dependent on the age of

scat, among other factors. For their target species, PCR success rates dropped below 50%

after 7-21 days. However, there was also a significant difference in PCR success rates

between the two canid species, and applying their findings to another species is not

necessarily appropriate. Similar research on cougar scat might provide a reliable scat

degradation timeframe, outside of which PCR failure would prevent samples from being

incorporated into a genetic detection history regardless of their being detected and collected in the field.

Our study objectives were to determine the density of a cougar population in northwest Wyoming using conventional capture and radio-collar methods (i.e., invasive method), and then apply three noninvasive survey methods to the same population and area to evaluate and compare their accuracy and efficacy in determining population density. The noninvasive field methods included two annual sessions of a) genetic mark-recapture using cougar hair collected from snow transects, b) photographic mark-recapture using remote camera trapping, and c) genetic mark-recapture using cougar scat collected with detection dogs. We used multiple types of analyses for each method, including conventional capture-mark-recapture (CMR) models, spatially explicit capture-recapture (SECR) models, and capture with replacement (CAPWIRE) to determine population size and density.

STUDY AREA

The study area encompassed ~5,120 km^2, including much of the Jackson Hole basin and adjacent lands in northwest Wyoming. The area was delineated by the Teton Range in Grand Teton National Park (GTNP) on the west, the Gros Ventre Range on the east, the Teton Wilderness Area on the north, and on the south by Wyoming state highway 22 and the Cache Creek drainage (Fig. 3.1). Most lands within the study area were administered by the U.S. Forest Service (Bridger-Teton National Forest), the National Park Service (Grand Teton National Park), and U.S. Fish and Wildlife Service (National Elk Refuge). A small percentage (~ 5%) was privately owned ranches or

residential areas. Elevations in the study area ranged from ~1,800 m in the Jackson Hole

basin to >3,600 m in the mountains. The area was characterized by short, cool summers

and long winters with frequent snowstorms. Average monthly temperature minimums

and maximums ranged from -17.3°C and -3.4°C in January, to 5.3°C and 26.9°C in July.

Precipitation occurred mostly as snow, and mean maximum snow depths ranged from

100 cm at lower elevations to >245 cm at intermediate elevations of 2,000 – 2,400 m

(Grand Teton National Park 2015).

Plant communities included cottonwood (*Populus angustifolia*) riparian zones

interspersed by sagebrush (*Artemisia spp.)* uplands at lower elevations. At intermediate

elevations, aspen (*P. tremuloides*), Douglas-fir (*Pseudotsuga menziesii*), and lodgepole

pine (*Pinus contorta*) were the dominant species. Spruce (*Picea engelmannii*) and fir

(*Abies lasiocarpa*) were the primary tree species at higher elevations (Marston and

Anderson 1991, Knight 1996).

Primary prey species available to cougars included mule deer (*Odocoileus

hemionus*), elk (*Cervus elaphus*), white-tailed deer (*O. virginianus*), moose (*Alces alces*),

bighorn sheep (*Ovis canadensis*), and various small to medium sized mammal and avian

species. The study area also included all historically occurring carnivores: grizzly bears,

black bears, and gray wolves (*Canis lupus*), as well as coyotes and red foxes (*Vulpes

vulpes*), and possibly bobcats (*Lynx rufus*) and lynx (*Lynx canadensis*).

METHODS

Our research was part of a long-term cougar ecology study in northwestern

Wyoming that incorporated the capture and GPS-tracking of resident adult cougars. We

previously reviewed various methods to enumerate cougars in a defined area (Chapter 2).

We then determined an estimate of density for the core region of the study area,

delineated by the effective trapping area or "area divisor". Our method used GPS-

telemetry data to enumerate the proportional residency of cougars in the area divisor

(McLellan 1989, Cooley et al. 2009a) for the years 2011, 2012, and 2013 (defined

annually as Sept 1 – Aug 31). We also included detected-but-unmarked cougars (based

on remote video and photo detections) when residency could be confidently assigned, and

backlogged subsequently captured cougars to previous years based on age and sex

(Logan and Sweanor 2001). Density estimates were scaled to cougars per 100 km^2. The

mean of these density estimates constituted our reference estimate to which we compared

the noninvasive results.

We delineated the noninvasive survey areas to correspond approximately with the

area divisor from Chapter 2 (Fig. 3.2). These survey areas encompassed ~1,600 km^2, and,

as with the area divisor, were defined generally by the Gros Ventre and Buffalo Valley

drainages where the majority of cougar detection and trapping efforts occurred. Over the

history of the long-term cougar ecology study (2001 – 2013), 93% of cougar capture

locations (n = 154 cougars) and 80% of GPS telemetry locations (n = 47,563 locations)

occurred within this core area. We employed three types of noninvasive surveys: remote

camera surveys, winter tracking for genetic sampling, and genetic sampling using scat-

detection dogs. We limited our CMR analyses to relatively well known methods that

were readily accessible to wildlife managers.

Cost comparison.— We compared the resource requirements of each survey type

using the rate of animal detection as the unit of measure. We only included detections

used in final population estimates (i.e., genetic samples that were collected but did not

yield individual identity did not count in the cost analysis). We calculated cost-per-

detection in dollars, and effort-per-detection in person-days of labor. We estimated the

true costs of donated equipment and volunteer labor to the best of our knowledge,

referencing similar, commercially available equipment or median salaries for comparable

positions (Bureau of Labor Statistics 2015)

Detections of radio-collared cougars.— CMR analysis produced estimates of

detection probability for each survey; we also produced alternate estimates of detection

probabilities based on noninvasive detection of radio-collared individuals. We applied a

simple two-sample Lincoln Peterson estimator (Krebs 2001), using the Chapman

estimator for small samples (Chapman 1951). We used captured and radio-collared

animals as the first sample, and noninvasive survey detections as the second sample:

$$\hat{N} = \left(\frac{(n_1 + 1)(n_2 + 1)}{m_2 + 1} \right) - 1$$

where $\hat{N}$ is the abundance estimate, n_1 and n_2 are animals captured or detected in the two

sampling sessions, and m_2 is the number of radio-collared animals detected in the second

sample. We then solved for $\hat{p}$ using the formula:

$$p_i = \frac{C_i}{\hat{N}}$$

where *p* is the probability of detection, *C* is the number of animals detected, and *i* is the

sample occasion.

We also examined detection success using Poisson regression analysis to examine

the number of detections of radio-collared cougars as a function of density of detectors

per individual home range. Density of detector dd_i was defined for cameras as the number

of camera stations per km^2 of home range *i* (defined by 95% kernel density estimation;

see Chapter 2). For transect based surveys, we measured dd_i by kilometers surveyed per

km^2 of home range *i*. Home ranges were delineated annually by 95% KDE (see Chapter 2

for details on home range calculation).

Photographic Sampling

Field methods.— We established an array of remote cameras stations across the

core study area during the summer months of 2012 and 2013, using two types of camera

station design. The majority of sites (n = 43) used a blood-based non-reward lure; the

remaining sites (n = 10 in 2012; n = 12 in 2013) were set up using conventional camera

survey methods with cameras placed along high-use trails (e.g., Karanth 1995, Negrões et

al. 2010). For the blood-lure stations, we first divided the core study area (described

above) into 36 km^2 cells. This cell size was based on the low densities of the target

animal (Rovero et al. 2013), and chosen so an average home-range size of a female

cougar would overlap the spatial equivalent of four cells. This resulted in 43 contiguous

sampling cells covering 1,548 km^2, divided between the Gros Ventre (n = 21 sampling

cells) and Buffalo Valley (n = 22 sampling cells) drainages. One camera station was

setup for each cell. Camera stations were active from approximately June 15 to

September 15 for each year. We selected the exact locations of the camera stations within

each cell based on topographic or vegetative features typical of cougar habitat or travel

routes. These sites were typically characterized by ridgelines, drainage bottoms, or edge

habitat where cougars were either known (via telemetry or natural sign) or suspected to

travel (Fig. 3.2). Due to our choice of blood-based attractant (see below) and the potential

for human-bear conflict, we were restricted from placing camera stations near roads,

human development, or high-use trails where humans regularly traveled. We installed

two models of motion-activated cameras at each station. The first type was a non-

commercial model designed by Panthera (Panthera Inc., New York, NY), which used a

visual-light xenon flash for nighttime images. The second camera type was a

commercially available infrared model: either the Reconyx PC800 or Reconyx Silent

Image (Reconyx, Inc., Holmen, WI). All camera models used a passive infrared sensor

for motion-triggered activation. The Reconyx camera used infrared lighting at night,

which resulted in black and white images. The Panthera model always used visual light,

either from ambient daytime light or from the xenon flash, and thus produced color

images. The xenon flash was relatively slow to recharge, so the Panthera cameras

generally produced fewer night images than the Reconyx cameras. We fixed the cameras

to tree trunks approximately 50 to 80 cm off the ground and 10-15 m apart, with both

cameras aimed in a manner to capture two sides of an animal as it passed through the site.

We placed an 80 cm high wood post between the cameras marked at 10 cm increments to

help estimate animal height and aid in individual identification (Fig. 3.3). To increase

detection probability and number of photos per event, we used a non-reward lure

comprised of aged cattle blood. This type of attractant was chosen based the low success

rate of non-food based scent attractants reported by Long et al. (2003), Choate et al.

(2006), and Sawaya et al. (2011), and anecdotal evidence that cougars responded to blood-based attractants at grizzly bear trapping sites (D. Thompson, Wyoming Game and Fish Department, pers. comm.). The lure was suspended in an open container (a repurposed laundry detergent jug) between trees by rope at least 4 m above the ground, directly above the measurement post. Sodium citrate was mixed with the blood to prevent coagulating and thus retain odor (Haroldson and Anderson 1996). We also suspended a repurposed compact-disc to act as a visual attractor. We use the terms "lure" and "attractant" loosely, in that the blood mixture and the compact disc were used in order to provoke the curiosity of any cougar already passing through the area, as opposed to attracting cougars from large distances. We hoped this would in turn generate a maximum number of photos, based on the assumption that additional photos would increase our ability to individually identify cougars.

The second type of camera station (hereafter referred to as "trail camera stations") was setup at an additional 10 -12 sites. The trail camera stations were setup as a method to compare detection rates of our novel blood-lure technique with the conventional placement method used in other cougar camera trapping studies (e.g., Kelly et al. 2008, Negrões et al. 2010). These trail cameras used a single Panthera or Reconyx camera, fixed approximately 50 to 80 cm off the ground. A small amount of cologne-based lure comprised of "Calvin Klein Obsession for Men" (Calvin Klein Inc., New York City, NY) and synthetic civet musk or catnip oil (Grawe's Lures, Wahpeton, ND) was placed in front of the camera. Field crews visited stations at a minimum of every two weeks to download images and perform any needed site maintenance. We replenished the blood lure every 4 weeks, or as needed.

Density estimate.— Photographic captures of cougars at camera stations were cataloged as "events" and generally consisted of multiple, sequential images of the captured individual. Events were considered separate if >6 hours elapsed between photos of the same cougar. We identified and distinguished individual cougars in photographs based on artificial tags, physical features (i.e., kinked tails, pelage markings, facial features, or size), and spatial/temporal distance between detections. We used resulting capture data to run conventional closed capture models (Otis et al. 1978; see Karanth 1995, Kelly et al. 2008) and spatially explicit capture-recapture methods (SECR; Efford 2004, Royle and Nichols 2009) to calculate densities, both separately and together for the Buffalo Valley and the Gros Ventre drainages.

For the conventional closed model, we used program MARK (White 2008), implemented through the R package RMark (Laake and Rexstad 2008). Detections were organized into capture histories of 8 occasions. In order to calculate density estimates, we estimated the effective trapping area of the camera station array by buffering camera station locations by the average female home range radius (analogous to the commonly used MMDM metric; see Soisalo and Cavalcanti (2006); see Chapter 2). To calculate the buffer distance, we calculated female home ranges during the remote camera survey months (June – September) from all GPS-collar data spanning the history of the study. Home ranges were only calculated if the individual's seasonal home range was comprised of a minimum of 50 relocations, as recommended by Seaman et al. (1999), and incorporated a minimum of 100 days. Home ranges were defined by 95% kernel density estimation (KDE) using the plug-in bandwidth (Jones et al. 1996). We used the geometric radius of the average female seasonal home range, weighted by individual, to determine

the buffering distance. All spatial analyses were completed in the R programming environment (R Version 3.0, www.r-project.org, accessed 10 Oct 2013), using the adehabitat package (Calenge 2011) and the ks package (Duong 2014), as outlined by Walter and Fischer (2015). We also used the R packages maptools (Roger et al. 2014), rgeos (Bivand and Rundel 2011), and shapefiles (Stabler 2014) to construct trapping buffers. Visualization of processes were implemented in ArcMap 10.2 (Environmental Systems Resource Institute 2013).

To estimate density directly, we used a Bayesian inference model designed for mark-recapture studies (Royle et al. 2009) in the R package SPACECAP (Gopalaswamy et al. 2012*a*). SPACECAP is designed specifically for noninvasive surveys with a user-friendly platform with a graphical user interface. SPACECAP has been used to estimate density for other elusive felids using remote camera surveys, including leopards (*Panthera pardus fusca*; Thapa et al. 2014), Scottish wildcats (*Felis silvestris silvestris*; Kilshaw et al. 2014), and Amur tigers (*Panthera tigris altaica;* Hernandez-Blanco et al. 2013). SPACECAP employs Bayesian inference by Markov chain Monte Carlo (MCMC) methods, using the Metropolis algorithm (Gelman et al. 1996) to estimate parameters: notably density D, probability of detection at an individual's home range center λ_0, and a measure of an individual's home range size as probability of detection decreases towards zero σ. The model used by SPACECAP applies to binary observations *y(i,j,k)* for individual *i*, trap *j*, and sample occasion *k*. The model is a binary regression model in which *y(i,j,k) ~ Bernoulli(p(i,j,k))*, where p is the probability of detection; see Gopalaswamy et al. (2012a) and Royle et al. (2009) for more information on the modeling details. We input encounter histories, camera station locations, and a spatial

mask layer of potential home range centers representing the state-space S. Since spatially explicit models incorporate trap location, we ran the SPACECAP models using the additional trail camera detections despite the non-uniform trap spacing that would not have been suitable for conventional CMR models. The mask layer was a grid of points spaced evenly at 2,236 m, with each point representing a "pixel" of 5 km^2. SPACECAP produced an estimated density at each pixel. Pixel size was approximately 1/32nd of the target animal's home range, following protocols suggested by Gopalaswamy et al. (2012b). The state-space S extended 20 km around the camera station array, in order that it included all potentially existing cougar home ranges that could be detected at camera stations (see below for details on delineation of state-space). We extracted a canopy cover value to the mask layer, and assigned '1' to all points that had no canopy cover (defined as percent canopy cover <1%), effectively eliminating open water and open sage habitats from the array of potential home range centers. We ran models with and without a behavioral trap response. SPACECAP allows for two types of detections functions: half-normal and the negative-exponential. We used the default half-normal function (see below for details on detection function selection). We performed a minimum of 200,000 MCMC iterations with a burn-in period of 50,000, and a thinning rate of 1 for each model. Iterations and burn-in were increased if models did not perform adequately. Model convergence was evaluated using the Geweke diagnostic statistic (Geweke et al. 1997), with z-scores between -1.6 and 1.6 indicating reasonable model performance. Model fit was evaluated using the Bayesian P-value (Royle et al. 2011), with values close to 0 or 1 indicating poor model fit. Models were also evaluated with a measure of

effective MCMC sample size adjusted for auto-correlation (Martyn et al. 2015). All evaluators were calculated within the SPACECAP platform.

Selection of detection function and delineation of state-space.— To evaluate the appropriateness of SPACECAP's available detection functions, we plotted the density of cougar locations as a function of distance from home range center. We performed this using the R packages maptools (Bivand and Lewin-Koh 2014), rgeos (Bivand and Rundel 2011), raster (Mattiuzzi et al. 2015) and unmarked (Fiske and Chandler 2011). We first separated all available GPS locations by individual and year (as defined by remote camera survey months June 15 to September 15). Remaining location sets were discarded if the number of locations was <50 and the time range was <30 days. We assumed an unprojected Cartesian coordinate system and re-referenced each location set around its geometric center defined as x = 0 and y = 0. We combined all re-referenced location sets and extracted distance-to-center for each GPS location (Fig. 3.4). The resulting density plot suggested that the half-normal detection was more appropriate than the negative exponential (Fig. 3.5). The density plot also suggested a low likelihood of encountering a cougar further than 20 km from its home range center, and we delineated the state-space *S* accordingly.

Reliability of identifying individual cougars in photographs.— Unlike certain other large felids, cougars do not exhibit unique pelage markings and there is some debate whether cougars are appropriate for photographic CMR methods (Kelly et al. 2008, Oliveira-Santos et al. 2010). Reliably identifying individual cougars in photo-captures was an important component of our measure of feasibility; however, our results were likely biased in this regard since at least a portion of the target population was

visually identifiable due to GPS-collars and ear tags. To examine the issue of

identifiability in an uncollared population, we tested the agreement to which independent

investigators distinguished individual cougars in our photographic captures without the

aid of artificial marks. We designed a photo database and electronic form in Microsoft

Access (Microsoft Corporation, Redmond, WA) that allowed independent investigator

participants to sort through photographic capture events and assign individual identity.

We selected a subsample of events from the 2013 survey, which included events from

both camera station designs. To create the subsample, we discarded events that had radio-

collared cougars or very poor photo quality. The Access form displayed events in pairs,

with an event displayed on each side of the computer monitor. The form allowed

investigators to scan through events on each side independently, as well as to sort through

the multiple images associated with each event (Fig. 3.6). For each event pairing, the

investigator was prompted to classify the pair as being from the same individual cougar,

or two different cougars. Also included were spatial and temporal data for each event,

with the spatial and temporal separation between the paired events automatically

calculated and displayed (e.g., "events A and B were 10.5 km and 51.3 hours apart"). We

considered this information "fair game", because we believed these data would logically

be included in a similar real-world research scenario, and should therefore not be ignored.

