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POPULATION ESTIMATION AND FIXED KERNEL ANALYSES OF ELK IN MICHIGAN

By

Daniel Paul Walsh

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Fisheries and Wildlife

2007

ABSTRACT

POPULATION ESTIMATION AND FIXED-KERNEL ANALYSES OF ELK IN MICHIGAN

By

Daniel Paul Walsh

Michigan proudly boasts an elk herd heavily utilized by a wide array of stakeholders from across the Midwest with varying recreational interests. Recently, significant changes have occurred within and surrounding the elk range, which have created concern among elk managers that historical techniques and management strategies may no longer be adequate to address the current issues facing Michigan's elk. This project was initiated and designed to gain valuable information and develop new techniques that will provide elk managers with the knowledge and tools for successful management of one of Michigan's most unique natural resources. I developed a population estimation procedure based on a sightability model framework using fixed-wing aircraft, which allowed for correction for visibility bias associated with missing elk groups. Incorporated into this technique was the ability to estimate group sizes, which reduced bias of population estimates and resulted in near nominal confidence interval coverage. Using this technique I estimated the Michigan elk herd to be approximately 905 (SE = 125). I collected 13,923 locations using triangulation procedures, and 728 visual observations of 58 radiocollared elk. I estimated individual home ranges for each animal using fixed-kernel estimation procedures, and determined that mean bull home range size (9,587 ha) was significantly larger than cow home range size (6,349 ha). Additionally, kernel surfaces were averaged to allow for population level inference about range use patterns. Analyses showed an uneven distribution of range use with many peaks and valleys in the probability density surface. There was considerable joint space use between elk from different summering areas based on dispersal patterns from capture sites, movement data and by examining the joint density surfaces calculated from the independent kernel density functions for each individual elk. Two large ranches in the center of the elk range, Black River and Canada Creek, received substantial use by elk throughout the year although use varied seasonally. Elk use within these ranches was highly localized, and changed in response to habitat manipulations. Also, movement patterns of bulls inhabiting Canada Creek Ranch indicated that these bulls are likely breeding bulls from across the range. Using the averaged kernel density surface, I demonstrated that management efforts focused on maintaining and enhancing wildlife openings are having the desired effect as elk used managed openings with a significantly higher probability than unmanaged openings. The elk range unfortunately lies within the endemic region for bovine tuberculosis (TB), which infects free-ranging deer in this area. Using the averaged kernel density with historical TB prevalence data, I identified high-risk areas for elk being exposed to TB. Three high-risk areas were delineated, and these areas corresponded well with locations of known TB positive elk. Lastly, I examined the range use patterns of a radiocollared cow that was infected with TB and her joint space use with other elk in the region. Results showed that this elk had a home range of 8,856 ha, potentially exposing numerous other individuals and species to infection either through direct or indirect contact. Elk population and management decisions must account for the dynamic movement patterns that exist in this region of the elk range to accommodate diverse recreational objectives.

ACKNOWLEDGEMENTS

This project was supported by the Federal Aid in Restoration Act under Pittman-Robertson project W-147-R, Michigan Agricultural Experiment Station and through generous contributions from the Rocky Mountain Elk Foundation and Safari Club International. I sincerely extend my gratitude to all these organizations for their support.

I want to extend special thanks to each of my graduate committee members for their contributions to this study as well as to my professional development. I especially want to thank Dr. Connie Page for her assistance when I would hit a "brick wall" while working out the variance equations for the population estimator. Without her I am not sure I would have ever finished this dissertation. I want to thank Dr. Dean Beyer for his logistical support, for providing an essential agency perspective, and for his amazing ability to tackle elk. I extend my gratitude to Dr. Scott Winterstein for his ability to put up with my "tough" questions, and to find the humor in every situation. Also I want to thank Dr. Graham Hickling for providing insights into TB issues, which stimulated many of the analyses with regard to elk and TB. Lastly, I want to thank my major professor Dr. Rique Campa for his friendship, constant support and insights into elk in Michigan which proved valuable at every step of this project, and for giving me this opportunity.

The success of this project is due in large part to the assistance I received from the many technicians that worked with me on this study. I learned much from each person with whom I worked. In particular, Amy Belson, Randy Havens, Greg Hochstetler, Mike Budd, Katie McIntyre, Tanner Dixson, Leslie Witter, Mark Tessmer and Chris Jeszke were outstanding employees as well as friends. I owe them a deep debt of gratitude.

The support for this project by the MDNR employees working in the elk range was amazing. I want to recognize, Unit Supervisor, Glen Matthews for his support and commitment to this project. Also Brian Mastenbrook, Elaine Carlson, Bill Green, Kevin Jacobs, Keith Fisher, Mark Monroe and Carrie Steen provided critical knowledge and assistance particularly during the development of the sightability model. I especially want to thank the Atlanta field crew for their help and more importantly their friendship. I learned more than I can say about elk and wildlife management from Dave Smith, it was truly a pleasure to have the opportunity to work with him. I will miss the stories and laughs I shared with Joe Valentine, Bruce Baker and Joe Molnar. They will be some of my fondest memories of working in the elk range. Lastly, there were numerous volunteers on this project particular during the flights, thank you all for your help.

I was also privileged to work with and count among my friends the other members of the *Ne Plus Ultra*, Ali Felix and Dan Linden. I was truly blessed to have had the opportunity to cross your paths on the walk of life, and what I have learned from knowing you and the memories I have shared will not be forgotten.

I must recognize my friends, too numerous to mention, who have always been there for me; I could never have made it without you all. Also I want to acknowledge my brothers and sisters, Bill, Rose, Sam, Joe, Rachel, John, Mary and Theresa for always being there for me, as well as the rest of my family.

Lastly, I am deeply indebted to my parents Bill and Dolores Walsh. Your sacrifices have allowed me to realize my dreams, and all my past, present and future successes are yours. Words cannot express my gratitude or how much I owe you.

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CHAPTER 1: INTRODUCTION

History

An extinct subspecies of elk (*Cervus elaphus canadensis*) once roamed the Lower Peninsula of Michigan, however, by the late 1800's the species was believed to be extirpated from the state (O' Gara and Dundas 2002). During the early 20th century, the state of Michigan initiated a series of reintroduction activities aimed at reestablishing the species in the northeastern region of the Lower Peninsula. It is generally believed among biologists that the entire Michigan elk herd arose from a 1918 reintroduction of 7 Rocky Mountain elk (*Cervus elaphus nelsoni*) southeast of Wolverine in Nunda Township of Cheboygan County (Moran 1973). But, based on historic and genetic evidence presented by Glenn and Smith (1993), it appears that the herd originated from multiple source populations with some evidence of founding individuals being Roosevelt elk (*Cervus elaphus roosevelti*). Thus, to explain the variability observed in the genetic data, it is likely that reintroductions other then the 1918 reintroduction were also successful, and/or private individuals were also releasing elk.

Despite the uncertainty of the origin of Michigan's elk herd, the population grew substantially until by 1964 the herd was estimated at over 2,000 elk (Moran 1973). With a population of this magnitude, tourism based on elk viewing became popular. However, increasing elk damage to forests, wildlife range and agricultural crops created conflicts that intensified throughout the 1960's. To address these conflicts, the Michigan Department of Natural Resources (MDNR) instituted hunts in 1964–1965. During these years, 477 elk were taken legally (Moran 1973). In the following years the elk herd decreased substantially. By 1975, when the MDNR conducted a combined aerial-snowmobile survey, they estimated only 200 animals comprised the entire herd (Beyer 1989). The serious decline was attributed to widespread poaching, lack of habitat management and human disturbances (Ruhl 1984). To combat these low population levels the MDNR developed the elk management plan, which focused on increasing the elk herd to 500–600 individuals through reduction of poaching activities and increased elk habitat management. By 1984, the population was estimated at 850 individuals, and conflicts similar to those observed in the 1960's were once again emerging. In response to these issues, the state began controlled hunting of the elk herd in 1984 (Beyer 1987). The same year, the MDNR formalized its elk management plan with the following objectives (Michigan Department of Natural Resources 1984: 24–25):

1. "Maintain a visible herd of 600–800 elk for public viewing.
2. When the elk herd reaches an optimal population level (easily viewable with minimal damage to agriculture and range), utilize a portion of the annual production through a controlled annual hunt.
3. Protect elk habitat.
4. Protect elk from illegal kill."

The elk plan had the desired effects, as the elk population has remained generally above 800 animals. Elk viewing remains a popular tourist attraction, and crop and forest damage complaints are minimal.

Current Issues

In recent years, there has been a noticeable change in the distribution of elk throughout their range. The historical elk range encompasses an area of approximately 1550 km^2

centered on the Pigeon River State Forest. Recently, there has been a noticeable range expansion in the southerly and easterly directions (Figure 1), and it has been estimated the range has expanded by approximately over 50% from where it had occurred in 1984 (D. E. Beyer, Michigan Department of Natural Resources, unpublished report). These range expansions are not entirely understood. However, it is likely that the 1998 ban on baiting and winter feeding of elk and white-tailed deer (*Odocoileus virginianus*), intended to minimize the transmission and spread of bovine tuberculosis (TB), is a major causative factor contributing to this expansion. This expansion created concern among elk managers and researchers that current management activities are no longer adequate, as elk are distributing themselves away from areas dominated by public lands to regions with a greater amount of private lands and agricultural activities. Also the easterly range expansion shifts elk into regions with higher TB prevalence in the white-tailed deer herd, creating concerns of increased TB transmission from deer to elk (Hickling 2002). Thus, understanding how elk in Michigan are currently utilizing the range is crucial from a management perspective.