All combinations of event pairings were evaluated. Note that this method can result in a

large sample if a sufficient number of events are compared:

$$C = \frac{n!}{2!(n-2)!}$$

where C is the number of combinations to evaluate, and n is the number of events.

We distributed the Access database to independent participants. Only wildlife researchers with considerable experience with cougars were considered for participation. A segment of the participants included biologists who performed cougar research in the study area and were familiar with the individual cougars in the photo database. Participants were not privy to our own identification assessment, capture history, or CMR results. We used the R package irr (Gamer et al. 2014) to calculate agreement level. We used simple percent agreement, similar to the metric that Kelly et al. (2008) used, as well as Fleiss's kappa (Fleiss 1971). We included Fleiss's kappa as it was a more statistically rigorous metric of agreement between assessors than simple percent agreement (Gwet 2010). A kappa of 1 indicated perfect agreement, and 0 indicated a level of agreement consistent with completely random assessments by participants. We stress the above analysis was not intended to confirm whether participants were correct in their assessment of individual cougar identity; our goal was to test for disagreement, thereby suggesting photographic CMR results may not be suitable for cougars due to an inability to reliably identify individuals. We also examined our hypothesis that a greater number of photos per detection would increase our ability to identify individuals. We used Poisson regression to examine the count of participants in agreement for each event pairing as a function of the total number of photos in the event matching.

Genetic Sampling

Field methods for winter tracking transects.— We delineated 226 km of transects across the study area, split between the Buffalo Valley (54%) and the Gros Ventre (46%) drainages. Transects were performed during the winters of 2011-2012 and 2012-2013.

Transects were performed by truck (21%), snowmobile (60%), or on snowshoes/skis (19%). Transects were selected based on topographic features characteristic of cougar habitat or travel routes, and ease of access for trackers (Fig. 3.2). Transects were the same routes that were used for detecting and capturing study animals for radio-collaring (see Chapter 2). Snowshoe/ski transects were typically characterized by ridgelines, drainage bottoms, or edge habitat where cougars were either known (via telemetry) or suspected to use. Truck and snowmobile transects were based additionally on accessibility and ability of researchers to quickly transect large amounts of terrain. We attempted to schedule transects at least 24 hours after a snowfall, but not later than 72 hours. This schedule was chosen in order to maximize the sampling window of time when cougars were potentially traveling, without compromising an observer's ability to detect tracks due to being obscured by other animal tracks or wind/weather. When cougar tracks were detected, researchers backtracked (or forward tracked if backtracking was not feasible) until a genetic sample (either hair or scat) could be collected. Hair was collected at bedsites, vegetative snags, or within tracks. We followed general collection recommendations outlined by Schwartz and Monfort (2008). To avoid genetic cross-contamination, each sample was collected using fresh latex gloves and sterilized thumb forceps. Hair samples were stored in small paper envelopes, which were then placed in 50 mL plastic FALCON® tubes, each with approximately 20 mL of silica gel. Scat samples were collected in unused "ziplock" type bags with silica gel (silica gel was added at approximately 2 times the estimated weight of the scat sample). All samples were stored out of direct sunlight at room temperature before being transferred to a laboratory for genetic analysis.

Field methods for scat detection dogs.— We used a single handler/dog team (Find It Detection Dogs, Walden, CO) to survey 20 transects across the core study area, divided between the Buffalo Valley (n = 8) and Gros Ventre (n = 12) drainages. Transects were run in late summer of 2013 and 2014. Transects were chosen based on terrain features characteristic of cougar habitat (similar to winter track transect selection described below), as well as accessibility. Detection dogs were restricted from entering Grand Teton National Park, which limited our ability to run transects in certain areas in the western portion of the area divisor (see Chapter 2). The initial transect delineations were course and approximate; these course transect lengths totaled 140 km (55 km in the Buffalo Valley drainage; 85 km in the Gros Ventre drainage), with an average transect length of 7.0 km. The dog handler team followed these transects using a handheld GPS device, but was given flexibility to choose exact routes while in the field (Fig. 3.2). Dogs were primarily trained using cougar scat collected from other regions, with a "refresher" training using locally collected scat performed immediately prior to our survey. Detection dogs were trained to walk off leash while searching for cougar scat, staying within approximately 25 m of the handler. When scat was detected, dogs were trained to signal the handler without touching the scat, allowing the handler to approach and verify. Unless scat was unmistakably a non-target species, all scat indicated by the dog was assumed to be cougar. Scat was sampled using sterile thumb forceps to collect approximately 0.5 mL of fecal material from the outside of the scat (Stenglein et al. 2010). The sample was placed in a 2 mL screw-top plastic tube containing 1.5 mL of DET buffer (Davidson et al. 2014), and agitated to saturate the sample. We stored

samples at room temperature and out of direct sunlight until transferring them to a
genetics laboratory.

   DNA extraction and analysis.— Analysis of genetic samples was split between
two labs depending on the year of collection. Hair samples and scat samples collected in
2013 were analyzed at the Sackler Institute for Comparative Genomics (Center for
Conservation Genetics, American Museum of Natural History, New York) as follows:
genomic DNA from scat samples was extracted using the QIAmp DNA Stool Mini Kit
(QIAGEN, Valencia, California) with modifications as outlined in Caragiulo et al.
(2013). Genomic DNA from hair was extracted with the DNeasy Blood and Tissue Kit
(QIAGEN, Valencia, California), using the manufacturer's recommended protocols. All
samples were initially tested for species identification as described in Caragiulo et al.
(2014), and screened out of further analysis if not identified as cougar. We used 21
cougar specific microsatellite primers which were developed by Kurushima et al. (2006).
Polymerase chain reactions (PCR) were carried out in 12.5 μL multiplex reactions
containing 2 to 5 μL of extracted DNA, 0.65 μL of each forward and reverse 10 μM
primer, and 5 μL Qiagen Mutliplex PCR Master Mix, 1 μL Q-solution, and the remaining
volume was RNAse-Free water (QIAGEN, Valencia, California, USA). We grouped
primers into four multiplex reactions based on fluorescent tag and amplicon size.
Thermocycling conditions were the same for all primers and multiplexes: initial
denaturation for 15 minutes at 95 °C, 13 cycles of denaturation at 94 °C for 30 seconds,
annealing with touchdown at 62.4 -0.3 °C for 90 seconds, and elongation at 72 °C for 60
seconds, followed by 32 cycles of denaturation at 94 °C for 30 seconds, annealing at 60
°C for 90 seconds, and elongation at 72 °C for 60 seconds, followed by a final elongation

at 60 °C for 30 minutes. We prepared samples for analysis by mixing 1 µL of PCR

product with 9 µL of an 8.82 µL: 0.18 µL mixture of Hi-Di formamide: GeneScan 500

LIZ size standard (Applied Biosystems, Carlsbad, California, USA). Samples were heat-

shocked for 3 minutes at 95 °C and genotypes were analyzed using an ABI 3730xl DNA

analyzer (Applied Biosystems, Carlsbad, California, USA). We scored genotypes with

GeneMapper v. 4.0 software (Applied Biosystems, Carlsbad, California, USA) and

individually verified them by visual inspection. To identify possible allelic dropout, we

performed all microsatellite amplifications at least four times using the multi-tube

approach (Taberlet et al. 1996). Allelic dropout and PCR success was quantified per

locus, based upon sample type (scat vs. blood/tissue vs. historic specimen) using the

program GIMLET (Valière 2002) and manual inspection. Consensus genotypes were

defined for each sample by comparing results from a consensus genotype inference

method using program GIMLET (Valière 2002), as well as manual inspection. Samples

that did not produce reliable consensus genotypes for at least 10 loci were excluded from

further analyses.

The 2014 scat survey samples were analyzed at the Laboratory for Ecological,

Evolutionary and Conservation Genetics (University of Idaho, Moscow, Idaho) using

protocols outlined by Davidson et al. (2014). Protocols were similar to those outlined

above, apart from the main difference of using 10 microsatellite loci from the domestic

cat (*Felis catus*) for individual identification (Menotti-Raymond et al. 1999, 2005), as

opposed to the Kurushima et al. (2006) microsatellites.

Statistical Analysis.— We analyzed consensus genotypes in the R package

allelematch (Galpern 2015) to determine the individual identities of cougars represented

in the samples. Noninvasively collected genetic data can be especially prone to genotyping errors and missing data (Waits and Paetkau 2005); allelematch was written specifically for analyzing this type of data for the purpose of identifying unique individuals in a population of unknown size (Galpern et al. 2012). Allelematch accommodates these imperfect datasets by calculating a pairwise similarity score between genotypes, and then identifying an optimal parameter of acceptance for imperfect allele matches (or a "mismatch tolerance"; see Fig. 3.9). Allelematch then produces an estimate of the number of unique genotypes represented in the sample. See Galpern et al. (2012) for details on the framework and application of the software.

Density estimation.— The resulting capture histories were comprised of one sampling occasion. Consequently, we were limited to single-occasion approaches such as the abundance estimator CAPWIRE (Miller et al. 2005) or certain SECR models. CAPWIRE was designed specifically for genetic sampling under the concept that this type of sampling is often "approximately done with replacement" (Miller et al. 2005), and usually performed on a single sampling occasion. CAPWIRE may be ideal for genetic sampling techniques such as ours, in which 1) there is only one sample occasion, 2) sampling is completely passive, and modeling for trap response behavior is not applicable, and 3) the sampled population is relatively small. Small population size is significant in that detections may be relatively rare, and therefore more informatively valuable. CAPWIRE retains all capture data, whereas traditional CMR techniques often must pool captures of an individual into a finite number of occasions, potentially squandering information. We note that Bromaghin (2007) critiqued CAPWIRE for utilizing a mathematically invalid likelihood function. However, this may be a minor

issue, as repairing the likelihood function does not alter CAPWIRE's abundance estimation (Bromaghin 2007). Furthermore, a genetic mark-recapture study by Davidson et al. (2014) used CAPWIRE to produce abundance estimates of cougars that were comparable to more traditional CMR methods. We ran CAPWIRE as implemented in the R package capwire (Pennell et al. 2013) using two models: the "equal catchability model" (ECM) and the "two innate rates model" (TIRM), and evaluated them using a likelihood-ratio test. The ECM and TIRM are analogous to homogenous and heterogeneous probabilities of detection in the traditional CMR framework. We calculated 95% confidence intervals for the model results using a parametric bootstrap, as implemented in the CAPWIRE package. To convert CAPWIRE abundance estimates into density, we delineated an effective trapping area around the sampling transects. The effective trapping area for the winter tracking transects was identical to the area divisor (Chapter 2). The effective trapping area for the detection dog survey was calculated identically to the method for the remote camera survey, using the geographic centers of scat transects as the buffering points.

We used the R package secr (Efford 2015) to estimate population density directly. The secr package allowed for single occasion detection histories, as well as the use of transect lines as the detector, whereas SPACECAP was limited to point-based trap arrays. Package secr uses spatially explicit capture-recapture models analogous to SPACECAP, but instead of a Bayesian framework, secr implements maximum likelihood to determine the spatial detection model. Parameters estimated were analogous to SPACECAP, but secr uses the notation g_0 instead of λ_0. We inputted the trap transects as a single-occasion detection history, and a spatial mask layer of potential home range center points, spaced

at 5 km, analogous to the SPACECAP methods outlined above. We ran the null secr

models, as well as models that incorporated a spatially varied density estimate that

attempted to fit a gradient in cougar density along latitude or longitude (as was observed

between the Buffalo Valley and Gros Ventre sampling areas). We also ran group models

based on sex class, when that information was available. Behavioral models were not

applicable due to our use of a single occasion. Models were evaluated using the corrected

Akaike's Information Criterion (AIC$_c$; Burnham and Anderson 2002).

     Demographic correction factor.— Since genetic surveys are not able to

distinguish age classes, our genetic surveys essentially used a different sampling frame

than that for the photographic and reference methods. To address this issue in the context

of comparing photographic and genetic sampling results, we estimated a correction factor

based on likely number of dependent juveniles in the population. Based on average male

to female ratios and number of dependent young observed in several cougar populations

(Quigley and Hornocker 2010), we used a male : female : juvenile age class ratio of 1.0 :

2.5 : 2.5 to estimate that the total population (as estimated by the genetic sampling

efforts) was 1.7 times greater than the adult population (as estimated by photographic and

reference methods).

RESULTS

Photographic Sampling

     Blood lure detections.— We were logistically constrained by the size of and

number of stations in the camera trap array, and camera stations were not all active for

the exact same time period or number of days. For the respective years, the average

number of days sampled per blood-lure camera station were 73.5 (± 3.9 SD) and 79.4 (±

8.1 SD), and the total number of sampling days were 3,160 and 3,414. The mean total

length of the sampling windows (calculated from the first camera activation to last

deactivation) was 100.0 days (± 5.0 SD, n = 2). We recorded 17 and 16 cougar photo-

events in 2012 and 2013, respectively (Table 3.1). The average detection rate for the

blood-lure stations was 0.15 detections per 30 sampling days. There was an average of

17.03 (± 9.67 SD) photos per detection event. Based on physical characteristics

(including artificial tags) and spatial/temporal distances between detections, we identified

5 and 7 unique individuals, respectively. Based on detections per sampling day,

detections were significantly more likely to occur in the Gros Ventre (n = 25) than the

Buffalo Valley (n = 7; two sample test for equality of proportions: $\chi^2 = 7.74$, df = 1, $P <$

0.01). The mean number of recaptures per cougar was 3.0 (± 2.3 SD) for 2012, and 2.3 (±

1.1 SD) for 2013.

Trail cameras.— The trail camera arrays recorded 6 and 9 additional cougar

detection events for 2012 and 2013, respectively (Table 3.1). For the respective years, the

average number of days sampled per camera station were 34.9 (± 9.7 SD) and 52.6 (± 9.2

SD), and the total number of sampling days were 349 and 579. The average detection rate

was 0.52 detections per 30 days, significantly higher than that of the blood cameras (two

sample test for equality of proportions: $\chi^2 = 13.90$, df = 1, $P < 0.001$). There was an

average of 5.6 (± 6.3 SD) photos per detection event, significantly lower than that for the

blood cameras (Welch two-sample test; $P < 0.001$).

Conventional CMR.— Due to low numbers of detections and unique individuals,

we were limited to relatively simple closed-population CMR models. We applied the null

model (M_0), behavioral model (M_b), and the heterogeneity model (M_h). Likely due to the low numbers of detections and of unique individuals, the models essentially produced the minimum abundances: all models for 2012 produced abundance estimates of 5 cougars, and all models for 2013 produced abundance estimates of 7 cougars. Confidence intervals were close to zero for all models except for the behavioral model in 2012; this model found a relatively strong "trap happy" response with low initial capture probability, thus increasing the abundance estimate. However, the behavioral model for 2013 indicated a "trap shyness" response (Table 3.2). The average female home range size during camera trapping months was 190.0 km^2 ($\pm$ 109.3 SD, n = 15). The effective trapping area was thus calculated with a buffering distance equal to the radius of this area: 7,769 m. This resulted in effective trapping area sizes of 1,215 km^2, 1,474 km^2, and 2,333 km^2 for the Buffalo Valley, Gros Ventre, and combined areas, respectively. The abundance estimates calculated in program MARK converted to density estimates of 0.21 cougars per 100 km^2 for 2012 and 0.30 cougars per 100 km^2 for 2013. We also note here that the detector generated ½ MMDM (based on our assessment of individual identity) was 4,825 m in 2012 and 2,519 m in 2013. The ½ MMDM metric was significantly lower than the telemetry derived buffer amount, consistent with findings for jaguars by Soisalo and Cavalcanti (2006). Due to poor model performance, we limited the density estimate to the combined area and did not attempt to subdivide abundance estimates for the Buffalo Valley or Gros Ventre areas.

Spatially explicit model.— Based on the Geweke diagnostic, models that incorporated a behavioral response performed poorly and were discarded. For behaviorally null models, SPACECAP produced posterior mean densities of 0.36 (95%

HPD = 0.18 – 0.64) and 0.84 (95% HPD = 0.40 – 1.40) cougars per 100 km^2 for 2012 and 2013, respectively (Table 3.3). Models restricted to the Gros Ventre were not consistent in performance, and models restricted to the Buffalo Valley were not run due to low numbers of detections. Density estimates were generally in agreement with home range centers (Fig. 3.7) as calculated in SPACECAP.

Detections of radio-tagged cougars.— In the 2012 season, 7 of the 23 total photo detections (29.2%) were detections of radio-collared cougars. In 2013, 5 of the 25 total photo detections (20.0%) were radio-collared. There were 8 radio-collared individuals present on the remote camera array in 2012. Based on our assessment of individual identity, 5 out of the 8 individuals photographed were not collared (62.5%). There were 7 radio-collared individuals on the remote camera array in 2013. Of the 12 photo-detected individuals, 8 were uncollared (66.7%). The two-sample Lincoln-Petersen estimator produced abundance estimates of 19.25 (95%CI = 9.39 – 29.11), with photo detection probability (p_2) of 0.42 (given p_1 of 0.42), and 19.80 (95%CI = 11.80 – 27.80), with photo detection probability of 0.61 (given p_1 of 0.35), for the respective years.

We used a generalized linear mixed-effect model (GLMM) with a Poisson distribution to examine if the density of camera stations within an individual's home range was related to the count of that individual's detections. We used the GLMM framework in order to add individual ID as a random effect and account for the variability between and autocorrelation within the individuals' location sets. We found a negative but insignificant correlation between number of detections and detectors per km^2 (β = -15.31, SE = 14.2, P = 0.28).