Additionally, elk researchers and managers were concerned the current population estimation procedure, since it does not account for these changes in elk range utilization patterns, it is no longer adequate for management purposes.

Objectives

The objectives of this study were focused on addressing the current issues facing elk managers as described above. The objectives were as follows:

1. Document elk movement patterns and range use throughout both the historical range as well as areas of range expansion.

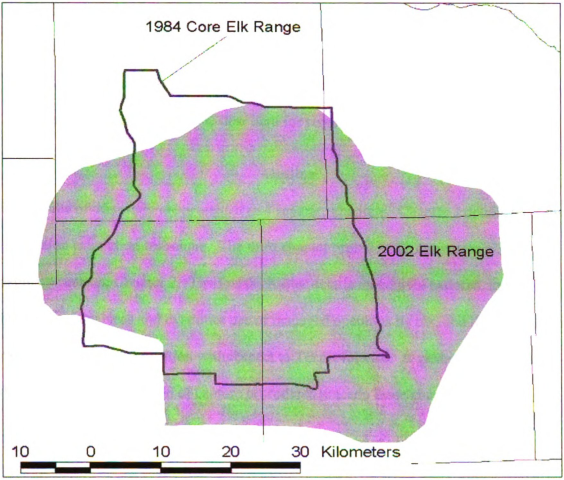


Figure 1. The areas of range expansion outside the historical elk range in Michigan, 2002 (adopted from D.E. Beyer, Michigan Department of Natural Resources, unpublished report).

2. Develop a population estimation procedure that will produce accurate and precise estimates while accounting for shifting elk distributions.
3. Determine areas of the elk range that exhibit a high level of elk usage as well as a high TB prevalence in the deer herd for targeted management efforts.

Outline

The results of this study are presented in 4 separate chapters. Chapter 2 details the new population estimation technique. The third chapter provides the derivation of the estimator used in Chapter 2. The fourth chapter details movement patterns, individual home range analyses and examines use of managed openings by elk, and the final chapter examines elk range utilization with respect to TB prevalence. A general study area description and description of capture procedures precede these chapters.

Study Area

The elk range in Michigan encompasses portions of 4 counties, Cheboygan, Montmorency, Otsego and Presque Isle, in the northeastern corner of the Lower Peninsula of Michigan (Figure 2). The historic or core elk range occupies approximately 1,550 km^2, and is centered on the Pigeon River State Forest near Vanderbilt, Michigan (Bender 1992). The entire elk range accounting for areas of recent range expansion encompasses approximately 3,450 km^2 (D.E. Beyer, Michigan Department of Natural Resources, unpublished report). This study focused mainly on the eastern region of the elk range near Atlanta in Montmorency County (Figure 3). Over 33% of the elk range is publicly owned, with another 3% controlled by 2 large private hunting clubs in the center of the range (Michigan Department of Natural Resources 2000).

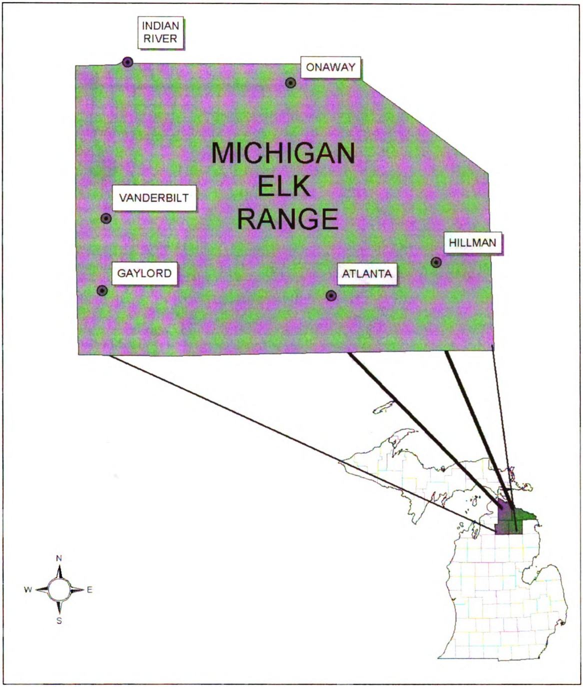


Figure 2. General location of Michigan elk range in Michigan, 2003.

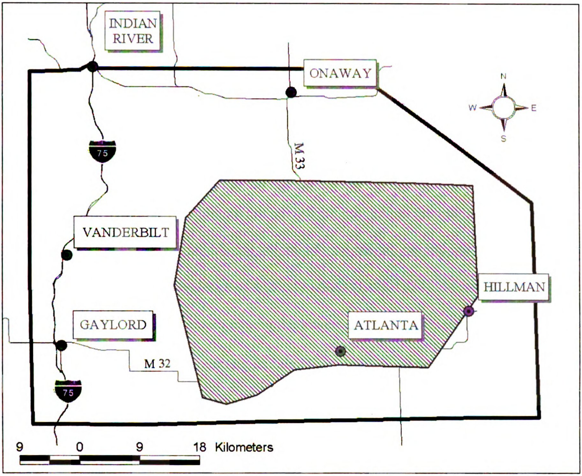
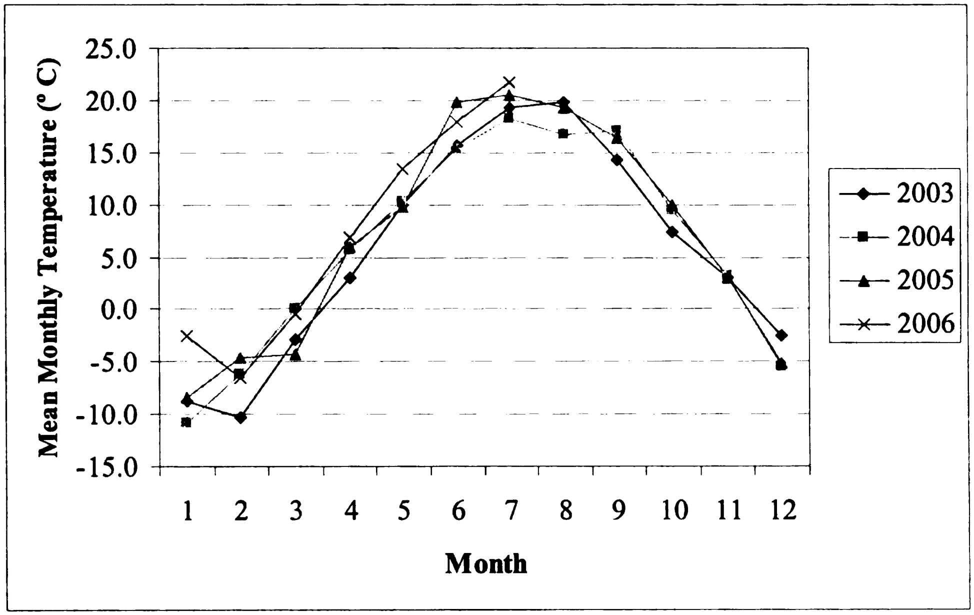


Figure 3. General location of the study area (cross-hatched area) within the elk range in Michigan, 2006.

Topography of the area slopes northerly and consists of flat-topped ridges interspersed with headwater swamps and outwash plains created through glacial actions (Moran 1973). Originating in these headwater swamps are the Black, Pigeon and Sturgeon rivers, which drain the study area (Ruhl 1984). Podzol soils characterize the region, and range from relatively infertile, dry sandy soils on outwash plains to medium high fertility soils on till plains and moraines (Moran 1973).

Climatic conditions are less affected by the Great Lakes than other regions in the state with most noticeable effects being increased cloudiness, moderation of fall and early winter temperatures and prevalence of westerly winds (Ruhl 1984). Mean annual temperature is 6.3° C with January having the lowest mean monthly temperature (-7.7° C) and the highest (19.7° C) occurring in July (NOAA 2006). The maximum mean monthly temperatures during the study (2003–2006) was 20.4° C in July 2005, and the minimum mean monthly temperature was -10.8° C in January 2004 (Figure 4). With the exception of 2003, generally mean monthly temperatures were above the long-term average for the study years (Figure 5). Mean annual rainfall is 67.3 cm, and mean annual snowfall is 189 cm (NOAA 2006) with precipitation being generally well distributed throughout the year. The maximum monthly precipitation total, 12.52 cm, occurred in August 2005, and the minimum monthly precipitation total, 0.48 cm, occurred in January 2003 (Figure 6). Mean monthly precipitation totals throughout the study were generally below the long-term average (Figure 7).