Reliability of identifying individual cougars in photographs.— We subsampled 15 events (resulting in 105 combinations of event pairs) from the 2013 remote camera survey to distribute to independent participants. We collected results from 7 participants. Each set of results included the list of 105 event pair combinations with participants' scoring of each pairing as "same cougar" or "different cougars". The number of unique individuals identified by participants ranged from 4 to 13. The mean number of identified individuals was 9 ($\pm$ 3.5 SD). Using the R package irr (Gamer et al. 2014), we found a 46.7% simple agreement between participants. Using Fleiss's kappa, we found a kappa value of 0.183 ($P = 0$). Although interpretation of kappa values is somewhat subjective (Gwet 2010), this value would usually be categorized as "slight" (Landis and Koch 1977) or "poor" agreement (Fleiss et al. 1981). Of the event pairings with full participant agreement, 100% were for differentiated individuals; there were no cases of full agreement when ascribing the paired events to the same individual. Out of the 105 event pairings, there were only 6 with >50% of participants ascribing them as "same". The mean distance between pairings with >50% of participants differentiating individuals was 18.1 km ($\pm$ 8.4 km SD, n = 99), and the mean distance between pairings with >50% of participants ascribing "same" status was 1.3 km ($\pm$ 3.1 km SD, n = 6). Of the 6 pairings with >50% "same" agreement, 4 were from event pairs occurring at the same camera station. Our simple agreement level of 46.7% was much lower than a similarly derived agreement level of 79.3% reported by Kelly et al. (2008). Of note, Kelly at al. (2008) used approximately three times as many detection events in their survey, despite a similar average number of identified individual cougars. Interestingly, we used 7 independent investigators, and Kelly et al. (2008) used 3 independent teams. This is notable because

we found that percent agreement decreased as the number of investigators increased: we reran our calculations for percent agreement using all possible combinations and subsets of the participant pool. The mean percent agreement for any subset of three investigators increased to 71.4% (± 13.5 SD) and ranged from 54.3% - 91.4% (Fig. 3.8).

To examine our hypothesis that a greater number of photos per event would aid in identification, we performed a generalized linear model with a Poisson distribution to examine the level of agreement for an event matching as a function of the number of photos used in the matching. We found no significant correlation (β = -0.009, SE = 0.008, P = 0.24). We also used a spatial-temporal measure of the minimum speed required for an individual cougar to be present at both events in a matching. We used the natural log transformation to normalize the value and found a significant negative correlation (β = - 0.21, SE = 0.03, P < 0.001) between higher minimum speed and count of "same" designations indicating that distance and time were likely important in participant's assessments, although it is uncertain if participants made decisions mainly based on spatial-temporal data, or if participant's decisions were correct, and supported by the spatial-temporal data.

Genetic Sampling

Winter tracking transects.— We surveyed 454 km of transects in the 2012 season, and 824 km in the 2013 season, totaling 1,276 km. The mean survey length was 102.0 days (± 17.0 SD, n = 2). The mean sampling window was 2.21 days of cougar travel time after snowfall per transect (± 1.04 SD). Between 1 and 8 observers participated in transects per snowfall event (n = 13, $\bar{x}$ = 3.6 ± 1.8 SD). We encountered 11 and 8 suspected cougar tracks for the two seasons, respectively. Over the course of the study,

tracks were encountered on average once per 67.26 km transected, and once per 0.68

days of sampling. Based on sampling effort, tracks were more likely to be encountered in

the Gros Ventre than the Buffalo Valley area (n = 5 in Buffalo Valley; n = 14 in Gros

Ventre; two sample test for equality of proportions: χ^2 = 4.71, df = 1, P < 0.05). We

collected usable hair samples from 9 of these encounters. Using mitochondrial analysis, 6

samples were identified as cougar hair. The other three were identified as Canid (n = 2)

or "unknown species" (n = 1). Only 2 of the samples were amplified to the individual

level, negating any subsequent mark-recapture analysis.

Scat detection dogs.— We completed 20 transects across the study area both in

2013 and 2014. The mean survey length was 26.0 days (±1.4 SD, n = 2), although, due to

the uncertainty of scat DNA degradation, this should not be interpreted as the sampling

window. Based on handheld-GPS data, handlers transected approximately 199 km per

year (76.5 km in the Buffalo Valley, 106.3 km in the Gros Ventre). The mean transect

length was 9,928 m (± 1,633.7 SD). A total of 219 scat samples were collected: 129 in

2013 and 90 in 2014. The mean number of scats collected per transect was 5.4 (± 5.2

SD), with 3.4 (± 2.1 SD) in the Buffalo Valley and 6.8 (± 6.2 SD) in the Gros Ventre. Of

these, 78.1% were determined to be cougar scat based on mDNA analysis. The remaining

scat samples were either non-target species or were unable to be verified due to poor

quality of sample (86.4% success rate for field detection when excluding those samples

that failed to yield a species identification). Non-target species were generally identified

as canid (red fox, coyote, grey wolf, or unknown canid). Two samples were identified as

ursid, one as cervid, and 15 samples were identified as unknown, non-target species.

After discarding non-target scats via mDNA analysis, the number of cougar scats

collected for each year differed by only 3.6% (n = 87 in 2013; n = 84 in 2014). This may

have indicated an improvement in detection ability between the two years: of the samples

that provided an mDNA-based species identification, 29.9% were non-target in 2013, and

1.2% were non-target in 2014. However, since two different labs and lab analyses were

used in the two years, this comparison is not necessarily appropriate. Based on scats

detected per length of transect, there were significantly more cougar scats detected in the

Gros Ventre than the Buffalo Valley (n = 40 in Buffalo Valley; n = 131 in Gros Ventre;

two sample test for equality of proportions: χ^2 = 17.223, df = 1, P < 0.001). Of these

verified cougar scats, 83 were genotyped (48.5% success rate for microsatellite analysis

of confirmed cougar scat) and analyzed with the R package allelematch. In 2013,

allelematch determined an optimum mismatch tolerance parameter of 6 (Fig. 3.9). Using

this parameter, allelematch identified 28 unique genotypes within 50 of the genotyped

scats. Two genotypes were discarded due to missing alleles which created high ambiguity

of identity. Of the 28 unique genotypes, 22 were in the Gros Ventre (78.6%), 5 were in

the Buffalo Valley (17.9%), and 1 was detected in both areas (3.6%). In 2014,

allelematch determined an optimum mismatch tolerance parameter of 4, and identified 17

unique genotypes within the 32 genotyped scats. Of the 17 unique genotypes, 9 were in

the Gros Ventre (52.9%) and 8 were in the Buffalo Valley (47.1%). The relatively similar

number of individuals detected between the Gros Ventre and Buffalo Valley in 2014 was

surprising. However, this was likely due to the uneven PCR success rate between the two

areas: the Gros Ventre samples were 28.1% successful in individual genetic

identification, and Buffalo Valley samples were 50.0% successful. As a comparison,

these values in 2013 were 42.3% and 32.0%, respectively.

CAPWIRE models.— The CAPWIRE equal catchability model (ECM) produced a maximum likelihood abundance estimate of 38 (95% CI = 29 – 50) in 2013, and 27 (95% CI = 19 – 38) in 2014. The two-innate rates model (TIRM) produced abundance estimate of 55 (95% CI = 42 – 89) in 2013 and 48 (95% 34 - 98) in 2014. The model fit comparison tests produced high values for the likelihood ratio: in 2013 the likelihood ratio was 12.94 ($P < 0.05$), and in 2014 the likelihood ratio was 13.98 ($P = 0$), strongly suggesting that we could reject the null equal catchability model. In order to calculate density, we buffered transects from their geographic centers by 7,769 m (similarly to the remote cameras) to delineate the effective trapping areas. The Buffalo Valley, Gros Ventre, and combined areas were 648 km^2, 816 km^2, and 1,401 km^2, respectively. The resulting TIRM density estimates for the Buffalo Valley, Gros Ventre, and combined areas, respectively, were 2.78, 5.51, and 3.93 cougars per 100 km^2 in 2013, and 2.78, 4.04, and 3.43 cougars per 100 km^2 in 2014 (Table 3.4).

Spatially explicit models.— Based on AIC$_c$ ranking, the top SECR model in 2013 incorporated a density gradient along north-south and east-west lines, reflecting the different cougar densities in the Buffalo Valley and Gros Ventre areas (Table 3.5). For the Gros Ventre area, the top 2013 model was the null model. Due to lack of re-detections in the Buffalo Valley in 2013, we could not run any SECR models. In 2014, the top model for the Gros Ventre, Buffalo Valley, and combined areas was the null model (Table 3.6). In 2014 we also ran group models incorporating the genetically determined sex of the individuals. Genetic classification of sex was 10.4% unsuccessful, and detections with unknown sex had to be excluded from the group models. Due to small sample size, we discarded models with greater than 6 parameters; these models

performed poorly, and failed to produce AIC_c scores. The null models were the highest

ranked for the Gros Ventre and Buffalo Valley. For the combined areas, there was

approximately equal evidence for a group effect for g_0 (Table 3.7) indicating a higher

probability of detection for males, which is possible given that transect routes generally

followed ridgelines and travel routes where cougar scrape sites were common, and where

males may be more likely to deposit scat (Harmsen et al. 2010). We used model

averaging, as implemented in Package secr, to determine results for the combined area

(Table 3.8).

 Detections of radio-tagged cougars.— Due to differing lab protocols, we were

only able to cross-reference genetic samples collected directly from radio-collared

animals to the scat data collected in 2013. Of the 28 unique genotypes detected in the scat

samples from 2013, 4 were identified as previously captured and radio-collared

individuals. We determined there were 7 radio-collared individuals on the transect array

during 2013. We used a generalized linear mixed-effect model (GLMM) with a Poisson

distribution to examine if the density of scat detection transects within an individual's

home range was related to the number of times an individual was detected. We found a

positive but nonsignificant correlation between the number of detections and detectors

per km^2 ($\beta = 0.531$, SE $= 0.486$, $P = 0.275$).

Comparisons with Reference Estimates

 Expressed as a density estimate of cougars per 100 km^2, the mean of the

telemetry-derived density estimates for 2011 – 2013 was 1.07 in the Gros Ventre area (n

$= 3, \pm 0.15$ SD), 0.26 in the Buffalo Valley area (n = 3, SD = 0.07), and 0.82 for the

combined areas (n = 3, ± 0.10 SD) (Chapter 2). After adjusting to include the non-adult

residents that were likely in the population and detected in genetic sampling, the respective estimates were 1.82 (n = 3, ± 0.26 SD), 0.45 (n = 3, ± 0.12 SD), and 1.40 (n = 3, ± 0.16 SD). Density estimates from the noninvasive techniques varied spatially and annually (Table 3.9) with some in agreement to density estimates derived from the radio-collared sample of cougars (Fig. 3.10).

Our survey of independent investigators (see above) suggested that our photographic detection histories were likely unreliable, due to inability to accurately assign individual identification to cougars. For the moment we ignore this caveat, and report the following comparisons under the assumption that our photographic tagging process was accurate. Our conventional CMR (MARK) based analysis of photographic captures produced results that were on average 68.3% lower than the reference estimate. Since our reference estimate included a small number of uncollared individuals for whom we were not 100% certain of residency (see Chapter 2), it was not categorically a minimum count. Nonetheless, it remains unlikely that the true density was lower than this reference estimate. The SECR-based models using SPACECAP produced more plausible results, likely in part due to our inclusion of trail camera photos in the encounter histories which increased the number of detections by an average of 45.8% per year. Promisingly, the 2013 SPACECAP estimate (D = 1.1) was less than 2% different than the reference estimate (D = 1.07). However, SPACECAP results had relatively high variance between the two seasons (relative SD = 56.5%), and, despite the greater number of detections, there were still issues of low sample size. The number of independent MCMC chains modeled (a measure of effective sample size for each model parameter) were especially problematic for σ, likely due to the low number of multi-detector recaptures (see Table

3.3). Both remote camera surveys coincided with telemetry-based surveys (2012 and 2013). We overlaid concurring annual home ranges of GPS-collared cougars on the pixel density maps produced by SPACECAP (Fig. 3.7). Home ranges were delineated by kernel density estimation, using the plugin bandwidth (Chapter 2).

Due to poor collection rates and genotyping success, the winter tracking transects did not provide density estimates with which to compare to the reference estimate. For the genetic sampling using scat detection dog surveys, the SECR-based density estimates were 71.8% greater than the adjusted telemetry-based reference estimates. The CAPWIRE estimates were on average 162.9% greater. Of note, the CAPWIRE equal catchability model (ECM) produced estimates closer to those for the reference estimate. However, based on the likelihood ratio test, the two innate rates model (TIRM) was more likely. Indeed, the TIRM was also more biologically appropriate given the high probability that a subset of the population included dependent young with lower innate capture probabilities than adults. Conversely, the AIC_c scores as implemented in Package secr favored models that generally did not incorporate heterogeneous mixtures for any of the parameters (including capture probability), despite their biological plausibility.

Cost Comparison

Estimated costs for the noninvasive surveys varied widely (Table 3.10). Some costs had to be estimated due to our use of volunteer support, as well as equipment and lab analysis that was donated in-kind. Outside of fuel costs, we did not account for the costs of trucks, snowmobiles, or ATVs. Remote camera surveys and winter tracking transects were intensive in their vehicle requirements, generally needing multiple vehicles per day of effort. The detection dog team provided its own vehicle, which was

accounted for in the personnel cost. Also, we did not include time spent on data analysis; this is especially relevant to the remote camera surveys, for which considerable time was spent in the process of sorting photographs and individually identifying cougars.

As a point of interest, we also report an estimate of the telemetry based "cost per enumeration" (i.e., the physical capture, tagging and radio-collaring as described in Chapter 2). We added the amount spent on GPS collars, collar refurbishments, houndsman services, immobilization drugs, and capture equipment over the course of 18 captures (including recaptures for collar replacement) that occurred between 2011 and 2014. Divided between the 14 individuals tracked, this results in a cost per enumeration of $5,426. This amount does not include general overhead costs: since captures were performed as part of a large scale ecological study on cougars, we were unable to parse out the costs of personnel, vehicles, and gas used in capture efforts from those of the wider study, and this estimate should be considered a minimum. Furthermore, we stress that it is not necessarily appropriate to directly compare this amount to the cost per noninvasive detection described above.

DISCUSSION

Using our techniques and analyses, scat detection dogs were more efficient in generating detections of cougars than the other methods attempted. Based on our survey of independent investigators' agreement in identifying photo-captured cougars, scat detection dogs were also less prone to error. More research is needed to determine the effective sampling window of scat detection dogs, although, based on work by Lonsinger et al. (2015), the sampling window of our scat detection dog survey was unlikely greater

than that for the remote camera or winter tracking surveys. Based on the detections of collared individuals, the scat detection surveys were slightly more effective: the 2013 scat survey detected 4 out of the 7 collared individuals (57.1%) present on the trapping array. The remote cameras detected 3 out of 8 and 4 out of 7 for the respective years, for an average of 47.3%. Based on our regression analyses of detectors per individual home range, there was no significant relationship between the density of detectors (either remote camera or scat transect) in a home range and the probability of being detected. Possibly a more important factor for remote camera detections was the placement of camera stations as opposed to the number of stations (i.e., one well-placed camera along a travel route will outperform several camera stations placed in less traveled locations). This highlights the difficulties in point-trapping animals with large home ranges over heterogeneous terrain, for which the detection probability of individual traps will vary significantly. Our analysis of density of scat transects per home range also failed to show any significant association. However, the relationship was nonetheless positive, and the model was limited to a single season.

For both remote cameras and scat detection dogs, SECR–based analyses produced results more comparable to the reference estimate than non-SECR analyses. Presumably, SECR has better applicability to cougar populations because conventional CMR assumptions for cougars are particularly problematic, such as closure issues related to large home ranges extending beyond the edge of the trapping array. Large home ranges were also problematic for determining the trapping buffer for non-SECR methods. We used GPS telemetry data to determine the buffer length, whereas a naively determined buffer width would have used the ½ MMDM metric determined from trap locations. The

mean remote camera generated estimate was 52.7% less than the telemetry-derived home range radius; the estimate from the scat detection dog transects was 51.5% less.

Alternative field techniques for the surveys may have changed their resulting estimates to some degree. For example, problems for the winter tracking transects included both very low detection rates and low success in genotyping samples. Sampling rate issues were possibly due to having too strict of protocols for the timing of transects: weather conditions were rarely ideal, and often did not provide a distinct sampling window with 2-3 days of calm tracking conditions. In addition, winter travel restrictions were in effect in certain parts of the study area, thereby limiting access to backtrack and collect hair samples. A subset of samples was identified as a canid species using mDNA analysis. All investigators were well trained in identifying cougar tracks; therefore this was most likely due to cross contamination at bedsites or in snow tracks as opposed to misidentification of tracks. Poor genotyping success was likely due to insufficient hair quantity, reinforcing statements by Kendall and McKelvey (2008) and genotyping success rates reported by Sawaya et al. (2011) and Russell et al. (2012). Potentially, the low rates of genotyping success accompanying shed cougar hair are not appropriate to relatively low density cougar populations such as ours. Based on our research, we would recommend that winter transects be performed with greater than our average of 3.5 observers per sampling stint. Observers should also collect a greater amount of hair (our samples were generally 4 – 5 hairs per sample), or increase tracking length to collect a more viable scat sample. Regardless, the scat detection dog surveys were 127.4 times more fruitful than the winter track transects in terms of detections per person-day of effort. This is in part due to the poor genotyping success of the collected hair samples:

winter transects only yielded a track-detection-to-individual-identity ratio of 11%. Given a hypothetical scenario of 100% genotyping success with all collected samples, the scat detection dog team would have still generated 33.3 times as many genotypes per person-day as the winter transects.

For the remote camera surveys, the most critical finding was that our photographic survey estimates were unreliable, mainly due to the inability to reliably identify individual cougars. Conceivably improved photo quality, either using improved camera technology or field techniques, would alleviate this problem. This issue has important implications regarding other remote camera density estimates for cougars that rely on photographic identification of individuals (e.g., Kelly et al. 2008, Negroes et al. 2010, Urios et al. 2010). Conceivably, these studies' use of conventional camera station setups (one or two cameras placed along high use trails without a lure to prolong detection events and increase photo quantity) resulted in more accurate individual identification. However, we found no correlation between investigator agreement and number of photos within a detection event. Kelly et al. (2008) also found no significant relationship between photo quality and ability of investigators to assign identification. Nevertheless, given the success of camera trapping studies on other felids (e.g., Karanth 1995, Trolle and Kéry 2003, Soisalo and Cavalcanti 2006), further research on the field techniques of photo-trapping cougars is still warranted. Disregarding the issue of identifiability, we found a 71% higher rate of detection for the trail sites over the blood lure stations, suggesting the trail camera setup was a more efficient method for generating detections. This discrepancy was possibly due in part to the blood stations being restricted from human use trails, which often overlapped topographic features where

cougars were more likely to be detected (e.g., ridgelines, drainage bottoms), supporting

our impression that well-placed passive detectors may be more effective than less ideally

placed baited detectors. Trail sites were also less costly; the blood lure camera stations

had a higher maintenance cost than the trail cameras due to the need to regularly replace

the blood lure. Furthermore, due to the possibility of bear encounters, safety protocols

prohibited visits to blood lure stations with fewer than two technicians, whereas trail sites

could be visited solo. Regardless, the scat detection surveys produced 730% more

detections per unit of survey length than the trail cameras and at a lower cost. We did not

calculate the trail cameras' detections per person day of effort. The blood-lure sites had a

261% greater number of photos taken per detection event over the trail sites, supporting

our hypothesis that cougars would spend more time investigating the site because of the

lure. However, we were wrong in our hypothesis that a greater number of photos would

increase an observers' ability to identify unique individuals. There was a promising

spatial correlation between the SPACECAP produced estimates of density and the

concurrent GPS-collar derived home ranges. Although the reliability of our density

estimates was uncertain, this spatial correlation suggested some promise assuming

resolutions to the issues outlined above.

Our survey methods were not necessarily comparable to work by Davidson et al.

(2014), due to that study's greater survey effort, smaller sampling area, and use of

multiple sampling occasions of scat dog transects allowing for conventional CMR using

program MARK. However, it is worth noting that Davidson et al. (2014) reported a

similar scat collection rate, number of unique genotypes, and genotyping success. Of

note, Davidson et al. (2014) reported some of the largest capture probabilities published

for felids (0.25-0.99), whereas our SECR based capture probabilities ranged from 0.03-0.05 (Table 3.6). Our sampling transects were sparse relative to the Davidson et al. (2014) study; however, the average spacing between nearest transect neighbors (calculated from transect center points) was 4,028 m and unlikely to only cover a single cougar home range. The scat detection dog encounter histories nevertheless had a high number of singletons (i.e., unique genotypes that were only encountered once): 60.7% and 70.6% of individual genotypes were detected only once in 2013 and 2014, respectively. These singletons could be explained by low sampling effort, inherently low detection probabilities for some portion of the population, or both. An increase in sampling effort would very likely increase our estimated capture probabilities, and potentially reduce singleton detections. However, another explanation is that the population during the sample included a high number of transient cougars. In this scenario, there would be erroneously inflated population estimates to some degree, due to transient individuals' inherently low detection probability, depending on the length of time spent on the transect array. To examine this, we reran the top SECR models for the combined areas, excluding the singleton detections. The 2013 model estimated a density of 0.81 cougars/100 km^2 (95% CI = 0.32 – 2.06); the 2014 model estimated 0.50 cougars/100 km^2 (95% CI = 0.19 – 1.30). These estimates were low compared to the reference estimate of 1.40 cougars/100 km^2. Although detection count was probably related to residency status, the singletons in our sample likely included residents as well as transients, given the relatively low recapture counts: the mean detection count per individual was 1.78 (n = 45, ± 1.43 SD), and the mean detection count for non-singleton individuals was 3.33 (n = 15, ± 1.59 SD). The inclusion of transients in the sample is

essentially an issue of population closure; despite SECR models' relaxed assumptions of closure, truly transient individuals (as opposed to temporary immigrants or emigrants; see Kendall et al. (1997); Gardner et al. (2009)) are problematic given there would not be any home range to be modeled. Survey timing may help with this issue. Ruth et al. (2011) found >90% of dispersing subadult cougars in the Greater Yellowstone Ecosystem migrated between April and September. Our surveys were performed in the late summer months; depending on the temporal sampling window, we likely sampled from this migratory period. This issue reiterates the issue of uncertainties in the temporal sampling window for cougar scat surveys given different environmental conditions that likely affect scat detectability and DNA integrity at various rates (Lonsinger et al. 2015). We recommend timing detection dog transects after spring snowmelt, but before the likelihood of detecting transient individuals increases. An ideal collection time may be further refined given more information on the DNA degradation rate for cougar scat samples.

Many carnivore species have undergone significant contractions in their historic distributions due to habitat loss, habitat fragmentation, or direct persecution by humans (Laliberte and Ripple 2004), resulting in a call for increased effort in carnivore conservation (Gittleman et al. 2001). Reliable population estimates are vital for the implementation and evaluation of any conservation effort, and noninvasive methods to determine these estimates may provide researchers the ability to measure population size at relatively low cost. In this thesis, we examined a current issue related specifically to the management and conservation of cougars: the need for a low cost alternative to the costly "gold standard" method of capturing and radio-collaring all individuals in a

population to determine its size. We examined several noninvasive techniques which have been used to survey cougar populations, but not necessarily in conjunction with other noninvasive methods or a comparative "gold standard" estimate. Based on our "gold standard" estimate (Chapter 2), the remote camera surveys and scat dog surveys both produced plausible density estimates. However, financial cost being a chief motivation behind the need for accurate noninvasive survey methods, we emphasize that our scat detection dog surveys were an order of magnitude less expensive than the other types of surveys (in terms of cost per detection). Future research should address the timing, temporal sampling window, and statistical power of this method. We also determined that photographic detections of cougars are likely unsuitable for CMR analyses, demonstrating a critical difference between survey options for cougars and other conspicuously pelaged felids such as tigers, leopards and jaguars. However, some researchers may prefer to use remote cameras, for reasons such as being able to detect multiple species without the need for scent training a dog to specific species. Therefore, future research is warranted provided that consideration is given to the issue of identifiability, as well as the method's relatively lower detection rate.

LITERATURE CITED

Anderson, C. R., and F. G. Lindzey. 2005. Experimental evaluation of population trend and harvest composition in a Wyoming cougar population. Wildlife Society Bulletin 33:179–188.

Beier, P. 2009. A focal species for conservation planning. Pages 177–189 *in* M. Hornocker and S. Negri, editors. Cougar: ecology and conservation. University Of Chicago Press, Chicago, Illinois, USA.

Beier, P., and S. Cunningham. 1996. Power of track surveys to detect changes in cougar populations. Wildlife Society Bulletin 24:540–546.

Bivand, R., N. Lewin-Koh. 2014. maptools. R package version 0.8-30. <https://cran.r-project.org/web/packages/maptools/maptools.pdf>. Accessed 8 Mar 2014.

Bivand, R., and C. Rundel. 2011. rgeos: interface to geometry engine-open source (GEOS). R package version 0.1-8. <http://cran.r-project.org/package=rgeos>. Accessed 25 April 2014.

Bromaghin, J. F. 2007. The genetic mark-recapture likelihood function of capwire. Molecular Ecology 16:4883–4885.

Bureau of Labor Statistics. 2015. Occupational Outlook Handbook. <http://www.bls.gov/ooh/life-physical-and-social-science/zoologists-and-wildlife-biologists.htm>. Accessed 10 Jul 2015.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.

Calenge, C. 2011. Home range estimation in R: the adehabitatHR package. <https://cran.r-project.org/web/packages/adehabitatHR/adehabitatHR.pdf>. Accessed 8 Mar 2014.

Caragiulo, A., I. Dias-Freedman, J. A. Clark, S. Rabinowitz, and G. Amato. 2014.
    Mitochondrial DNA sequence variation and phylogeography of Neotropic pumas
    (*Puma concolor*). Mitochondrial DNA 25:304–312.

Chapman, D. G. 1951. Some properties of the hypergeometric distribution with
    applications to zoological sample censuses. University of California Publications
    in Statistics 1:131–160.

Choate, D., M. Wolfe, and D. Stoner. 2006. Evaluation of cougar population estimators
    in Utah. Wildlife Society Bulletin 34:782–799.

Cooley, H. S., R. B. Wielgus, G. Koehler, and B. Maletzke. 2009*a*. Source populations in
    carnivore management: cougar demography and emigration in a lightly hunted
    population. Animal Conservation 12:321–328.

Cooley, H. S., R. Wielgus, G. M. Koehler, H. S. Robinson, and B. T. Maletzke. 2009*b*.
    Does hunting regulate cougar populations? A test of the compensatory mortality
    hypothesis. Ecology 90:2913–2921.

Cougar Management Guidelines Working Group. 2005. Cougar Management Guidelines.
    T. Beck, J. Beecham, P. Beier, T. Hofstra, M. Hornocker, F. Lindzey, K. Logan,
    B. Pierce, H. Quigley, I. Ross, H. Shaw, R. Sparrowe, and S. Torres, editors.
    WildFutures, Bainbridge Island, Washington, USA.

Davidson, G. A., D. A. Clark, B. K. Johnson, L. P. Waits, and J. R. Adams. 2014.
    Estimating cougar densities in northeast Oregon using conservation detection
    dogs. Journal of Wildlife Management 78:1104–1114.

Dempsey, S. J., E. M. Gese, and B. M. Kluever. 2014. Finding a fox: an evaluation of survey methods to estimate abundance of a small desert carnivore. PLoS ONE 9:e105873.

Dice, L. R. 1938. Some census methods for mammals. Journal of Wildlife Management 2:119–130.

Duong, T. 2014. ks: Kernel smoothing. R package version 1.9.3. <https://cran.r-project.org/web/packages/ks/ks.pdf>. Accessed 8 Mar 2014.

Efford, M. G. 2004. Density estimation in live-trapping studies. Oikos 3:598–610.

Efford, M. 2015. secr. R package version 2.9.5. <https://cran.r-project.org/web/packages/secr/secr.pdf>. Accessed 4 Mar 2015.

Ernest, H. B., M. C. Penedo, B. P. May, M. Syvanen, and W. M. Boyce. 2000. Molecular tracking of mountain lions in the Yosemite valley region in California: genetic analysis using microsatellites and faecal DNA. Molecular ecology 9:433–441.

Fiske, I. J., and R. B. Chandler. 2011. Unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. Journal of Statistical Software. Volume 43.

Fleiss, J. L. 1971. Measuring nominal scale agreement among many raters. Psychological Bulletin 76:378–382.

Fleiss, L., B. Levin, and M. C. Paik. 1981. The measurement of interrater agreement. Pages 598 – 626 *in* K. McPherson, editor. Statistical methods for rates and proportions. John Wiley & Sons, Inc, Hoboken, New Jersey, USA.

Galpern, P., M. Manseau, P. Hettinga, K. Smith, and P. Wilson. 2012. Allelematch: An R package for identifying unique multilocus genotypes where genotyping error and missing data may be present. Molecular Ecology Resources 12:771–778.

Galpern, P. 2015. allelmatch. R package version 2.5. <https://cran.r-project.org/web/packages/allelematch/allelematch.pdf>. Accessed 6 June 2014.

Gamer, M., J. Lemon, I. Fellows, and P. Singh. 2014. irr. R package version 0.84. <https://cran.r-project.org/web/packages/irr/irr.pdf>. Accessed 3 Mar 2014.

Gardner, B., J. A. Royle, and M. T. Wegan. 2009. Hierarchical models for estimating density from DNA mark-recapture studies. Ecology 90:1106–1115.

Gelman, A., G. Roberts, and W. Gilks. 1996. Efficient metropolis jumping rules. Bayesian Statistics 5:599–607.

Geweke, J. F., M. P. Keane, and D. E. Runkle. 1997. Statistical inference in the multinomial multiperiod probit model. Journal of Econometrics 80:125-165.

Gittleman, J. L., D. W. MacDonald, R. K. Wayne, and M. Gosling. 2001. Why "carnivore conservation"? Pages 1–7 *in*. J. L. Gittleman, S. M. Funk, D. W. Macdonald, and R. K. Wayne, editors. Carnivore conservation. Cambridge University Press, London, United Kingdom.

Goossens, B., L. P. Waits, and P. Taberlet. 1998. Plucked hair samples as a source of DNA: Reliability of dinucleotide microsatellite genotyping. Molecular Ecology 7:1237–1241.

Gopalaswamy, A. M., J. A. Royle, J. E. Hines, P. Singh, D. Jathanna, N. S. Kumar, and K. U. Karanth. 2012*a*. Program SPACECAP : software for estimating animal

density using spatially explicit capture-recapture models. R. Freckleton, editor. Methods in Ecology and Evolution 3:1067–1072.

Gopalaswamy, A. M., J. A. Royle, and J. E. Hines. 2012*b*. SPACECAP. R package version 1.0.6. <https://cran.r-project.org/web/packages/SPACECAP/SPACECAP.pdf>. Accessed 27 Mar 2014.

Grand Teton National Park. 2015. <http://www.nps.gov/grte/naturescience/weather.htm>. Accessed 10 Apr 2014.

Gwet, K. L. 2010. Handbook of Inter-Rater Reliability: the definitive guide to measuring the extent of agreement among raters. Advanced Analytics, LLC, Gaithersburg, Maryland, USA.

Harihar, A., B. Pandav, and S. P. Goyal. 2009. Subsampling photographic capture-recapture data of tigers (*Panthera tigris*) to minimize closure violation and improve estimate precision: a case study. Population Ecology 51:471–479.

Harmsen, B. J., R. J. Foster, S. M. Gutierrez, S. Y. Marin, and C. Patrick. 2010. Scrape-marking behavior of jaguars (*Panthera onca*) and pumas (*Puma concolor*). Journal of Mammalogy 91:1225–1234.

Harmsen, B. J. 2006. The use of camera traps for estimating abundance and studying the ecology of jaguars (*Panthera onca*). Thesis, University of Southampton, England, United Kingdom.

Haroldson, M., and C. Anderson. 1996. Effectiveness of attractants to lure grizzly bears into hair collection sites for future DNA fingerprinting. Yellowstone grizzly bear

investigations: annual report of the Interagency Grizzly Bear Study Team. Bozeman, Montana, USA.

Hernandez-Blanco, J. a, V. V Rozhnov, V. S. Lukarevskiy, S. V Naidenko, M. D. Chistopolova, P. a Sorokin, M. N. Litvinov, and a K. Kotlyar. 2013. Spatially explicit capture-recapture method (SECR, SPACECAP): A new approach to determination of the Amur tiger (*Panthera tigris altaica*) population density by means of camera-traps. Doklady biological sciences : proceedings of the Academy of Sciences of the USSR, Biological sciences sections / translated from Russian 453:365–8.

Jones, M. C., J. S. Marron, and S. J. Sheather. 1996. A brief survey of bandwidth selection for density estimation. Journal of the American Statistical Association 91:401–407.

Karanth, K., and J. Nichols. 1998. Estimation of tiger densities in India using photographic captures and recaptures. Ecology 79:2852–2862.

Karanth, K. U. 1995. Estimating tiger Panthera tigris populations from camera-trap data using capture-recapture models. Biological Conservation 71:333–338.

Kays, R., and K. Slauson. 2008. Remote cameras. Pages 110–140 *in* R. A. Long, P. Mackay, W. J. Zielinski, and J. Ray, editors. Noninvasive survey methods for carnivores. Island Press, Washington, D.C.

Kelly, M. J., A. J. Noss, M. S. Di Bitetti, L. Maffei, R. L. Arispe, A. Paviolo, C. D. De Angelo, and Y. E. Di Blanco. 2008. Estimating puma densities from camera trapping across three study sites: Bolivia, Argentina, and Belize. Journal of Mammalogy 89:408–418.

Kendall, K. C., and K. S. McKelvey. 2008. Hair collection. Pages 141–182 *in* R. A. Long, P. Mackay, W. J. Zielinski, and J. Ray, editors. Noninvasive survey methods for carnivores. Volume 106. Island Press, Washington, D.C.

Kendall, W. L., J. D. Nichols, and J. E. Hines. 1997. Estimating temporary emigration using capture-recapture data with Pollock's robust design. Ecology 78:563–578.

Kilshaw, K., P. Johnson, A. M. Kitchen, and D. Macdonald. 2014. Detecting the elusive Scottish wildcat Felis silvestris silvestris using camera trapping. Oryx 49:207-215.

Knight, D. H. 1996. Mountains and plains: the ecology of Wyoming landscapes. Yale University Press, New Haven, Connecticut, USA.

Knopff, K. H., A. A. Knopff, A. Kortello, and M. S. Boyce. 2010. Cougar kill rate and prey composition in a multiprey system. Journal of Wildlife Management 74:1435–1447.

Krebs, C. J. 2001. Ecology: the experimental analysis of distribution and abundance. Benjamin Cummings, San Francisco, California, USA.

Kurushima, J. D., J. A. Collins, J. A. Well, and H. B. Ernest. 2006. Development of 21 microsatellite loci for puma (*Puma concolor*) ecology and forensics. Molecular Ecology Notes 6:1260–1262.