Due to variations in soil fertility, aspect and moisture levels, vegetation types are diverse and well interspersed. In addition logging, agriculture, and management activities further complicate the pattern of vegetation types throughout the area. Moran



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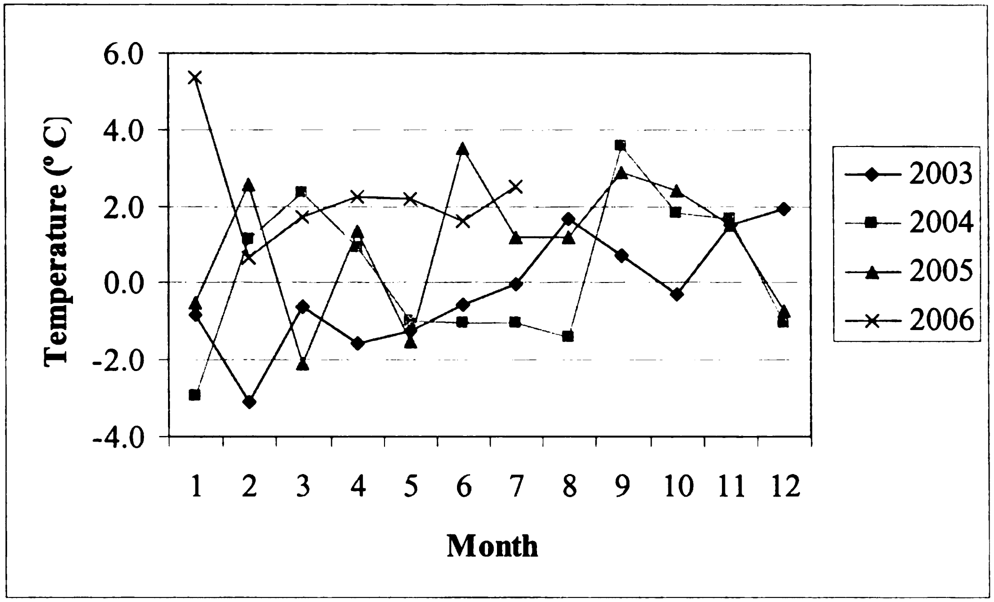


Figure 5. Differences in mean monthly temperature (° C) from long-term averages for the study area recorded at the National Oceanic and Atmospheric Administration weather station at Alpena Regional Airport, 2006.

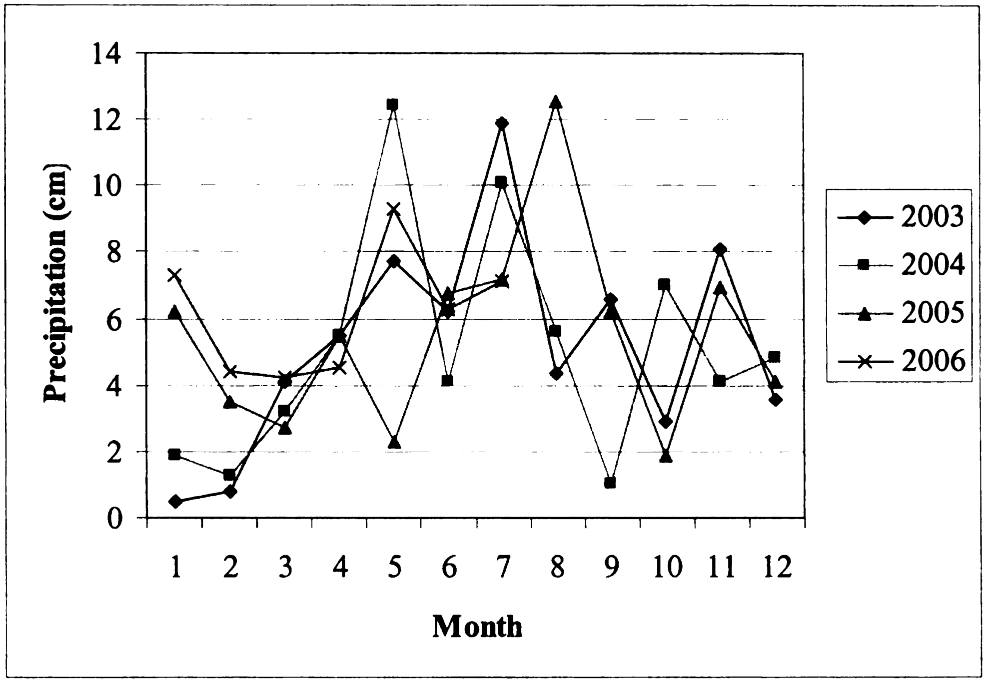


Figure 6. Monthly precipitation totals (cm) for the study area recorded at the National Oceanic and Atmospheric Administration weather station at Alpena Regional Airport, 2006.

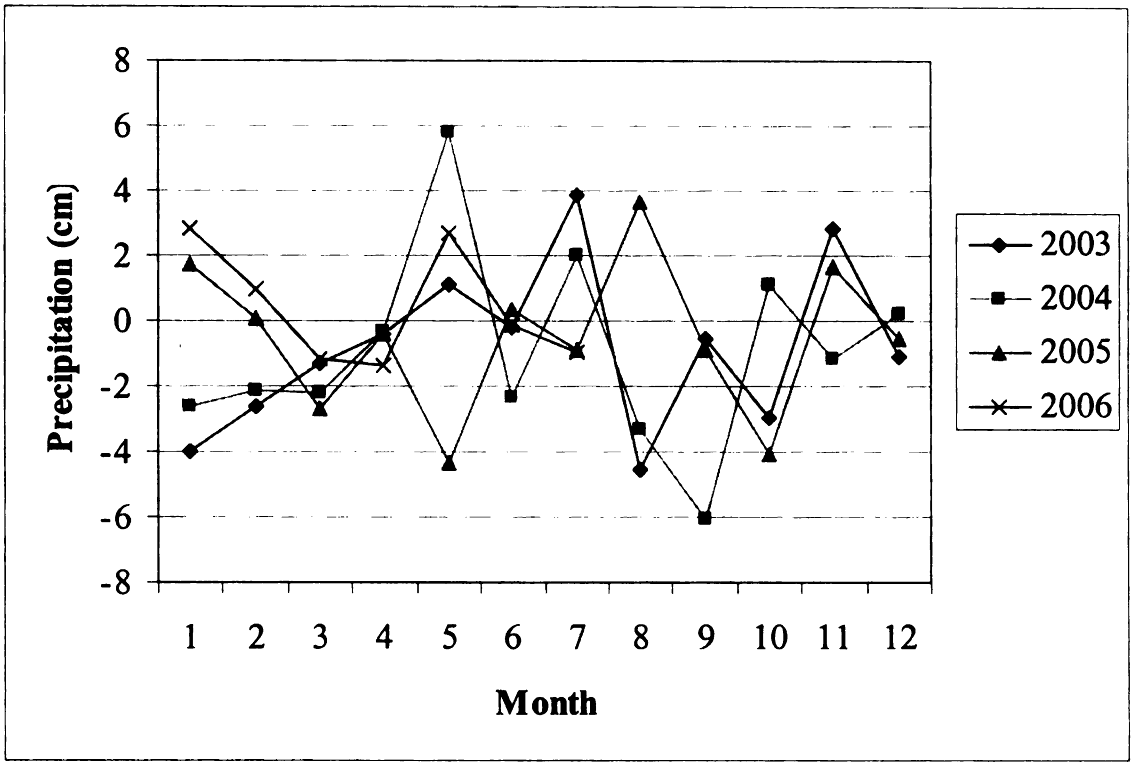


Figure 7. Differences in precipitation totals (cm) from long-term averages for the study area recorded at the National Oceanic and Atmospheric Administration weather station at Alpena Regional Airport, 2006.

(1973) gives a detailed description of the vegetation of the region. Typical vegetation found on moraine uplands consist of sugar maple (*Acer saccharum*), red pine (*Pinus resinosa*), white pine (*Pinus strobus*), hemlock (*Tsuga canadensis*), basswood (*Tilia americana*), red maple (*Acer rubrum*), and northern red oak (*Quercus borealis*). Aspen (*Populus tremuloides*), red oak, red pine and white pine are found on steep morainic slopes. Red maple, white birch (*Betula papyrifera*) and aspen characterize the outwash plain-morainic ecotone. Sandy outwash plains are typified by jack pine (*Pinus banksiana*), cherry (*Prunus spp.*) and willow (*Salix spp.*). Riverbanks and bottomlands support ash (*Fraxinus spp.*), speckled alder (*Alnus rugosa*), dogwoods (*Cornus spp.*), white cedar (*Thuja occidentalis*) and red elm (*Ulmus fulva*). Coniferous swamps typically contain white cedar, balsam fir (*Abies balsamea*), black spruce (*Picea mariana*) and balsam poplar (*Populus balsamifera*). These typical forest cover types are found throughout the study area in varying age classes and stocking rates.

Capture Procedures

Capturing and radiocollaring elk was critical to achieving all the objectives for this project. All capture operations were planned and conducted by MDNR and contractors, and therefore, this project was exempted by the All University Committee on Animal Use and Care (D. L. Garling, All University Committee on Animal Use and Care, written communication, 01 27 2003).

The eastern edge of the traditional elk range and areas of range expansion were targeted for elk captures, as this region represents areas of elk distribution shifts and incorporates a portion of the TB endemic area for white-tailed deer in Michigan (Garner 2001, Hickling 2002). Captures were conducted during the winter since elk are more readily located from the air against the snow background. Home range sizes tend to be smaller during this time period (Ruhl 1984) allowing for more consistent relocation of elk groups by capture crews. Also during winter, group sizes of bull/cow groups and bull only groups are largest (Beyer 1987, Bender 1992) increasing the probability of large numbers of individuals being discovered and being captured. Lastly, Moran (1973) provided some anecdotal evidence of intermingling of elk from various portions of the elk range during winter, based on dispersal of marked individuals. Thus, winter captures likely allowed for the marking of a more representative sample of animals from across the range.