Laake, J., and E. Rexstad. 2008. RMark–an alternative approach to building linear models in MARK. Pages C1–C115 *in* E. Cooch and G. White, editors. Program MARK: a gentle introduction. <http://www.phidot.org/software/mark/docs/book>. Accessed 10 Oct 2013.

Laliberte, A., and W. Ripple. 2004. Range contractions of North American carnivores and ungulates. BioScience 54:123–138.

Landis, J., and G. Koch. 1977. The measurement of observer agreement for categorical data. Biometrics 33:159–174.

Logan, K., and L. Sweanor. 2001. Desert puma: evolutionary ecology and conservation of an enduring carnivore. Island Press, Washington, D.C., USA.

Logan, K., and L. Sweanor. 2010. Behavior and social organization of a solitary carnivore. Pages 105–117 *in* M. Hornocker and S. Negri, editors. Cougar: ecology and conservation. University Of Chicago Press, Chicago, USA.

Long, E. S., D. M. Fecske, R. A. Sweitzer, J. A. Jenks, B. M. Pierce, and V. C. Bleich. 2003. Efficacy of photographic scent stations to detect mountain lions. Western North American Naturalist 63:529–532.

Lonsinger, R. C., E. M. Gese, S. J. Dempsey, B. M. Kluever, T. R. Johnson, and L. P. Waits. 2015. Balancing sample accumulation and DNA degradation rates to optimize noninvasive genetic sampling of sympatric carnivores. Molecular Ecology Resources 15:831–842.

Mace, R. D., S. C. Minta, T. L. Manley, and K. E. Aune. 1994. Estimating grizzly bear population size using camera sightings. Wildlife Society Bulletin 22:74–83.

Mackay, P., D. A. Smith, R. A. Long, and M. Parker. 2008. Scat detection dogs. Pages 183–222 *in* P. MacKay, W. J. Zielinski, R. A. Long, and J. Ray, editors. Noninvasive survey methods for carnivores. Island Press, Washington, D.C.

MacKay, P., W. J. Zielinski, R. A. Long, and J. C. Ray. 2008. Noninvasive research and carnivore conservation. Pages 1–7 *in* R. A. Long, P. Mackay, W. J. Zielinski, and

J. C. Ray, editors. Noninvasive survey methods for carnivores. Island Press, Washington, D.C.

Marston, R. A., and J. E. Anderson. 1991. Watersheds and vegetation of the Greater Yellowstone Ecosystem. Conservation Biology 5:338–346.

Martyn, A., N. Best, K. Cowles, K. Vines, D. Bates, R. Almond, and M. M. Plummer. 2015. coda. R Package version 0.17-1. <https://cran.r-project.org/web/packages/coda/coda.pdf>. Accessed 27 Mar 2014.

Mattiuzzi, M., M. Sumner, J. A. Greenberg, A. Bevan, A. Shortridge, and M. R. J. Hijmans. 2015. raster. R package version 2.3-33. <https://cran.r-project.org/web/packages/raster/raster.pdf>. Accessed 10 Jun 2015.

McLellan, B. 1989. Dynamics of a grizzly bear population during a period of industrial resource extraction. I. density and age-sex composition. Canadian Journal of Zoology 67:1856–1860.

Menotti-Raymond, M. A., V. A. David, L. L. Wachter, J. M. Butler, and S. J. O'Brien. 2005. An STR forensic typing system for genetic individualization of domestic cat (*Felis catus*) samples. Journal of Forensic Sciences 50:1061–1070.

Menotti-Raymond, M., V. David, L. Lyons, A. Schäffer, J. Tomlin, M. Hutton, and S. O'Brien. 1999. A genetic linkage map of microsatellites in the domestic cat (*Felis catus*). Genomics 57:9–23.

Miller, C. R., P. Joyce, and L. P. Waits. 2005. A new method for estimating the size of small populations from genetic mark-recapture data. Molecular Ecology 14:1991–2005.

Nakagawa, S., N. J. Gemmell, and T. Burke. 2004. Measuring vertebrate telomeres: Applications and limitations. Molecular Ecology 13:2523–2533.

Negrões, N., P. Sarmento, J. Cruz, C. Eira, E. Revilla, C. Fonseca, R. Sollmann, N. M. Tôrres, M. M. Furtado, A. T. A. Jácomo, and L. Silveira. 2010. Use of camera-trapping to estimate puma density and influencing factors in central Brazil. Journal of Wildlife Management 74:1195–1203.

Oliveira-Santos, L. G. R., C. A. Zucco, P. C. Antunes, and P. G. Crawshaw. 2010. Is it possible to individually identify mammals with no natural markings using camera-traps? A controlled case-study with lowland tapirs. Mammalian Biology 75:375–378.

Otis, D., K. Burnham, G. White, and D. Anderson. 1978. Statistical inference from capture data on closed animal populations. Wildlife Monographs 3–135.

Parker, P. G., A. A. Snow, M. D. Schug, G. C. Booton, and P. A. Fuerst. 1998. What molecules can tell us about populations: choosing and using a molecular marker. Ecology 79:361-382.

Pennell, M. W., C. R. Stansbury, L. P. Waits, and C. R. Miller. 2013. Capwire: a R package for estimating population census size from non-invasive genetic sampling. Molecular ecology resources 13:154–157.

Proulx, G., M. R. L. Cattet, and R. A. Powell. 2012. Humane and efficient capture and handling methods for carnivores. Pages 70–130 *in* L. Boitani and R. A. Powell, editors. Carnivore ecology and conservation: a handbook of techniques. Oxford University Press, New York, USA.

Quigley, H. B., and M. G. Hornocker. 2010. Cougar population dynamics. Pages 59–75
    in M. G. Hornocker and S. Negri, editors. Cougar: ecology and conservation.
    University of Chicago Press, Chicago, USA.

Ripple, W. J., J. a Estes, R. L. Beschta, C. C. Wilmers, E. G. Ritchie, M. Hebblewhite, J.
    Berger, B. Elmhagen, M. Letnic, M. P. Nelson, O. J. Schmitz, D. W. Smith, A. D.
    Wallach, and A. J. Wirsing. 2014. Status and ecological effects of the world's
    largest carnivores. Science 343:1–11.

Rovero, F., F. Zimmermann, D. Berzi, and P. Meek. 2013. "Which camera trap type and
    how many do I need?" A review of camera features and study designs for a range
    of wildlife research applications. Hystrix 24:148-156.

Royle, J. A., R. B. Chandler, R. Sollmann, and B. Gardner. 2013. Spatial Capture-
    Recapture. Academic Press, Waltham, Massachusetts, USA.

Royle, J. A. J., K. U. Karanth, A. M. A. Gopalaswamy, and N. S. Kumar. 2009. Bayesian
    inference in camera trapping studies for a class of spatial capture-recapture
    models. Ecology 90:3233–3244.

Royle, J. A., M. Kéry, and J. Guélat. 2011. Spatial capture-recapture models for search-
    encounter data. Methods in Ecology and Evolution 2:602–611.

Royle, J., and J. Nichols. 2009. A hierarchical model for estimating density in camera-
    trap studies. Journal of Applied Ecology 118–127.

Russell, R. E., J. A. Royle, R. Desimone, M. K. Schwartz, V. L. Edwards, K. P. Pilgrim,
    and K. S. McKelvey. 2012. Estimating abundance of mountain lions from
    unstructured spatial sampling. Journal of Wildlife Management 76:1551–1561.

Ruth, T. K., M. a. Haroldson, K. M. Murphy, P. C. Buotte, M. G. Hornocker, and H. B. Quigley. 2011. Cougar survival and source-sink structure on Greater Yellowstone's Northern Range. Journal of Wildlife Management 75:1381–1398.

Sawaya, M. A., T. K. Ruth, S. Creel, J. J. Rotella, J. B. Stetz, H. B. Quigley, and S. T. Kalinowski. 2011. Evaluation of noninvasive genetic sampling methods for cougars in Yellowstone National Park. Journal of Wildlife Management 75:612–622.

Schwartz, M. K., and S. L. Monfort. 2008. Genetic and endocrine tools for carnivore surveys. Pages 238–262 *in* R. A. Long and W. J. Zielinski, editors. Noninvasive survey methods for carnivores. Island Press, Washington, D.C.

Seaman, D. E., J. J. Millspaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke, and R. A. Gitzen. 1999. Effects of sample size on kernel home range estimates. Journal of Wildlife Management 63:739–747.

Seber, G. A. F. 1982. The estimation of animal abundance and related parameters. Second edition. Volume 2. Charles Griffith and Company, Ltd, London, United Kingdom.

Smith, D. A., K. Ralls, B. L. Cypher, and J. E. Maldonado. 2005. Assessment of scat-detection dog surveys to determine kit fox distribution. Wildlife Society Bulletin 33:897–904.

Smith, D. A., K. Ralls, A. Hurt, B. Adams, M. Parker, B. Davenport, M. C. Smith, and J. E. Maldonado. 2003. Detection and accuracy rates of dogs trained to find scats of San Joaquin kit foxes (*Vulpes macrotis mutica*). Animal Conservation 6:339–346.

Soisalo, M. K., and S. M. C. Cavalcanti. 2006. Estimating the density of a jaguar population in the Brazilian Pantanal using camera-traps and capture–recapture sampling in combination with GPS radio-telemetry. Biological Conservation 129:487–496.

Soria-Díaz, L., C. Rodríguez-Soto, O. Monroy-Vilchis, C. Rodríguez-Soto, M. Zarco-González, and V. Urios. 2010. Variation of abundance and density of *Puma concolor* in zones of high and low concentration of camera traps in Central Mexico. Animal Biology 60:361–371.

Stabler, B. 2014. shapefiles. R package version 0.7. <https://cran.r-project.org/web/packages/shapefiles/shapefiles.pdf>. Accessed 10 Feb 2014.

Stenglein, J. L., M. De Barba, D. E. Ausband, and L. P. Waits. 2010. Impacts of sampling location within a faeces on DNA quality in two carnivore species. Molecular ecology resources 10:109–114.

Taberlet, P., S. Griffin, B. Goossens, S. Questiau, V. Manceau, N. Escaravage, L. P. Waits, and J. Bouvet. 1996. Reliable genotyping of samples with very low DNA quantities using PCR. Nucleic Acids Research 24:3189–3194.

Thapa, K., R. Shrestha, J. Karki, G. J. Thapa, N. Subedi, N. M. B. Pradhan, M. Dhakal, P. Khanal, and M. J. Kelly. 2014. Leopard *Panthera pardus fusca* density in the seasonally dry, subtropical forest in the Bhabhar of Terai Arc, Nepal. Advances in Ecology 2014:1-12.

Trolle, M., and M. Kéry. 2003. Estimation of ocelot density in the Pantanal using capture–recapture analysis of camera-trapping data. Journal of Mammalogy 84:607–614.

Valière, N. 2002. GIMLET: a computer program for analysing genetic individual identification data. Molecular Ecology Notes 2:377–379.

VanSickle, W., and F. Lindzey. 1991. Evaluation of a cougar population estimator based on probability sampling. Journal of Wildlife Management 55:738–743.

Waits, L., and D. Paetkau. 2005. Noninvasive genetic sampling tools for wildlife biologists: a review of applications and recommendations for accurate data collection. Journal of Wildlife Management 69:1419–1433.

Walter, W. D., and J. W. Fischer. 2015. Manual of applied spatial ecology. Walter Applied Spatial Ecology Lab, Pennsylvania State University. University Park, Pennsylvania, USA.

Wasser, S. K., B. Davenport, E. R. Ramage, K. E. Hunt, M. Parker, C. Clarke, and G. Stenhouse. 2004. Scat detection dogs in wildlife research and management: application to grizzly and black bears in the Yellowhead Ecosystem, Alberta, Canada. Canadian Journal of Zoology 82:475–492.

White, G. C. 2008. Closed population estimation models and their extensions in Program MARK. Environmental and Ecological Statistics 15:89–99.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations: modeling, estimation, and decision making. Academic Press, New York, USA.

Wilson, K., and D. Anderson. 1985. Evaluation of two density estimators of small mammal population size. Journal of Mammalogy 66:13–21.

Wolfe, M. L., E. M. Gese, P. Terletzky, D. C. Stoner, and L. M. Aubry. 2016. Evaluation of harvest indices for monitoring cougar survival and abundance. Journal of Wildlife Management 80:27–36.

Woods, J. G., D. Paetkau, D. Lewis, B. N. McLellan, M. Proctor, C. Strobeck, and J. G. Woods. 1999. Genetic tagging of free-ranging black and brown bears. Wildlife Society Bulletin 27:616–627.

Yoshizaki, J., K. H. Pollock, C. Brownie, and R. A. Webster. 2009. Modeling misidentification errors in capture-recapture studies using photographic identification of evolving marks. Ecology 90:3–9.

Table 3.1. Comparison of detection and photo rates for blood lure camera stations and conventional trail cameras for sampling cougars

noninvasively, northwestern Wyoming, 2012-2013.

Camera station design	Year	Number of camera stations	Number of detections	Total sampling days	Detection rate per 30 days	Mean photos per event	± SD photos per event
Blood lure sites	2012	43	17	3160	0.149	16.8	10.7
	2013	43	16	3414	0.141	27.3	8.8
Trail sites	2012	10	6	348	0.517	8.6	9.0
	2013	12	9*	579	0.466	3.6	2.7

*one detection event comprised 2 kittens with an adult; the kittens were not included

in the total

Table 3.2. Parameter estimates for cougars sampled noninvasively in northwestern Wyoming, as determined from program MARK. Density was calculated using the effective trapping buffer determined from mean home range size.

Year	Model	Parameter	Estimate	SE	95% Lower CI	95% Upper CI	Density	Density range
2012	M_0	N	5.00	0.00	5.00	5.00	0.21	(0.21-0.21)
		p	0.33	0.07	0.20	0.48	-	-
	M_b	N	5.88	3.49	5.03	28.62	0.25	(0.22-1.23)
		p	0.17	0.18	0.02	0.71	-	-
		c	0.44	0.12	0.24	0.67	-	-
	M_h	N	5.00	0.00	5.00	5.00	0.21	(0.21-0.21)
		p	0.33	0.07	0.20	0.48	-	-
		π	0.50	0.00	0.50	0.50	-	-
2013	M_0	N	7.00	0.00	7.00	7.00	0.30	(0.30-0.30)
		p	0.29	0.06	0.18	0.42	-	-
	M_b	N	7.00	0.00	7.00	7.00	0.30	(0.30-0.30)
		p	0.35	0.11	0.18	0.57	-	-
		c	0.25	0.07	0.14	0.41	-	-
	M_h	N	7.00	0.00	7.00	7.00	0.30	(0.30-0.30)
		p	0.29	0.06	0.18	0.42	-	-
		π	0.50	0.00	0.50	0.50	-	-

Table 3.3. Parameter estimates for a cougar population in northwestern Wyoming, as determined from remote camera surveys using spatially explicit models as implemented in SPACECAP.

Year	Area	Camera array	Parameter	Posterior mean	Geweke diagnostic	Effective sample size	Posterior SD	95% Lower HPD level	95% Upper HPD level
2012	Total Study Area	Blood lure cameras	σ	6,058	-0.33	455.3	3,087	2,925	10,891
			λ_0	0.077	0.27	1,023.6	0.047	0.011	0.169
			ψ	0.238	-0.73	2,617.1	0.115	0.049	0.462
			N	14.979	-0.69	2,239.2	6.932	5.000	28.000
			D	0.331	-	-	0.153	0.110	0.618
			p	0.073	-	-	0.042	0.011	0.155
		All cameras	σ	10,254	-0.43	512.4	4,160	5,329	1,6391
			λ_0	0.032	-0.54	1,731.8	0.015	0.007	0.062
			ψ	0.247	0.45	2,889.6	0.105	0.076	0.452
			N	16.278	0.31	2,367.3	6.482	8.000	29.000
			D	0.359	-	-	0.143	0.177	0.640
			p	0.031	-	-	0.015	0.007	0.060
	Gros Ventre	Blood lure cameras	σ	258,423	-1.18	6.0	301,789	2,827	862,310
			λ_0	0.056	4.79	1,780.3	0.064	0.004	0.179
			ψ	0.141	3.33	3,635.1	0.094	0.021	0.335
			N	6.894	3.23	2,617.9	4.596	4.000	17.000
			D	0.210	-	-	0.140	0.122	0.518

Year	Location	Camera	Parameter						
			p	0.053	-	-	0.056	0.004	0.164
		All cameras	σ	10,652	0.40	1,105.3	4,812	5,472	17,572
			λ_0	0.029	-1.37	3,554.7	0.013	0.007	0.056
			ψ	0.221	0.62	10,619.3	0.085	0.078	0.391
			N	14.466	0.65	7,893.7	4.903	8.000	24.000
			D	0.441	-	-	0.149	0.244	0.732
			p	0.028	-	-	0.013	0.007	0.054
	Buffalo Valley	Blood lure cameras	N/A	N/A	N/A	N/A	N/A	N/A	N/A
		All cameras	N/A	N/A	N/A	N/A	N/A	N/A	N/A
2013	Total Study Area	Blood lure cameras	σ	5,924	-0.84	653.3	1,953	3,198	9,646
			λ_0	0.062	1.10	1,220.6	0.031	0.013	0.124
			ψ	0.321	-0.47	3,753.1	0.131	0.097	0.582
			N	21.195	-0.46	2,893.0	8.212	8.000	37.000
			D	0.468	-	-	0.181	0.177	0.817
			p	0.060	-	-	0.029	0.013	0.117
		All cameras	σ	6,437	-0.25	738.2	1692	3872	9,872
			λ_0	0.034	-0.93	1,657.4	0.014	0.011	0.063
			ψ	0.526	0.37	2,291.4	0.170	0.222	0.875
			N	37.906	0.33	2,166.3	11.929	16.000	61.000

		D	0.837	-	-	0.263	0.397	1.391
		p	0.034	-	-	0.014	0.011	0.061
Gros Ventre	Blood lure cameras	σ	22,926	-0.29	30.8	45,443	2,891	119,292
		λ_0	0.062	-1.56	1,630.5	0.043	0.004	0.144
		ψ	0.224	-1.05	2,611.2	0.137	0.031	0.498
		N	13.974	-1.02	2,266.4	8.604	5.000	31.000
		D	0.426	-	-	0.262	0.152	0.945
		p	0.059	-	-	0.040	0.004	0.134
	All cameras	σ	4,481,923	-9.76	1,169.0	612,443	2,938,274	5,404,512
		λ_0	0.008	1.04	21,628.5	0.002	0.003	0.012
		ψ	0.222	-0.47	39,325.2	0.076	0.089	0.370
		N	12.565	-0.73	24,531.4	3.396	9.000	19.000
		D	0.004	-	-	0.001	0.003	0.006
		p	0.008	-	-	0.002	0.003	0.012
Buffalo Valley	Blood lure cameras	N/A	N/A	N/A	N/A	N/A	N/A	N/A
	All cameras	N/A	N/A	N/A	N/A	N/A	N/A	N/A

Table 3.4. Cougar density as estimated by CAPWIRE, comparing the equal catchability model (ECM) and two innate rates model (TIRM). Density was estimated using the ad hoc buffering method. Northwest Wyoming.