Two different capture techniques were employed to capture animals. Helicopter net-gunning techniques were used to capture elk in February, 2003 (Carpenter and Innes 1995). Hawkins and Powers Aviation (Greybull, Wyoming, USA) was contracted for this operation. Once captured, each animal was radiocollared with a 550 g, Telonics (Mesa, Arizona, USA), MOD-600HC radiocollar transmitting on a unique frequency in the 150-152 MHz range with brown leather collar bands. Collars have a predicted battery life of 4 years and are equipped with a MS6A, 6 hr mortality sensor. Upon capture blind folds and ear plugs were placed on the animal. Personnel recorded the sex of each animal, ear-tagged, and obtained blood, fecal, and hair samples for analysis if condition of the animal permitted. Capture personnel monitored the condition of an animal during handling by observing coloration of mucous membranes, which indicates proper blood pressure and blood oxygen levels. Also respiration rate, pulse and body temperature were monitored as indicators of animal condition. Average normal body conditions include the following: mucous membranes of a pinkish color, respiration rate typically between 6–12 breaths/min., pulse of 60–70 beats/min., and temperature of 38.3 °C (Michigan Department of Natural Resources 2003). If a captured individual's body temperature reached a maximum of 40.6 °C, if respiration became shallow and rapid, or if mucous membranes became gray or blue, the individual was immediately released. Lastly, personnel gave most animals an intramuscular injection of 5–10 cc of the long-lasting antibiotic, Flocillian (Bristol Laboratories, Syracuse, New York, USA) to minimize infection.

Chemical immobilization techniques were used by MDNR personnel in July 2004 to capture elk (Roffe et al. 2005). Carfentanil was administered by intramuscular injection using a dart gun (Pneudart, Williamsport, Pennsylvania, USA) in the rear hindquarter. Once an animal succumbed to the anesthesia, personnel followed the same procedures as describe for net-gunning. Naltrexone at 125 times the carfentanil dose was injected into the jugular as a reversal.

In February 2005, MDNR in conjunction with Quiksilver Air (Fairbanks, Alaska, USA), collared additional elk using net-gunning techniques. Also 4 animals that had grown significantly since 2003 were recollared. Capture techniques and protocol were as before. However, 5 of these animals were collared with Advanced Telemetry System's (Isanti, Minnesota, USA) G2000 GPS collars, rather than the standard VHF radiocollars. These collars were programmed to take fixes every 7 hours.

Capture Results, Mortalities, Current Status

The MDNR personnel captured 58 elk throughout the study (Table 1). Twenty adult bulls and 20 adult cows were captured in 2003, 2 adult cows were darted in 2004, and 16 adult cows were captured in 2005. No mortalities as a result of capture occurred during this study. Capture locations were distributed throughout the eastern portion of the range (Figures 8–9). Images in this dissertation are presented in color.

A total of 20 mortalities occurred during the study period (Table 1). Ten of these elk died as a result of legal or illegal hunting activities. During the mandatory hunter orientation before the 2003–2006 elk hunts, hunters were asked to avoid shooting collared animals to allow for collection of long-term datasets, however there were no legal mandates against shooting a collared animal. Generally, hunters willingly complied with this request, and many hunters at the check station reported seeing and passing up shots on collared animals. Of the hunters harvesting collared elk, all but 1 individual reported that they did not see the collar on the animal prior to harvest.

Other mortalities factors included: 1 cow died of old age (22 yr), 1 cow died of exhaustion after becoming mired in an old beaver pond, 1 cow broke her neck running into a fence, 1 cow died of a meningeal worm (*Parelaphostroneylus tenuis*) infection, and 1 bull died of unknown causes, although age (14 yr) may have been a contributing factor. Additionally, the 5 GPS collars were removed in October 2005 off of 2 bulls and 3 cows. As of January 2007, there were currently 33 active collars on 11 bulls and 22 cows.

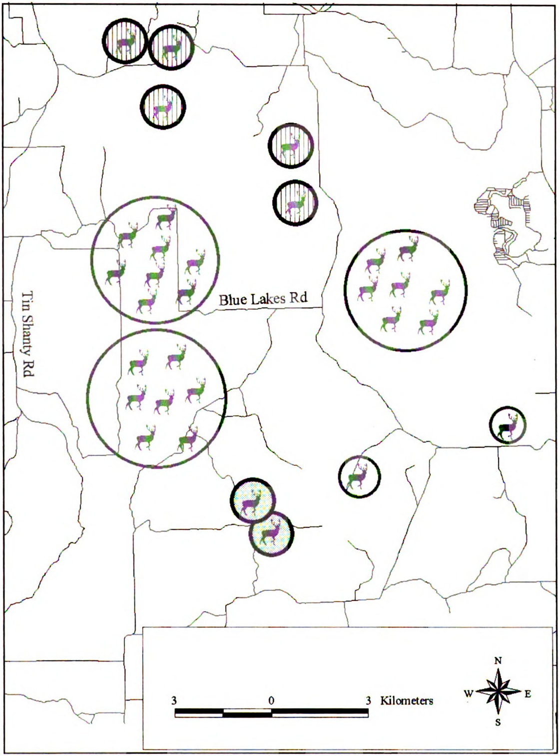


Figure 8. Location of elk captured from the western portion of the study area (unfilled circles represent 2003 capture locations, cross-hatched circles represent 2004 capture locations, and circles filled with lines represent 2005 captures) in Michigan, 2003–2005.

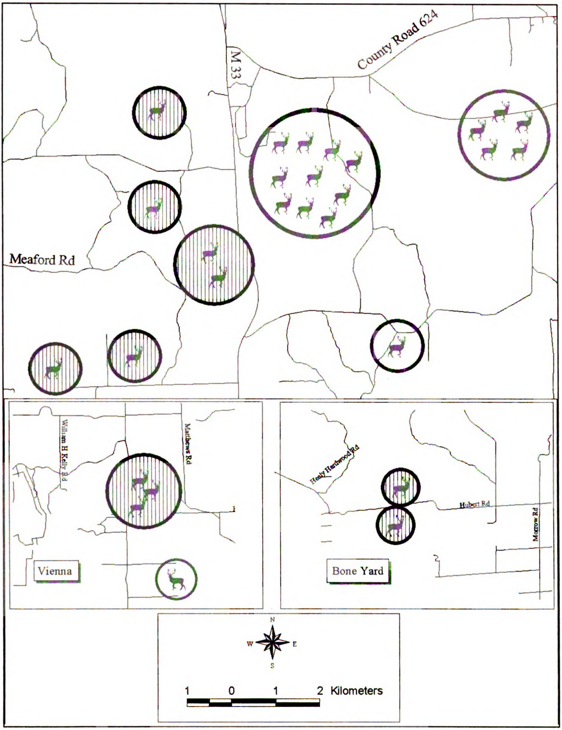


Figure 9. Location of elk captured from the eastern portion of the study area (unfilled circles represent 2003 capture locations and circles filled with lines represent 2005 captures) in Michigan, 2003–2005.

Table 1. Capture record, age[a], mortalities, and current status (January 2007) of radiocollared elk in Michigan, 2003–2006.

Elk Number	Date Capture	Left Ear Tag	Right Ear Tag	Sex	Age	Current Status (date recovered)
1	2/12/2003	673	673	F	A	Active
2	2/9/2003	674	674	F	22.0	Old age (3/30/05)
3	2/12/2003	675	675	M	A	Active
4	2/9/2003	676	676	F	A	Active
5	2/9/2003	677	677	F	A	Active
6	2/12/2003	678	678	M	A	Active
7	2/9/2003	679	679	F	4.0	Broken neck-fence (2/16/05)
8	2/9/2003	680	680	F	A	Shot (1/07)
9	2/12/2003	681	681	F	A	Illegally shot (9/10/05)
10	2/9/2003	682	682	M	A	Shot (12/7/04)
11	2/11/2003	683	683	F	A	Active
12	2/11/2003	684	684	F	A	Active
13	2/12/2003	685	685	M	A	Shot (12/7/05)
14	2/12/2003	686	686	M	A	Active
15	2/9/2003	687	687	M	A	Active
16	2/9/2003	688	688	M	Y	Active
17	2/12/2003	689	689	F	A	Active
18	2/11/2003	690	690	M	14.5	Unknown cause (8/6/2003)
19	2/12/2003	691	691	F	11.0	Exhaustion - mired in beaver pond (6/9/05)
20	2/11/2003	692	692	M	A	GPS collar removed (10/23/05)
21	2/11/2003	693	693	F	A	Shot (1/07)
22	2/12/2003	694	694	M	4.5	Shot (12/7/04)
23	2/12/2003	695	695	M	A	Active
24	2/9/2003	696	696	F	A	Active
25	2/11/2003	697	697	M	A	GPS collar removed (10/23/05)
26	2/9/2003	698	698	F	A	Active
27	2/9/2003	699	699	F	A	Active

[a] Age estimates are provided for mortalities based on cementum aging (in years), for all other elk age is classified as adult = A or yearling = Y.