		Trap area	ECM	CI95%	CI95%	ECM density	CI95%	CI95%	TIRM	CI95%	CI95%	TIRM density	CI95%	CI95%
2013	GV	816	30.00	23.00	39.00	3.68	2.82	4.78	45.00	35.00	73.00	5.51	4.29	8.95
	BV	648	11.00	6.00	∞	1.70	0.93	∞	18.00	7.00	∞	2.78	1.08	∞
	TSA	1,401	38.00	29.00	50.00	2.71	2.07	3.57	55.00	42.00	89.00	3.93	3.00	6.35
2014	GV	816	16.00	11.00	24	1.96	1.35	2.94	33.00	19.00	156	4.04	2.33	19.12
	BV	648	10.00	8.00	18	1.54	1.23	2.78	18.00	9.00	45	2.78	1.39	6.94
	TSA	1,401	27.00	19.00	38	1.93	1.36	2.71	48.00	35.00	98	3.43	2.50	7.00

Table 3.5. AICc ranking for SECR models for cougar scat collection surveys in Northwest Wyoming, without sex grouping. x and y indicate a latitudinal or longitudinal gradient to density. ~1 indicates parameters that are held constant.

Year	Area	Model	K	logLik	AICc	dAICc	AICcwt
2013	Combined areas	D~x + y g$_0$~1 σ ~1	5	-198.889	410.506	0	0.653
		D~x g$_0$~1 σ ~1	4	-201.579	412.897	2.391	0.1976
		D~y g$_0$~1 σ ~1	4	-202.305	414.349	3.843	0.0956
		D~1 g$_0$~1 σ ~1	3	-204.249	415.498	4.992	0.0538
2013	Gros Ventre	D~1 g$_0$~1 σ~1	3	-164.446	336.154	0	0.3806
		D~x g$_0$~1 σ~1	4	-163.273	336.768	0.614	0.28
		D~y g$_0$~1 σ~1	4	-163.288	336.799	0.645	0.2757
		D~x + y g$_0$~1 σ~1	5	-163.099	339.728	3.574	0.0637
2014	Combined areas	D~1 g$_0$~1 σ~1	3	-125.071	257.988	0	0.7038
		D~y g$_0$~1 σ~1	4	-124.855	261.044	3.056	0.1527
		D~x g$_0$~1 σ~1	4	-125.065	261.464	3.476	0.1238
		D~x + y g$_0$~1 σ~1	5	-124.842	265.139	7.151	0.0197
2014	Gros Ventre	D~1 g$_0$~1 σ~1	3	-70.2986	151.397	0	0.9456
		D~x g$_0$~1 σ~1	4	-70.2223	158.445	7.048	0.0279
		D~y g$_0$~1 σ~1	4	-70.2704	158.541	7.144	0.0266
		D~x + y g$_0$~1 σ~1	5	-69.9603	169.921	18.524	0
2014	Buffalo Valley	D~1 g$_0$~1 σ~1	3	-53.4806	118.961	0	0.9905
		D~x g$_0$~1 σ~1	4	-53.4613	128.256	9.295	0.0095
		D~x + y g$_0$~1 σ~1	5	-53.1118	146.224	27.263	0
		D~y g$_0$~1 σ~1	4	-70.2704	158.541	39.58	0

Table 3.6. Population parameter estimates from top SECR models based on cougar scat collection (non-sex grouping models) in Northwest Wyoming. Data was not sufficient for the Buffalo Valley in 2013. Density estimates are in cougars per 100 km^2. Estimates for σ are in meters.

Year	Area	Top model	Density	SE	95% CI	G_0	SE	95% CI	σ	SE	95% CI
2013	Combined area	D ~ lat long	2.19	1.01	(0.92 - 5.19)	0.03	0.01	(0.01 - 0.05)	5,233	931	(3,702 - 7,396)
	Gros Ventre	null	5.70	2.25	(2.70 - 12.02)	0.03	0.01	(0.01 - 0.04)	4,409	1,054	(2,777 - 7,000)
	Buffalo Valley	null	-	-	-	-	-	-	-	-	-
2014	Combined area	null	2.62	0.97	(1.30 - 5.28)	0.02	0.02	(0.02 - 0.10)	3,920	817	(2,617 - 5,873)
	Gros Ventre	null	2.98	1.60	(1.11 - 8.00)	0.05	0.03	(0.02 - 0.13)	3,020	907	(1,698 - 5,372)
	Buffalo Valley	null	1.94	1.71	(0.44 - 8.56)	0.05	0.03	(0.01 - 0.13)	4,754	2,399	(1,870 - 12,090)

Table 3.7. AICc ranking for SECR models using genetics collected from cougar scat in Northwest Wyoming. Models incorporate a sex grouping (2014). ~g indicates a parameter with a group effect. x or y indicate a latitudinal or longitudinal gradient to the density estimate.

Area	model	K	logLik	AIC	AICc	dAICc	AICcwt
Combined areas	D~1 g_0~1 σ~1	3	-128.425	262.85	265.032	0	0.3249
	D~1 g_0~g σ~1	4	-126.909	261.819	265.819	0.787	0.2192
	D~+g g_0~g σ~1	5	-125.517	261.035	267.701	2.669	0.0856
	D~1 g_0~g σ~g	5	-125.905	261.81	268.477	3.445	0.058
	D~1 g_0~1 σ~g	4	-128.267	264.534	268.534	3.502	0.0564
	D~y g_0~1 σ~1	4	-128.356	264.712	268.712	3.68	0.0516
	D~x g_0~1 σ~1	4	-128.372	264.745	268.745	3.713	0.0508
	D~g g_0~1 σ~1	4	-128.392	264.783	268.783	3.751	0.0498
	D~y g_0~g σ~1	5	-126.839	263.679	270.345	5.313	0.0228
	D~x g_0~g σ~1	5	-126.864	263.728	270.395	5.363	0.0222
	D~1 + g g_0~1 σ~g	5	-127.716	265.432	272.099	7.067	0.0095
	D~y g_0~1 σ~g	5	-128.197	266.395	273.061	8.029	0.0059
	D~x g_0~1 σ~g	5	-128.211	266.422	273.089	8.057	0.0058
	D~x + y g_0~1 σ~1	5	-128.29	266.58	273.247	8.215	0.0053
	D~y + g g_0~1 σ~1	5	-128.323	266.645	273.312	8.28	0.0052
	D~x + g g_0~1 σ~1	5	-128.339	266.678	273.345	8.313	0.0051
	D~y + g g_0~g σ~1	6	-125.422	262.845	273.345	8.313	0.0051
	D~1 + g g_0~g σ~g	6	-125.423	262.847	273.347	8.315	0.0051
	D~x + g g_0~g σ~1	6	-125.452	262.903	273.403	8.371	0.0049
	D~y g_0~g σ~g	6	-125.82	263.641	274.141	9.109	0.0034
	D~x g_0~g σ~g	6	-125.856	263.712	274.212	9.18	0.0033
	D~x + y g_0~g σ~1	6	-126.782	265.563	276.063	11.031	0
	D~y + g g_0~1 σ~g	6	-127.641	267.283	277.783	12.751	0
	D~x + g g_0~1 σ~g	6	-127.645	267.29	277.79	12.758	0
	D~x + y g_0~1 σ~g	6	-128.128	268.255	278.755	13.723	0
	D~x + y + g g_0~1 σ~1	6	-128.257	268.513	279.013	13.981	0
Gros Ventre	D~1 g_0~1 σ~1	3	-71.8947	149.789	155.789	0	0.9385
	D~1 g_0~g σ~1	4	-71.0782	150.156	163.49	7.701	0.02
	D~g g_0~1 σ~1	4	-71.642	151.284	164.617	8.828	0.0114
	D~1 g_0~1 σ~g	4	-71.6513	151.303	164.636	8.847	0.0113
	D~x g_0~1 σ~1	4	-71.7595	151.519	164.852	9.063	0.0101
	D~y g_0~1 σ~1	4	-71.8945	151.789	165.122	9.333	0.0088

	D~g g$_0$~1 σ~g	5	-68.6729	147.346	177.346	21.557	0
	D~g g$_0$~g σ~1	5	-69.3885	148.777	178.777	22.988	0
	D~1 g$_0$~g σ~g	5	-70.3438	150.688	180.688	24.899	0
	D~x g$_0$~g σ~1	5	-70.9558	151.912	181.912	26.123	0
	D~y g$_0$~g σ~1	5	-71.068	152.136	182.136	26.347	0
	D~x + g g$_0$~1 σ~1	5	-71.5069	153.014	183.014	27.225	0
	D~x g$_0$~1 σ~g	5	-71.5258	153.052	183.052	27.263	0
	D~x + y g$_0$~1 σ~1	5	-71.6329	153.266	183.266	27.477	0
	D~y + g g$_0$~1 σ~1	5	-71.6419	153.284	183.284	27.495	0
	D~y g$_0$~1 σ~g	5	-71.648	153.296	183.296	27.507	0
	D~g g$_0$~g σ~g	6	-68.3351	148.67	232.67	76.881	0
	D~x + g g$_0$~1 σ~g	6	-68.5089	149.018	233.018	77.229	0
	D~y + g g$_0$~1 σ~g	6	-68.6635	149.327	233.327	77.538	0
	D~x + g g$_0$~g σ~1	6	-69.2373	150.475	234.475	78.686	0
	D~y + g g$_0$~g σ~1	6	-69.3614	150.723	234.723	78.934	0
	D~y g$_0$~g σ~g	6	-70.0387	152.077	236.077	80.288	0
	D~x g$_0$~g σ~g	6	-70.1548	152.31	236.31	80.521	0
	D~x + y g$_0$~g σ~1	6	-70.7602	153.52	237.52	81.731	0
	D~x + y + g g$_0$~1 σ~1	6	-71.3802	154.76	238.76	82.971	0
	D~x + y g$_0$~1 σ~g	6	-71.3895	154.779	238.779	82.99	0
Buffalo Valley	D~1 g$_0$~1 σ~1	3	-71.8947	149.789	155.789	0	0.9385
	D~1 g$_0$~g σ~1	4	-71.0782	150.156	163.49	7.701	0.02
	D~g g$_0$~1 σ~1	4	-71.642	151.284	164.617	8.828	0.0114
	D~1 g$_0$~1 σ~g	4	-71.6513	151.303	164.636	8.847	0.0113
	D~x g$_0$~1 σ~1	4	-71.7595	151.519	164.852	9.063	0.0101
	D~y g$_0$~1 σ~1	4	-71.8945	151.789	165.122	9.333	0.0088
	D~g g$_0$~1 σ~g	5	-68.6729	147.346	177.346	21.557	0
	D~g g$_0$~g σ~1	5	-69.3885	148.777	178.777	22.988	0
	D~1 g$_0$~g σ~g	5	-70.3438	150.688	180.688	24.899	0
	D~x g$_0$~g σ~1	5	-70.9558	151.912	181.912	26.123	0
	D~y g$_0$~g σ~1	5	-71.068	152.136	182.136	26.347	0
	D~x + g g$_0$~1 σ~1	5	-71.5069	153.014	183.014	27.225	0
	D~x g$_0$~1 σ~g	5	-71.5258	153.052	183.052	27.263	0
	D~x + y g$_0$~1 σ~1	5	-71.6329	153.266	183.266	27.477	0
	D~y + g g$_0$~1 σ~1	5	-71.6419	153.284	183.284	27.495	0
	D~y g$_0$~1 σ~g	5	-71.648	153.296	183.296	27.507	0
	D~g g$_0$~g σ~g	6	-68.3351	148.67	232.67	76.881	0
	D~x + g g$_0$~1 σ~g	6	-68.5089	149.018	233.018	77.229	0
	D~y + g g$_0$~1 σ~g	6	-68.6635	149.327	233.327	77.538	0
	D~x + g g$_0$~g σ~1	6	-69.2373	150.475	234.475	78.686	0
	D~y + g g$_0$~g σ~1	6	-69.3614	150.723	234.723	78.934	0

D~y g_0~g σ~g	6	-70.0387	152.077	236.077	80.288	0
D~x g_0~g σ~g	6	-70.1548	152.31	236.31	80.521	0
D~x + y g_0~g σ~1	6	-70.7602	153.52	237.52	81.731	0
D~x + y + g g_0~1 σ~1	6	-71.3802	154.76	238.76	82.971	0
D~x + y g_0~1 σ~g	6	-71.3895	154.779	238.779	82.99	0

Table 3.8. Results from top ranked SECR models using genetics collected from cougar scat in Northwest Wyoming. Models incorporate a sex grouping (2014). The combined area model was a model average. Density estimates are in cougars per 100 km^2. Estimates for σ are in meters.

Area	Top model	Sex	Density	SE	95% CI	G0	SE	95% CI	σ	SE	95% CI
Combined area	(null)+ (g0~sex)	Males	1.09	0.40	(0.54 - 2.2)	0.06	0.28	(0.03 - 0.14)	3,918	792	(2,645 - 5,802)
		Females	1.09	0.40	(0.54 - 2.2)	0.04	0.21	(0.02 - 0.11)	3,918	792	(2,645 - 5,802)
Gros Ventre	null	Males	1.22	0.66	(0.04 - 3.30)	0.05	0.03	(0.02 - 0.15)	3,012	901	(1,698 - 5,345)
		Females	1.22	0.66	(0.04 - 3.30)	0.05	0.03	(0.02 - 0.15)	3,012	901	(1,698 - 5,345)
Buffalo Valley	null	Males	0.73	0.78	(0.13 - 4.05)	0.05	0.03	(0.02 - 0.14)	5,081	2,957	(1,762 - 14,646)
		Females	0.73	0.78	(0.13 - 4.05)	0.05	0.03	(0.02 - 0.14)	5,081	2,957	(1,762 - 14,646)

Table 3.9. Density estimates for a population of cougars in Northwest Wyoming in cougars per 100 km^2. Columns 1-3 compare camera trapping estimates to a telemetry-based reference estimate; Columns 4-6 compare scat collection estimates to the telemetry-based estimate after being adjusted to estimate additional non-adults. We did not estimate a reference or perform camera trapping in 2014; we did not collect scat in 2012. Other missing values are due to inadequate sample size.

Year	Area	Reference est.	SPACECAP cameras (95% HPD)	MARK cameras (95% CI)	Adj. reference est.	SECR scat (95% CI)	CAPWIRE scat (95% CI)
2012	Gros Ventre	1.16	0.57 (0.4 - 0.9)	-	1.97	-	-
	Buffalo Valley	0.34	-	-	0.58	-	-
	Combined areas	0.91	0.57 (0.4 - 0.8)	0.21 (0.21 - 0.21)	1.55	-	-
2013	Gros Ventre	0.90	0.95 (0.4 - 0.8)	-	1.53	5.70 (2.70 - 12.02)	3.44 (2.68 - 5.59)
	Buffalo Valley	0.25	-	-	0.43	-	1.74 (0.68 - ∞)
	Combined areas	0.72	1.1 (0.7 - 1.6)	0.3 (0.3 - 0.3)	1.22	2.19 (0.92 - 5.19)	2.46 (1.88 - 3.97)
2014	Gros Ventre	-	-	-	-	2.98 (1.11 - 8.00)	4.04 (2.33 - 19.12)
	Buffalo Valley	-	-	-	-	1.94 (0.44 - 8.56)	2.78 (1.39 - 6.94)
	Combined areas	-	-	-	-	2.62 (1.30 - 5.28)	3.42 (2.56 - 7.00)

Table 3.10. Cost comparison for noninvasive survey methods used to determine population estimates of cougars, northwestern Wyoming.

Survey Method	Equipment cost	Lab cost	Fuel cost	Personnel cost**	Total cost	Number of detections	Person-days of effort	Detections per person-day	Cost per detection
Remote Cameras	$57,770.00	N/A	$4,200.00	$93,600.00	$155,570.00	48	650	0.0738	$3,241.04
Detection Dogs	N/A	$8,895.00	N/A	$19,378.07	$28,273.07	83*	40	2.0750	$340.64
Winter Transects	N/A	$450.00	$260.64	$14,544.00	$15,254.64	2*	101	0.0198	$7,627.32

*Total detections used in analysis; does not include encounters that failed to yield a genetic identification (219 scat samples were collected from detection dogs ; 19 sets of tracks were encountered in winter transects)

**Based on person-days of work at a wage of

$144 per day
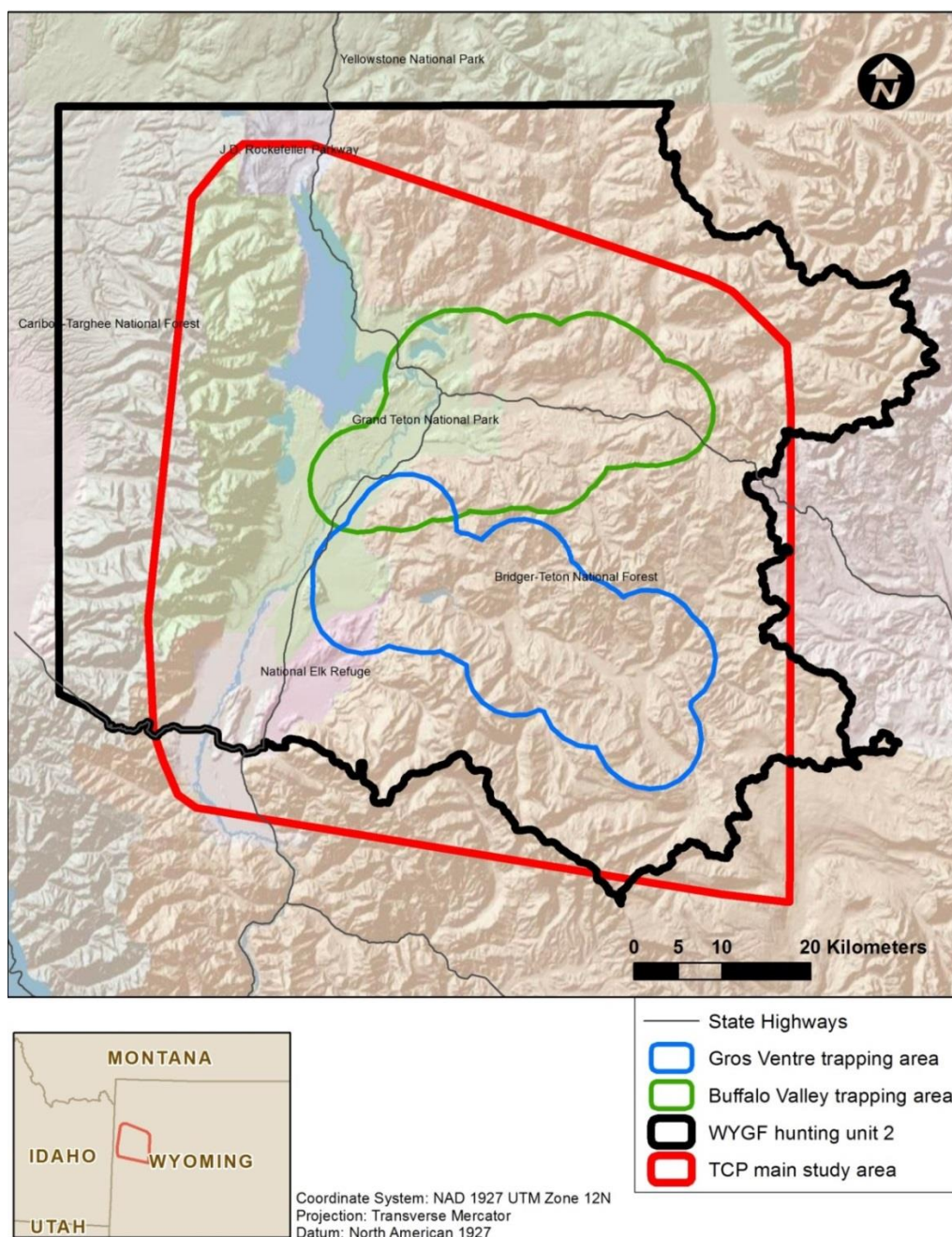
Figure 3.1. The study area, as defined by a minimum convex polygon of all recorded cougar locations over the course of the broader cougar ecology study (in red), northwestern Wyoming. The blue and green polygons delineate the area divisors for determination of the reference density.
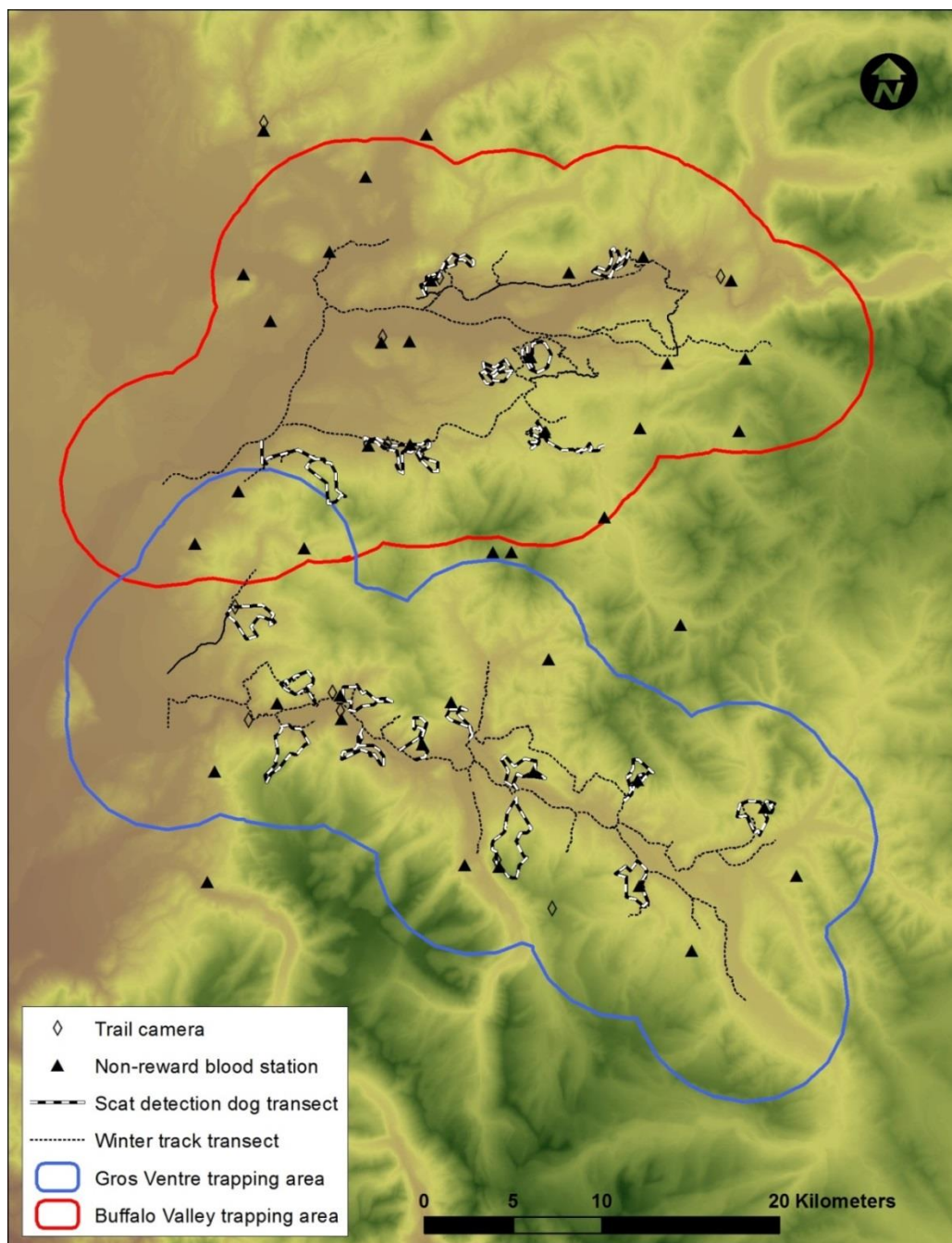
Figure 3.2. Locations of noninvasive detectors and the effective trapping area (area divisor) for detecting cougars, northwestern Wyoming.

Figure 3.3. An example of a photo detection of a cougar at a blood-lure station, northwestern Wyoming. This photo was one of several photos associated with this detection event.
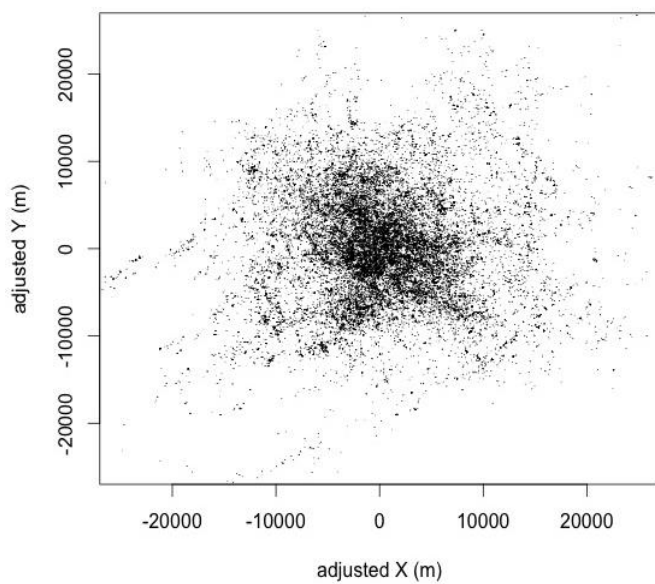
Figure 3.4. Multiple sets of cougar GPS locations, with each annual location set re-centered around the centroid of its respective home range, northwestern Wyoming.
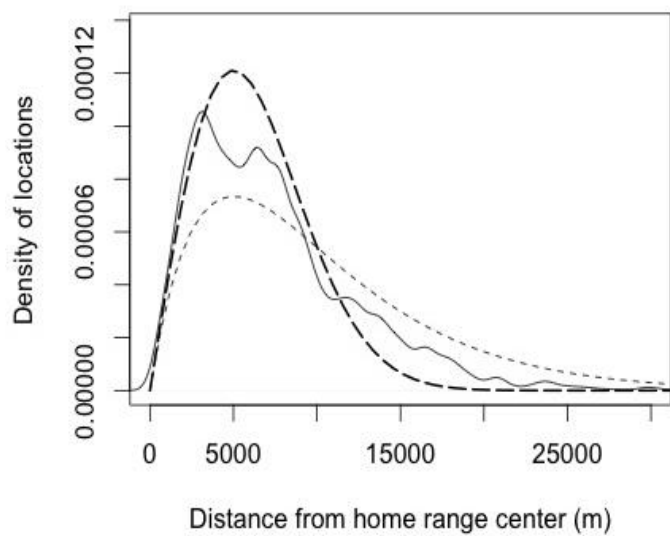
Figure 3.5. Density function for cougar GPS locations as a function of distance from individual

home range center. The solid line represents the GPS locations. Heavy dashed line is a half-

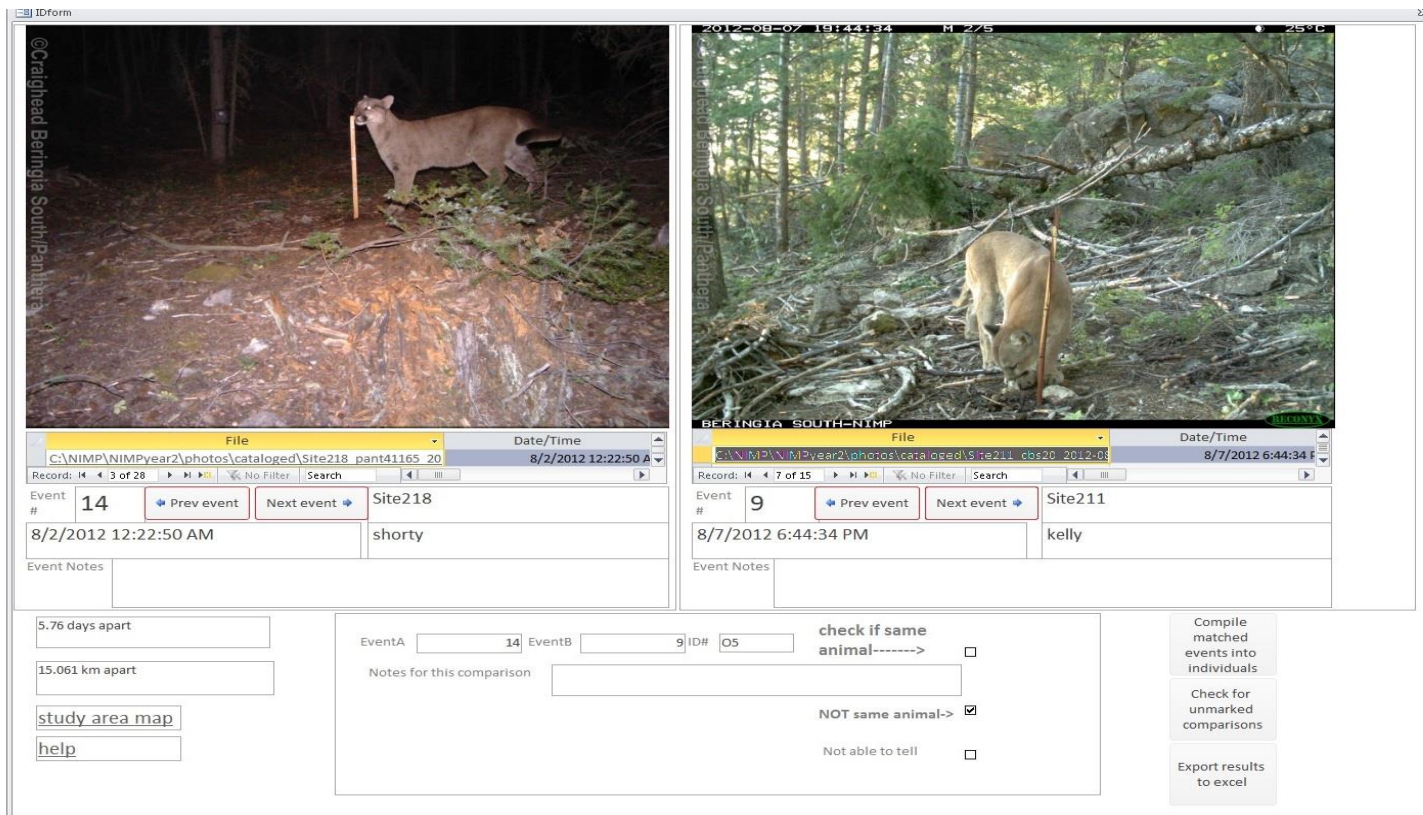normal function. The light dashed line is the negative-exponential function.