Table 1. (cont'd)

Elk Number	Date Capture	Left Ear Tag	Right Ear Tag	Sex	Age	Current Status (date recovered)
28	2/9/2003	602	602	F	A	Active
29	2/12/2003	618	618	M	A	Unknown (1/21/07)
30	2/12/2003	621	621	M	Y	Active
31	2/9/2003	630	630	F	A	Active
32	2/11/2003	632	632	F	A	Shot (12/13/03)
33	2/11/2003	639	639	M	A	Active
34	2/11/2003	110	111	M	A	Active
35	2/11/2003	112	113	M	A	Active
36	2/11/2003	114	115	M	Y	Active
37	2/12/2003	116	117	M	Y	Shot (12/10/03)
38	2/12/2003	118	119	M	A	Shot (12/5/06)
39	2/9/2003	120	121	F	A	Active
40	2/9/2003	122	123	F	5.5	Brainworm (10/9/03)
41	7/26/2004	478	477	F	6.5	Illegally shot (12/10/05)
42	7/28/2004	666	666	F	A	Active
46	2/12/2005			F	A	Active
48	2/12/2005	4	4	F	A	Shot (1/07)
49	2/12/2005	5	5	F	A	Active
50	2/12/2005	6	6	F	A	Active
51	2/12/2005	7	7	F	A	Active
52	2/12/2005			F	A	Shot (8/29/05)
53	2/12/2005	9	9	F	A	Active
54	2/12/2005			F	Y	Shot(1/07)
55	2/12/2005	11	11	F	A	Active
56	2/12/2005	12	12	F	A	Active
57	2/12/2005			F	A	Active
58	2/12/2005	14	14	F	A	GPS collar removed (10/24/05)

Table 1. (cont'd)

Elk Number	Date Capture	Left Ear Tag	Right Ear Tag	Sex	Age	Current Status (date recovered)
59	2/12/2005	15	15	F	A	GPS collar removed (10/23/05)
61	2/12/2005	NA	NA	F	A	GPS collar removed (10/23/05)
64	2/12/2005	NA	NA	F	A	Active
66	2/12/2005	21	21	F	A	Shot (8/30/05)

CHAPTER 2: POPULATION ESTIMATION OF MICHIGAN'S ELK HERD

Introduction

Estimating the size of free-ranging wildlife populations is one of the most daunting yet critical tasks faced by wildlife managers (White and Shenk 2001). In Michigan enumeration of wild elk (*Cervus elaphus*) populations has been problematic. Historically, estimation of annual population size was based on pellet group surveys, kill distributions and field observations (Moran 1973). Abundance estimates generated were both imprecise and likely biased as a result of the subjective nature of the surveys (Moran 1973, Beyer 1987). In 1975, the Michigan Department of Natural Resources (MDNR), in an effort to improve its elk survey technique, instituted a combined aerial and snowmobile survey technique to derive population estimates (Otten 1989). This technique involved gathering a group of 100+ volunteers as well as MDNR personnel, and assigning them in pairs to survey quadrats using snowmobiles. MDNR personnel and volunteers would attempt to count all elk within a quadrat. In conjunction with the snowmobile survey, an aircraft would survey quadrats that could not be accessed by snowmobiles such as private lands. Also some quadrats were simultaneously surveyed by volunteers and the aircraft, which provided an ad hoc check on volunteer counts.

There are several problems with the combined aerial and snowmobile survey technique. First, there is no correction for visibility bias (Caughley 1974, Samuel and Pollock 1981) to adjust counts for unseen animals, and therefore projections of population size are undoubtedly negatively biased (Samuel et al. 1992). Visibility bias arises from a multitude of causative factors including group size (i.e., larger groups are more likely to be observed), vegetation characteristics (i.e., the amount of conifer cover in a region) and animal behavior. Secondly, surveys focus primarily on areas of historically high elk densities without a standardized procedure for sampling the entire elk range. This results in areas of lower densities, such as regions of range expansion being excluded from the survey. Also, this survey provides only an index to the parameter of interest–population size. Differences in index values across years cannot be attributed exclusively to changes in elk numbers, but may result from changes in detection probability (i.e., the parameter of population size is confounded with detection probability) (Anderson 2001). Confounding of detection probability and population size prohibits managers from being able to confidently draw conclusions about any observed changes in counts. Since this technique is an index, and is not made using any sampling or statistical framework; no associated measure of precision can be developed for generated population estimates to assess their quality (White et al. 1982). Lastly, in recent years snow conditions in the elk range have not been adequate to allow the use of snowmobiles, which effectively crippled this survey technique.

As a result of these problems, Otten et al. (1993) developed an aerial survey procedure, which utilized sightability correction factors (Samuel et al. 1992) to correct for visibility bias in aerial counts of Michigan elk. The correction factors allowed for statistically defensible estimates of population size and calculation of associated measures of precision. Otten et al. (1993) also provided a standardized sampling procedure for conducting counts across the entire elk range to eliminate the problems of only sampling areas where elk historically occurred. However, this survey procedure was never employed. The major drawback was the technique's reliance on the availability of the Michigan State Police helicopter to conduct surveys, which is costly and often difficult to obtain during the narrow window of survey conditions allowable under Otten's survey protocol . Thus, currently managers still rely on the aerial and snowmobile survey with associated limitations for their management programs.

In recent years, growing public interest and increasing consumptive and non-consumptive use of the elk herd has created pressure to have an accurate and defensible estimation technique for elk managers. To meet these demands, I developed a fixed-wing survey technique based on sightability models (Samuel et al. 1987) and the following objectives:

1) To measure and determine variables which have a significant effect on sightability of elk from fixed-wing aircraft.
2) To use these variables to develop a fixed-wing sightability model for correcting aerial counts of the Michigan elk herd.
3) To develop a standardized, stratified sampling procedure to allow for rigorous survey of elk throughout their range.
4) Develop an economical survey technique that incorporates the sightability model corrections, allows for estimation of group size, and provides statistically defensible population estimates with associated measures of precision for the Michigan elk herd across the entire range.

Study Area

The study site selected for this project is the current elk range located primarily in Cheboygan, Montmorency, Otsego and Presque Isle counties in the northern portion of the Lower Peninsula of Michigan (Moran 1973). The historic range was estimated at approximately 1,550 km^2, including the Pigeon River State Forest near Vanderbilt, Michigan (Bender 1992). The current range size is estimated at approximately 3,450 km^2 (D. E. Beyer, Michigan Department of Natural Resources, unpublished report). We focused our study mainly on the eastern region of the elk range near Atlanta in Montmorency County.

Topography of the area slopes northerly and consists of flat-topped ridges interspersed with headwater swamps and outwash plains created through glacial actions (Moran 1973).

Mean annual temperature is 6.3° C with January having the lowest mean monthly temperature (-8.1° C) and the highest (19.7° C) occurring in July (NOAA 2006). Mean annual rainfall is 93 cm, and mean annual snowfall is 378 cm (NOAA 2006) with precipitation being generally well distributed throughout the year.

Due to wide array of soil fertilities, aspects and moisture levels, vegetation types are diverse and well interspersed. In addition human activities such as logging, agriculture and management practices further complicate the pattern of vegetation types throughout the area. Dominant cover types include deciduous and coniferous forests interspersed with typically human-induced openings. Moran (1973) provides a detailed description of the vegetation of the region.

Methods

Sightability Model Development–Detection Probability Estimation

Capture.—To facilitate sightability model development in February 2003, we captured and radiomarked 20 adult bulls and 20 adult cows using helicopter net-gunning techniques (Carpenter and Innes 1995). Hawkins and Powers Aviation (Greybull, Wyoming, USA) was contracted for this operation. The capture was exempted by the Michigan State University Animal Care and Use Committee (D. L. Garling, All University Committee on Animal Use and Care, written communication, 1 27 2003). In the summer of 2004, we supplemented our sample of radiomarked animals by capturing and radiomarking 2 additional adult cows using chemical immobilization techniques (Roffe et al. 2005). Thus after mortalities, 36 radiomarked elk were available for sightability model development during winters of 2004 and 2005.

Data Collection.– Prior to initiation of sightability model development, I met with MDNR wildlife biologists, MDNR pilots, administrators, and others that would be involved in the process to discuss protocol and expectations. Once all participants understood their respective roles, we conducted aerial surveys to develop an elk sightability model during the winters of 2004 and 2005. I chose winter for model development, since elk group size tends to be largest during the winter (Moran 1973, Beyer 1987) increasing the probability of observing elk groups (Samuel et al. 1987). Also snow conditions provide a good background against which elk can be observed from the air. We conducted all flights using Cessna 180 or Cessna 170 between 0900–1600 hours to take advantage of good light conditions and minimize shadow effects.

We attempted to make flights under clear skies with calm winds, temperatures at or above –12° C after a fresh snowfall (Otten 1989). However, due to the time constraints and the amount of data needed for adequate estimation of the sightability function, we conducted flights when conditions were deemed safe by the pilots. Flights consisted of 2 shifts, 2–3 hours in length, with a 1 hour break between shifts to allow for aircraft refueling and for recuperation of observers.

I divided the region encompassing the greatest extent of movements of radiocollared elk into 80 quadrats with length (N/S) 9.66 km and width (E/W) 3.22 km (Figure 10), and I gave each quadrat a unique identification. Parallel, 0.40 km wide, flight lines were created running north to south within each quadrat, and the starting point and ending point of each line was recorded (Figure 11). I created flight lines to assure 100% coverage of the quadrat.

We used 2 fixed-wing aircraft equipped with radiotelemetry gear and wheel covers removed. The first plane, the telemetry plane, contained a pilot and a telemetry operator. The second plane, the observation plane, contained a pilot, 2 experienced observers and a telemetry operator. Observers were seated at the rear of the plane, and the telemetry operator next to the pilot. Each plane was equipped with a radio for inter-plane communications, a book containing all the quadrat and flight line locations, andGlobal Positioning System (GPS) equipment for locating and flying flight lines and recording locations of observed elk groups and radiomarked individuals.

In the telemetry plane, the telemetry operator randomly selected a radiocollared animal for observation. Using the telemetry equipment, the telemetry plane located the group of animals containing the collared individual. The pilot recorded the location of the group using a GPS. Based on this GPS location, the operator determined the quadrat, which contained the marked individual. Lastly, the telemetry operator scanned all frequencies of marked individuals to determine if any other marked individuals were in the same quadrat. If additional animals were in the same quadrat, their location were also determined. Once all animals in the quadrat were located, the telemetry operator radioed the identification number of both the quadrat and the

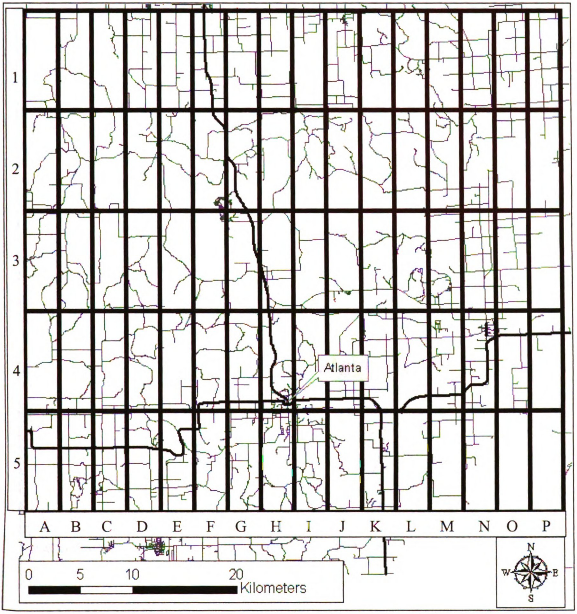


Figure 10. Region that contains the greatest extent of movement of radiocollared elk, and the locations of quadrats used in the sightability model development in Michigan, 2004–2005.

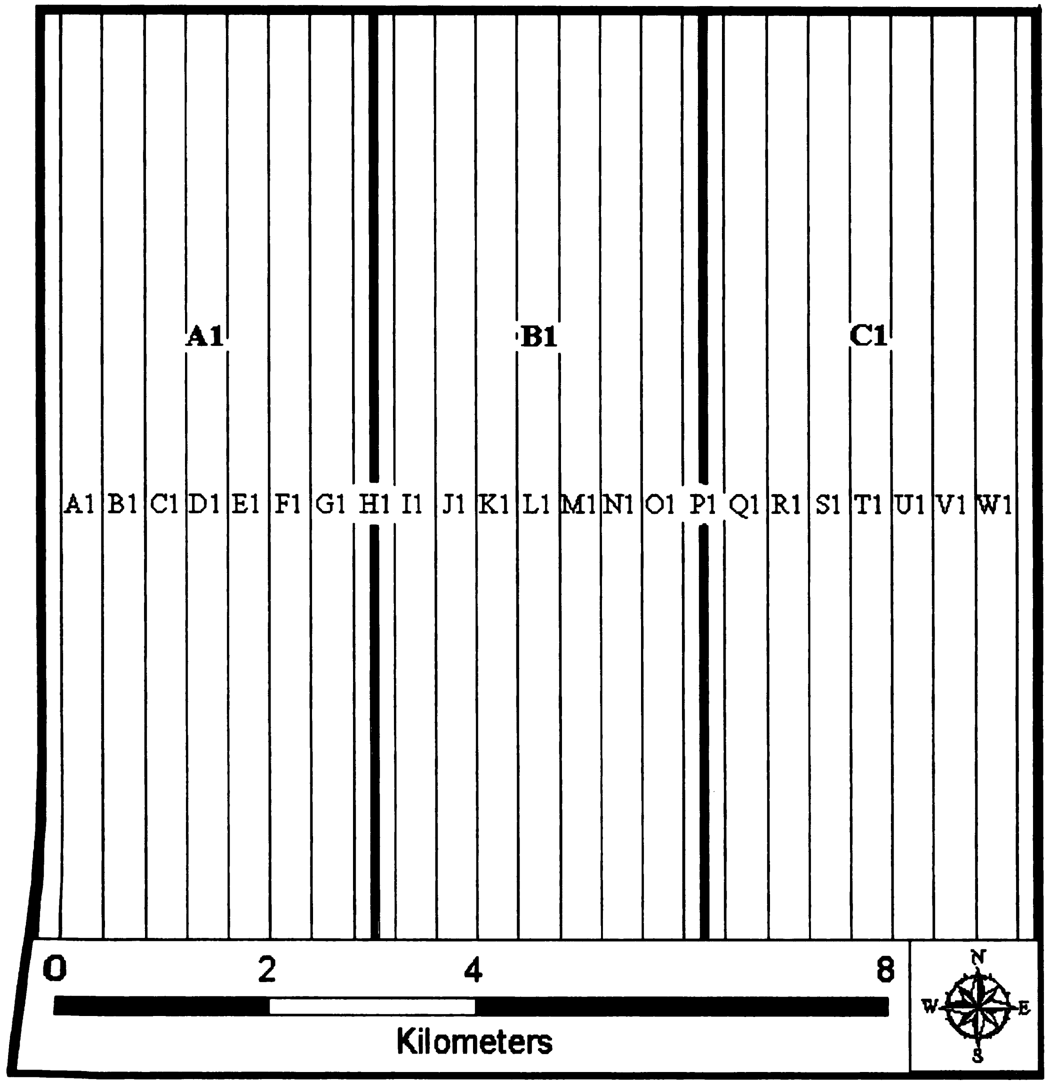


Figure 11. The location of 0.40 km flight lines in quadrats used to develop an elk sightability model for Michigan, 2004–2005.

radiomarked individual(s), and their GPS location(s) to the second telemetry operator in the observation plane. The telemetry plane then proceeded to the next closest radiocollared animal. However, for safety purposes a minimum separation of 1 quadrat was maintained between the telemetry and observation planes. If an elk group contained multiple radiomarked animals, this aggregate was treated as a single unit since the sampling unit is the group not the individual elk (Samuel et al. 1987).

Once the telemetry plane communicated the quadrat to be surveyed, the observation plane proceeded to the designated quadrat and flew the designated flight lines within the quadrat starting in the southwest corner of the quadrat. The observation plane flew the flight lines at an air speed of approximately 129 km/hr and at a height of 152 m above the ground. The 2 experienced observers visually scanned out each side of the plane to a distance of 0.20 km for elk groups. Markers on the wing struts aided searcher in searching the correct area.

If a group was located, observers communicated to the telemetry operator they located a group, if the operator determined the group contained the radio-marked individual(s), the pilot left the designated flight line and reduced altitude while circling the group, and recording the GPS location. While the pilot circled, 1 observer counted all elk in the group. A group was defined as all elk visible in an area. However, if distinct groups were clearly noticeable by the observer over the area (i.e., there is a clear separation between groups of animals), or if elk were distributed in areas of different conifer cover classes then these were treated as separate groups. The observer also recorded the number of bulls, cows and calves, the percent conifer cover at the group's location, behavior of the first animal (s) seen, wind speed, snow cover conditions and light conditions. The percent conifer cover was classified into 3 classes: 1) 0–33% conifer cover, 2) 34–66% conifer cover and 3) 67–100% conifer cover at a 10 m radius around the first elk initially sighted. Behavior was classified as bedded (B), standing (S) or both (B/S). Snow cover conditions were classified as 1) complete, 2) some low vegetations showing or some 3) bare ground showing. Lastly, light conditions were classified as bright light with high intensity (BH), bright light with medium intensity (BM), flat light with medium intensity (FM) and flat light with low intensity (FL). A standardized data sheet was provided to aid in data collection (Appendix A). These independent variables were selected a priori as likely to influence sightability of elk. When the first observer completed data collection, the pilot circled the plane in the opposite direction, and the second observer repeated the process. Observers did not communicate their findings until both completed data collection (i.e., observers were independent). After the group had been counted by both observers, the pilot returned to the flight line and continued to survey the quadrat if more radiocollared inviduals were in the quadrat. If the observers located and counted all groups with the radiomarked individuals then the telemetry operator communicated to the pilot the survey of the quadrat was complete. The telemetry operator did not communicate with observers until the group(s) containing the radiomarked individual(s) was located or the surveying of the quadrat was complete. If observers did not locate the group(s) containing the radiomarked individual during the survey of the entire quadrat, the telemetry operator located this animal(s) using the telemetry gear. Observers recorded telemetry equipment was used to locate the group containing the radiomarked animal (i.e., it will be classified as unseen) as opposed to the group being located during the normal survey of the quadrat, and the same procedure for data collection as just described was implemented.

In 2005, we attempted to ensure an even distribution of observations across the various class levels of the independent variables if possible (e.g., we sampled more intensively groups located in conifer class level 3 in 2005 as we had fewer observations of groups in this conifer class level).