Figure 3.6. A screenshot of the MS Access comparison form used to assess the agreement to which independent observers identified individual cougars photo-captured in northwest Wyoming. Users compared the two displayed events and assessed if the cougars were the same or different individuals.
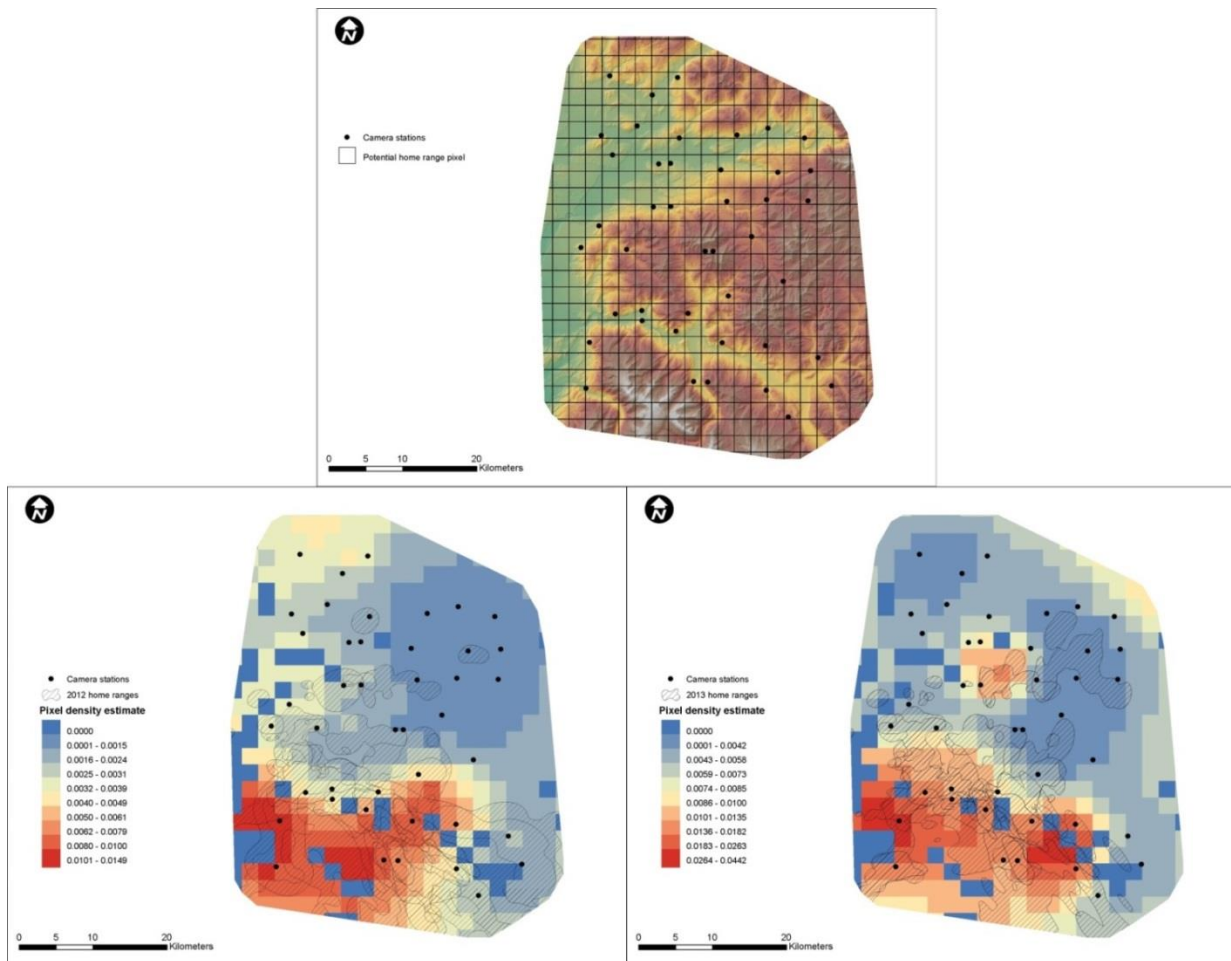
Figure 3.7. Maps with pixel density estimates for photo-captured cougars in northwest Wyoming, produced by SPACECAP. The top map displays the grid of empty 5 km² pixels representing potential home range centers. The bottom maps display 2012 and 2013 pixel density estimates, overlaid with home ranges derived from GPS telemetry.
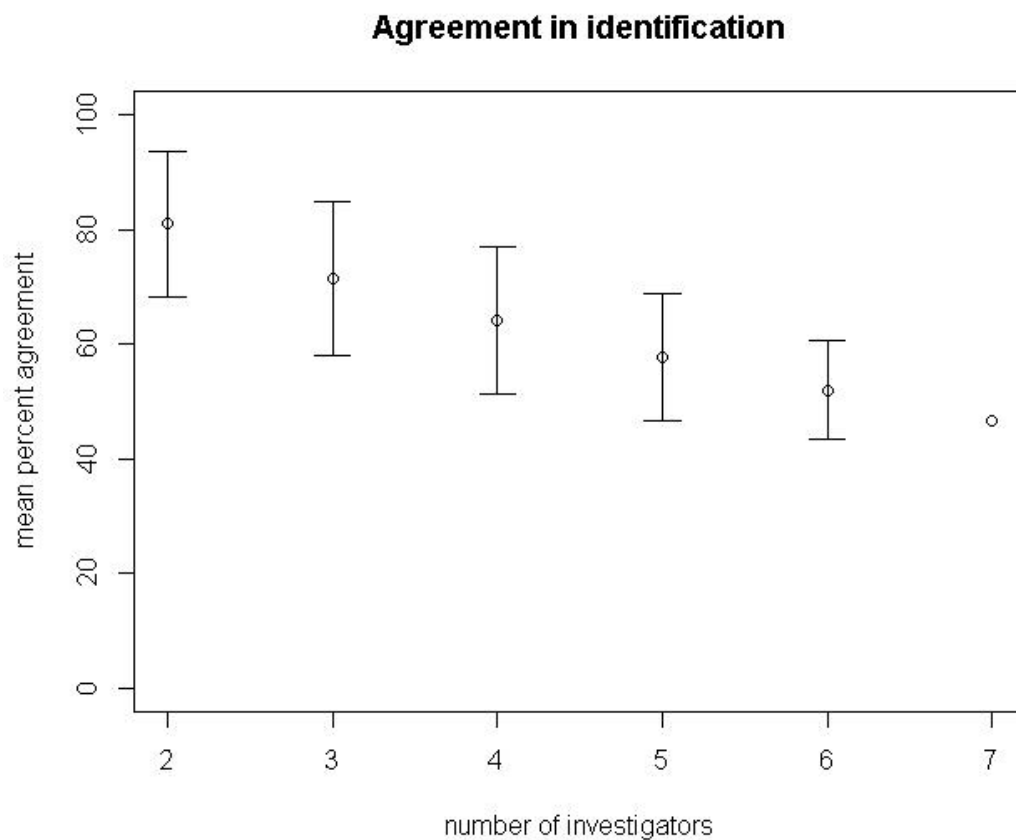
Figure 3.8. Percent agreement for identifying individual cougars from photographs as a function of the number of investigators queried; error bars indicate the standard deviation of the agreement level.
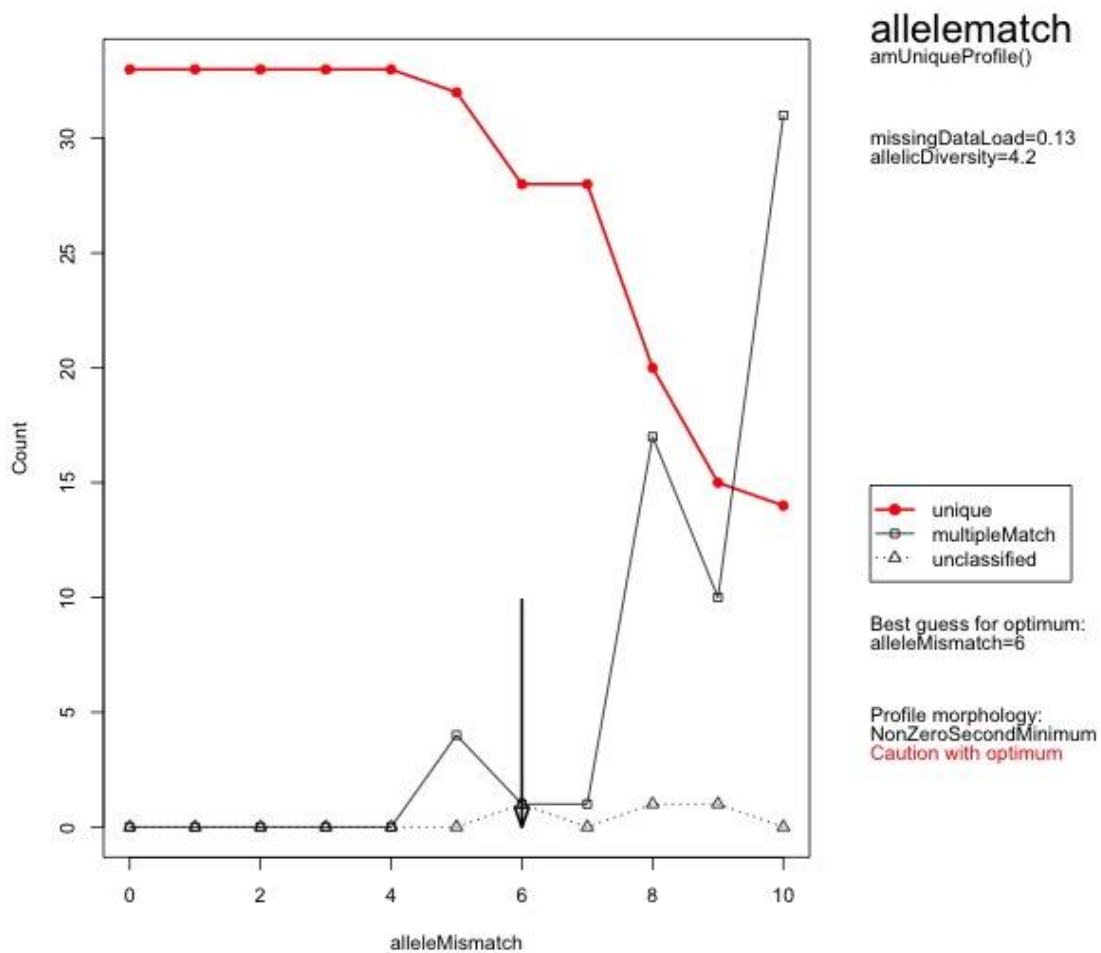
Figure 3.9. Output from the R package allelematch, indicating the optimum mismatch tolerance for determining matched genotypes of cougars sampled noninvasively by scat detection dogs in northwest Wyoming, 2013.
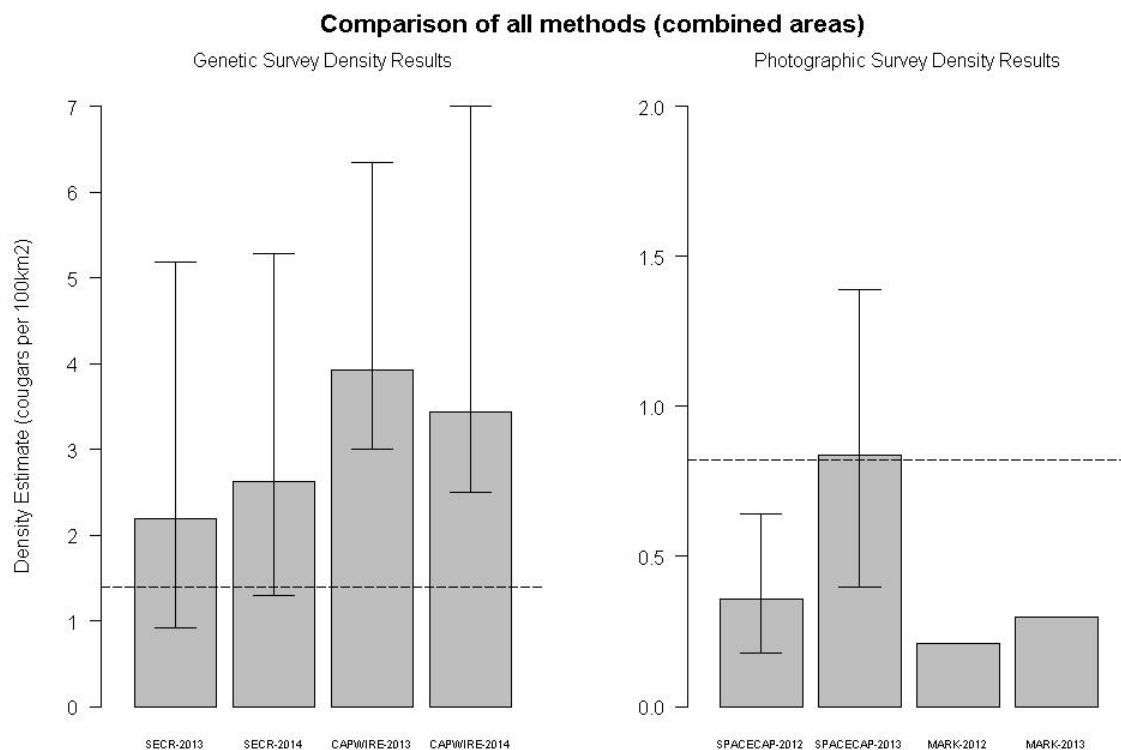
Figure 3.10. Yearly density estimates of cougars sampled noninvasively as determined by SECR, CAPWIRE, SPACECAP, and MARK in northwest Wyoming. The dotted line indicates the mean reference estimate (or adjusted mean reference estimate for genetic surveys), determined from 3 annual telemetry-based enumerations (2011 – 2013).

CHAPTER 4

CONCLUSIONS

This research should prove valuable to management and conservation entities responsible for monitoring cougar (*Puma concolor*) populations. In Chapter 2, we outlined the difficulties and biases associated with the "gold standard" methodology of determining cougar population size or density (i.e., capturing, collaring, and directly counting individuals; Cougar Management Guidelines Working Group 2005). Firstly, this research highlighted the potential for these capture based methods to underestimate cougar densities: acknowledging that different studies will have varying levels of capture effort and ability, our density estimates (for the combined area divisors) increased by an average of 65.2% (n = 3) when including resident cougars that were detected by remote camera, but missed by capture efforts. Secondly, we argued that these enumerative methods should be used in conjunction with an area divisor (i.e., the area over which population size is divided to compute density) that is based on capture-effort (e.g., McLellan 1989) as opposed to animal location (e.g., Cooley et al. 2009*a*, *b*; Elbroch and Wittmer 2012). This method reduces bias associated with "cougar aggregations" (Smallwood 1997), and is more informative when making comparisons to other survey methods covering the same area. Using this method, we estimated the density of a population of cougars in Northwest Wyoming, which was spatially comparable to the noninvasive densities estimated in Chapter 3.

In Chapter 3, we examined three types of noninvasive survey methods to estimate cougar density: winter tracking transects, remote camera surveys, and scat detection dog surveys. Most importantly, our results demonstrated that scat detection dogs were an

order of magnitude less expensive than the other methods, in terms of cost-per-detection. The scat detection dog surveys also produced a greater number of detections in a shorter collection time, although the true sampling window (i.e., the temporal window in which an individual cougar could be detected) was not known with certainty. The winter tracking surveys did not yield enough detections for any useful population analysis; we recommend careful consideration of the issues outlined in our discussion, as well as similar studies' results (e.g., Sawaya et al. 2011, Russell et al. 2012). The remote camera survey produced fewer detections over a greater time span, and, most importantly, our analysis of human ability to identify individual cougars in photographs indicated that this method is not reliable in a capture-mark-recapture framework. We also demonstrated that SECR models (Efford 2011, Royle et al. 2011) may be more applicable to cougar populations than conventional CMR models, due to cougars' large home ranges that can extend beyond the boundaries of a survey area.

Cougars, as with many large carnivores, have undergone major population declines and range contractions over the past century due to habitat loss, habitat fragmentation, and direct human persecution (Ripple et al. 2014). In recent decades, many cougar populations have exhibited signs of recovery at local range levels (Thompson and Jenks 2010, LaRue et al. 2012, Knopff et al. 2014), while others may still be susceptible to decline (Laundre et al. 2007, Knopff et al. 2010). Given cougars' vast historic range, and potential role as both a top-down regulator (Ripple and Beschta 2006) and an umbrella species (Beier 2009), identifying these areas of extirpation or recolonization should be a priority for conservationists and managers. In this thesis, we learned important lessons on the applicability and efficacy of three commonly proposed

noninvasive survey techniques for cougars. We also addressed several issues and difficulties that can hamper monitoring efforts, including those related to cougars' large home ranges (i.e., temporary immigration/emigration; Kendall et al. 1997) and tendency to shift in population aggregations over time (Smallwood 1997).

LITERATURE CITED

Beier, P. 2009. A focal species for conservation planning. Pages 177–189 *in* M. Hornocker and S. Negri, editors. Cougar: ecology and conservation. University of Chicago Press, Chicago, USA.

Cooley, H. S., R. B. Wielgus, G. Koehler, and B. Maletzke. 2009*a*. Source populations in carnivore management: cougar demography and emigration in a lightly hunted population. Animal Conservation 12:321–328.

Cooley, H. S., R. Wielgus, G. M. Koehler, H. S. Robinson, and B. T. Maletzke. 2009*b*. Does hunting regulate cougar populations? A test of the compensatory mortality hypothesis. Ecology 90:2913–2921.

Cougar Management Guidelines Working Group. 2005. Cougar Management Guidelines. T. Beck, J. Beecham, P. Beier, T. Hofstra, M. Hornocker, F. Lindzey, K. Logan, B. Pierce, H. Quigley, I. Ross, H. Shaw, R. Sparrowe, and S. Torres, editors. WildFutures, Bainbridge Island, Washington, USA.

Efford, M. G. 2011. Estimation of population density by spatially explicit capture-recapture analysis of data from area searches. Ecology 92:2202–2207.

Elbroch, L. M., and H. U. Wittmer. 2012. Puma spatial ecology in open habitats with aggregate prey. Mammalian Biology 77:377–384.

Kendall, W. L., J. D. Nichols, and J. E. Hines. 1997. Estimating temporary emigration using capture-recapture data with Pollock's Robust Design. Ecology 78:563–578.

Knopff, K. H., A. A. Knopff, A. Kortello, and M. S. Boyce. 2010. Cougar kill rate and prey composition in a multiprey system. Journal of Wildlife Management 74:1435–1447.

Knopff, K. H., N. F. Webb, and M. S. Boyce. 2014. Cougar population status and range expansion in Alberta during 1991-2010. Wildlife Society Bulletin 38:116–121.

LaRue, M. A., C. K. Nielsen, M. Dowling, K. Miller, B. Wilson, H. Shaw, and C. R. Anderson. 2012. Cougars are recolonizing the midwest: analysis of cougar confirmations during 1990-2008. Journal of Wildlife Management 76:1364–1369.

Laundre, J. W., L. Hernandez, and S. G. Clark. 2007. Numerical and demographic responses of pumas to changes in prey abundance: testing current predictions. Journal of Wildlife Management 71:345–355.

McLellan, B. 1989. Dynamics of a grizzly bear population during a period of industrial resource extraction. I. density and age-sex composition. Canadian Journal of Zoology 67:1856–1860.

Ripple, W. J., and R. L. Beschta. 2006. Linking a cougar decline, trophic cascade, and catastrophic regime shift in Zion National Park. Biological Conservation 133:397–408.

Ripple, W. J., J. A Estes, R. L. Beschta, C. C. Wilmers, E. G. Ritchie, M. Hebblewhite, J. Berger, B. Elmhagen, M. Letnic, M. P. Nelson, O. J. Schmitz, D. W. Smith, A. D. Wallach, and A. J. Wirsing. 2014. Status and ecological effects of the world's largest carnivores. Science 343:6167.

Royle, J. A., M. Kéry, and J. Guélat. 2011. Spatial capture-recapture models for search-encounter data. Methods in Ecology and Evolution 2:602–611.

Russell, R. E., J. A. Royle, R. Desimone, M. K. Schwartz, V. L. Edwards, K. P. Pilgrim, and K. S. McKelvey. 2012. Estimating abundance of mountain lions from unstructured spatial sampling. Journal of Wildlife Management 76:1551–1561.

Sawaya, M. A., T. K. Ruth, S. Creel, J. J. Rotella, J. B. Stetz, H. B. Quigley, and S. T. Kalinowski. 2011. Evaluation of noninvasive genetic sampling methods for cougars in Yellowstone National Park. Journal of Wildlife Management 75:612–622.

Smallwood, K. S. 1997. Interpreting puma (*Puma concolor*) population estimates for theory and management. Environmental Conservation 24:283–289.

Thompson, D. J., and J. A. Jenks. 2010. Dispersal movements of subadult cougars from the Black Hills: the notions of range expansion and recolonization. Ecosphere 1:1–11.