To prevent observer expectancy in regards to a cell containing a radiomarked individual, which could bias results, periodically cells known to not contain any radiomarked individuals, placebo cells, were surveyed. Due to limited resources we flew a maximum of 1 placebo cell per week. Only the telemetry operator on the observation plane knew the cell was devoid of marked animals.

Analysis.– Data collected during the elk sightability surveys resulted in observed elk groups being classified as seen or unseen. This dichotomous classification was the dependent variable in a logistic regression analysis with independent variables: group size, percent canopy cover, animal behavior, wind speed, snow conditions and light conditions. I followed the Samuel et al. (1987) recommendation of using the natural log transformation of group size in the analysis since they found it was a better predictor than the untransformed measure of group size. The logistic regression analysis allowed estimation of heterogeneous sighting probabilities for each elk group observed. The logistic model used in the analysis for estimating sighting probability closely followed Samuel et al. (1987):

$$P(y=1) = \frac{\exp(u)}{1+\exp(u)}, \qquad (1)$$

where $P(y=1)$ = sighting probability, and $u = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_j x_j$ is the usual linear regression equation of covariates $\left(x_1, x_2, \ldots, x_j\right)$ determined to be affecting elk sightability.

In addition to using the Samuel et al. (1987) formulation (SF) to calculate sighting probabilities, I modified their model by replacing group size, one of the covariates, by an estimate of group size and recalculated probabilities. Group size was estimated using a method of moments estimator (MME) (DasGupta and Rubin 2005: see Chapter 3):

$$\hat{m}_{i(k)} = \frac{X_{(w)}^{\alpha+1}\left(S^2\right)^{\alpha}}{\overline{X}^{\alpha}\left(X_{(w)} - \overline{X}\right)^{\alpha}}, \tag{2}$$

where $X_{(w)}$ = maximum of w observer counts of the size of the ith group in the kth quadrat, $\overline{X}$ = mean of the counts, S^2 = sample variance of the counts, and $\alpha = 0.10$. This α value was chosen as it was shown to minimize the mean squared error (MSE) for the range of population size and detection probability typical of elk aerial surveys in Michigan (see Chapter 3). If all counts of group size were identical then group size was assumed to be known. This estimator assumes that double counting of individual elk did not occur, and other species (e.g., white-tailed deer) were not counted as elk (i.e., there was no misclassification).

The approximate estimate of the asymptotic variance for estimate of group size is as follows:

$$\hat{\text{var}}(\hat{m}_{i(k)}) \approx \frac{2\alpha^2 \hat{m}_{i(k)}(\hat{m}_{i(k)} - 1)}{w}. \tag{3}$$

For both formulations, I created 63 *a priori* models based on all linear combinations of the independent variables. I estimated beta parameters for each model, and derived model averaged estimates and relative likelihood values based on the entire suite of models (Burnham and Anderson 2002).

I developed an unconditional covariance matrix for the beta parameters used in the SF (Burnham and Anderson 2002).

An estimate of the covariance matrix for the beta parameters in my formulation (GS) was complex and not available in a closed form, as I had to account for measurement error associated with estimating group size (Carroll et al. 1995). Therefore, I used a parametric bootstrap procedure to estimate the covariance matrix (Efron and Tibshirani 1993). I generated 10,000 datasets from the empirical distribution of data collected during sightability model development. Any observations with missing independent variable information were excluded from the resampling process. To incorporate variability associated with estimating group size, group size for each observation in the bootstrapped datasets, where counts were not identical, were generated from a Normal distribution with mean = $\hat{m}_{i(k)}$ and variance = $\dfrac{2\alpha^2\hat{m}_{i(k)}\left(\hat{m}_{i(k)}-1\right)}{w}$ distribution where $\hat{m}_{i(k)}$ = the estimate of group size for the ith group in the kth quadrat, $\alpha = 0.10$, and w = number of observer counts of group size for the selected observation (DasGupta and Rubin 2005). The elements of the covariance matrix were then estimated as follows for i, j = 1 to 7:

$$\hat{\Sigma}_{ij} = \frac{1}{10{,}000}\sum_{k=1}^{10{,}000}\left(\hat{\beta}_{ik}-\bar{\beta}_i\right)\left(\hat{\beta}_{jk}-\bar{\beta}_j\right), \tag{4}$$

where $\hat{\beta}_{ik}$ = the $\hat{\beta}$ corresponding to the i^{th} predictor variable from the sightability model at the k^{th} iteration, and $\overline{\beta}_i$ = the mean of the $\hat{\beta}$'s over the 10,000 iterations.

All analyses were done using SAS Macro Facility and PROC GLIMMIX (SAS Institute 2003).

Survey–Population Size Estimation

Data Collection.– Prior to implementation of the elk survey, I met with MDNR wildlife biologists, MDNR pilots, MDNR technicians, administrators, and others that would be involved in the process to discuss protocol and expectations. The protocol and datasheets used are in Appendix B. Once all participants understood their respective roles, we conducted an elk survey during late January through early February 2006. We maintained as much similarity as possible in observers, timing of flights and conditions between the survey and those used during the sightability model development to assure sightability during the survey mimicked conditions under which the correction factors for sightability were developed.

We used 2 fixed-wing aircraft to conduct the survey. Multiple aircraft shortened survey time and minimized potential problems associated with animal movements between quadrats. Both planes contained a pilot and 2-experienced observers, and were equipped with a book containing all the quadrat and flight line locations, and Global Positioning System (GPS) equipment for locating and flying flight lines and recording location of observed elk groups.

For the elk survey, I divided the entire elk range into 92 (N/S) 9.66 km by (E/W) 3.22 km quadrats (Figure 12), and each quadrat was assigned a unique identification. Parallel, 0.40 km wide, flight lines running north to south within each quadrat were

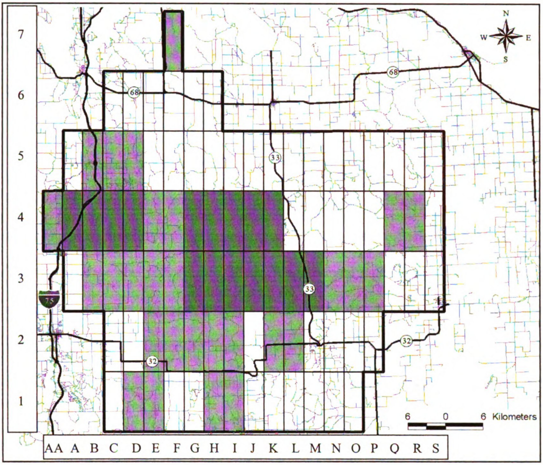


Figure 12. Location of quadrats of and expected elk densities of quadrats (dark gray–high elk density, light gray–medium elk density, white–low elk density) used during the elk survey in Michigan, 2006 (identifying labels are along the margins).

created, and the starting point and ending point of each line I provided to the pilots (Figure 11). I created an adequate number of flight lines to assure 100% coverage of the entire quadrat. Quadrats were classified into 3 strata of elk density: high (31 or more elk), medium (16–30 elk) and low (0-15 elk) based on recommendations of Otten (1989).

Radio-telemetry data, local biologists' knowledge, historic kill data, and information gained on observations of elk distributions made during past population surveys and sightability model development flights were the basis of stratification. The entire range was surveyed in 2006. We surveyed high density quadrats first, and we attempted to survey adjacent quadrats on the same day to minimize elk groups moving between quadrats. Once the high density quadrats were surveyed, we surveyed the remaining quadrats in a pattern radiating out from the high density quadrats to once again minimize movement of elk groups between quadrats.

When a quadrat was surveyed, the plane flew to the quadrat's southwest corner as a starting point, and then flew all flight lines within the quadrat. Pilots attempted to maintain the same air speed and altitude as used for development of the sightability model. The independent variables of group size, behavior, percent conifer cover, wind speed, snow cover conditions and light conditions for all elk groups observed by the 2 observers were recorded following the same protocol as developed for the sightability model. In addition to the 2 observers, the pilot also provided an independent count of the size of observed elk groups.

Analysis.– In conjunction with the sightability models developed, I used data collected on elk groups during the elk survey to generate population estimates of the Michigan elk herd using both my formulation correcting for group size (GS) and the

Samuel et al. (1987) formulation (SF). The estimate of population size for SF was calculated as follows (Steinhorst and Samuel 1989):

$$t = \sum_{k}^{l} \frac{1}{p_k} \sum_{i}^{n_k} m_{i(k)} \hat{\Theta}_{i(k)}, \tag{5}$$

where p_k = the probability the k^{th} land unit is selected as part of the sample (known), $m_{i(k)}$ = size (assumed to be known) of the i^{th} group in the k^{th} land unit, and $\hat{\Theta}_{i(k)}$ = is the inverse of the estimated sighting probability $(1/\hat{y}_{i(k)})$ for the i^{th} group in the k^{th} land unit calculated using the SF sightability model.

Estimating group size resulted in the following estimator:

$$t = \sum_{k}^{l} \frac{1}{p_k} \sum_{i}^{n_k} \hat{m}_{i(k)} \hat{\Theta}_{i(k)}, \tag{6}$$

where p_k = the probability the k^{th} land unit is selected as part of the sample (known), $\hat{m}_{i(k)}$ = method of moments estimate (Equation 2) of the size of the i^{th} group in the k^{th} land unit, and $\hat{\Theta}_{i(k)}$ = is the inverse of the estimated sighting probability $(1/\hat{y}_{i(k)})$ for the i^{th} group in the k^{th} land unit calculated using GS, which includes $\hat{m}_{i(k)}$ as a covariate in the estimation of $\hat{y}_{i(k)}$. If there was only 1 count on a group or if all counts for the i^{th} group in the k^{th} land unit were identical $\hat{m}_{i(k)} = m_{i(k)}$.

When using the SF, Steinhorst and Samuel (1989) provide the following equation for estimating the variance of t:

$$
\begin{aligned}
s_t^2 = &\sum_{k}^{l} \frac{1-p_k}{p_k^2} \hat{M}_k^2 + \sum_{k \neq k'}^{l} \sum^{l'} \frac{p_{kk'} - p_k p_{k'}}{p_{kk'} p_k p_{k'}} \hat{M}_k \hat{M}_{k'} + \\
&\sum_{k}^{l} \frac{1}{p_k} \sum_{i}^{n_k} \left(1 - \frac{1}{\hat{\Theta}_{i(k)}}\right) \left(m_{i(k)} \hat{\Theta}_{i(k)}\right)^2 + \sum_{j} \sum_{j'} a_j a_{j'} s_{\hat{\Theta}_j \hat{\Theta}_{j'}},
\end{aligned}
\tag{7}
$$

where $\hat{M}_k = \sum_{i}^{n_k} m_{i(k)} / \hat{y}_{i(k)}$, $p_{kk'}$ = probability both the k and k' land unit are selected in the sample, $a_j = \Sigma_{i(k)j}\, m_{i(k)} / p_k$ with j indexing all $i(k)$ where the independent variables are constant, and $s_{\hat{\Theta}_j \hat{\Theta}_{j'}} = \mathrm{e}^{-(\mathbf{x}_j + \mathbf{x}_{j'})'\hat{\boldsymbol{\beta}} - (\mathbf{x}_j + \mathbf{x}_{j'})'\hat{\Sigma}(\mathbf{x}_j + \mathbf{x}_{j'})/2} \left(\mathrm{e}^{\mathbf{x}_j' \hat{\Sigma} \mathbf{x}_{j'}} - 1 \right)$ with $\mathbf{x}_j$ = vector of independent variables, $\hat{\boldsymbol{\beta}}$ = vector of beta parameters estimated by the SF, and $\hat{\Sigma}$ = consistent estimator of the covariance matrix . All remaining variables are as in equation (5).

The approximate variance estimate for t when using GS is as follows (see Chapter 3 for derivation):

$$
\begin{aligned}
s_t^2 = {} & \sum_k^l \frac{1-p_k}{p_k^2}\hat{M}_k^2 + \sum_{k \neq k'}^l \sum^{l'} \frac{p_{kk'} - p_k p_{k'}}{p_{kk'} p_k p_{k'}} \hat{M}_k \hat{M}_{k'} + \sum_k^l \frac{1}{p_k} \sum_i^{n_k} \left(1 - \frac{1}{\hat{\Theta}_{i(k)}}\right) \left(\hat{m}_{i(k)} \hat{\Theta}_{i(k)}\right)^2 + \\
& \sum_k^l \frac{1}{p_k^2} \sum_i^{n_k} \left(1 + e^{-\sum_{j=1}^{7} \hat{\beta}_j x_{i(k)j}} (1 - \hat{\beta}_1) \right)^2 \hat{\sigma}^2_{\hat{m}_{i(k)}} \\
& + \sum_j \left[\sum_k^l \frac{1}{p_k} \sum_i^{n_k} - \hat{m}_{i(k)} x_{i(k)j} e^{-\sum_{j=1}^{7} \hat{\beta}_j x_{i(k)j}} \right]^2 \hat{\sigma}^2_{\hat{\beta}_j} \\
& + \sum_{j \neq j'} \sum \left[\sum_k^l \frac{1}{p_k} \sum_i^{n_k} - \hat{m}_{i(k)} x_{i(k)j} e^{-\sum_{j=1}^{7} \hat{\beta}_j x_{i(k)j}} \right] \\
& \times \left[\sum_k^l \frac{1}{p_k} \sum_i^{n_k} - \hat{m}_{i(k)} x_{i(k)j'} e^{-\sum_{j=1}^{7} \hat{\beta}_j x_{i(k)j}} \right] \hat{\sigma}_{\hat{\beta}_j, \hat{\beta}_{j'}} \\
& + \sum_{i(k) \neq i'(k')} \left[\frac{1}{p_k p_{k'}} \hat{m}_{i(k)} \hat{m}_{i'(k)'} s_{\hat{\Theta}_{i(k)}, \hat{\Theta}_{i'(k)'}} \right],
\end{aligned}
\tag{8}
$$

where $\hat{M}_k = \sum_i^{n_k} \hat{m}_{i(k)} / \hat{y}_{i(k)}$, $\hat{\beta}_j$ = is the j^{th} beta parameter estimated from the GS formulation, $\hat{\beta}_1$ = is the estimated beta parameter associated with the independent variable of estimated group size, $x_{i(k)j}$ = is the j^{th} predictor variable i^{th} group in the k^{th} land unit from the sightability model, $\hat{\sigma}^2_{\hat{m}_{i(k)}}$ = is the estimated variance of the group size estimate for the i^{th} group in the k^{th} land unit derived in equation (3), and $\hat{\sigma}^2_{\beta_j \beta_{j'}}$ =

estimated covariance of $\hat{\beta}_j$ and $\hat{\beta}_{j'}$ for all j derived in equation (4). If there was only 1 count or if all counts for a group were identical, then $\hat{\sigma}^2_{\hat{m}_{i(k)}} = 0$.

The first 2 terms in this equation are the error associated with sampling, the third term is the error associated with sightability (i.e., the fact that animals are missed during aerial surveys). The fourth term can generally be thought of as the error associated with estimating group size with a component accounting for the estimate of sighting probability being a function of group size. The next 2 terms correspond to the error associated with estimating the sightability of elk groups with a component accounting for group size estimation. The last term is accounting for the covariance between each group's sighting probabilities, since they were derived from using the same sightability model. This last term is a point estimate approximation for the following expectation:

$\sum_{i(k) \neq i'(k')} \mathrm{E}_{m_j m_{j'}} \left[\frac{1}{p_k p_{k'}} \hat{m}_{i(k)} \hat{m}_{i'(k')} \operatorname{cov}\left(\hat{\Theta}_{i(k)}, \hat{\Theta}_{i'(k')}\right) \right]$, with the $\operatorname{cov}\left(\hat{\Theta}_{i(k)}, \hat{\Theta}_{i'(k')}\right)$

estimated by

$$s_{\hat{\Theta}_{i(k)} \hat{\Theta}_{i'(k')}} = e^{-(\mathrm{x}_{i(k)} + \mathrm{x}_{i'(k')})'\hat{\beta} - (\mathrm{x}_{i(k)} + \mathrm{x}_{i'(k')})'\hat{\Sigma}_{\hat{\beta}}(\mathrm{x}_{i(k)} + \mathrm{x}_{i'(k')})/2} \left(e^{\mathrm{x}'_{i(k)} \hat{\Sigma}_{\hat{\beta}} \mathrm{x}_{i'(k')}} - 1 \right)$$

, where $\mathbf{x}_{i(k)}$ = the vector of predictor variables used in the sightability model for the $i(k)^{\text{th}}$ group, $\hat{\boldsymbol{\beta}}$ = vector of beta parameters estimated using GS, and $\hat{\Sigma}_{\hat{\beta}}$ = estimated covariance matrix for the beta parameters estimated using GS. This approximation results in only a slight positive bias in variance estimates (see Chapter 3). Thus, Equation (8) can be rewritten more succinctly in matrix notation. Let $\hat{\mathbf{m}}$ = vector of estimated or known group sizes for all groups observed in the survey, $\hat{\boldsymbol{\beta}}$ = vector of beta parameters estimated using GS, $\boldsymbol{\eta} = \begin{pmatrix} \hat{\mathbf{m}} \\ \hat{\boldsymbol{\beta}} \end{pmatrix}$, $\boldsymbol{\delta}$ = vector of partial derivatives of t with respect to

$\hat{m}_{i(k)}$ and $\hat{\beta}_j$ evaluated at $\boldsymbol{\eta}$, thus for the i[th] group in the k[th] land unit

$\delta_{\hat{m}_{i(k)}} = \frac{1}{p_k}\left(1 + e^{-\mathbf{x}_{i(k)}\hat{\boldsymbol{\beta}}}\left(1 - \hat{\beta}_1\right)\right)$ and for the j[th] beta estimate

$\delta_{\hat{\beta}_j} = \sum_k^l \frac{1}{p_k} \sum_i^{n_k} - \hat{m}_{i(k)} x_{i(k)j} \cdot e^{-\sum_{j=1}^{7} \hat{\beta}_j x_{i(k)j}}$, and lastly $\hat{\boldsymbol{\Sigma}} = \begin{bmatrix} \hat{\Sigma}_{\sigma^2_{\hat{m}_{i(k)}}} & 0 \\ 0 & \hat{\Sigma}_{\hat{\beta}} \end{bmatrix}$

where $\hat{\Sigma}_{\sigma^2_{\hat{m}_{i(k)}}}$ = a diagonal matrix of $\hat{\sigma}^2_{\hat{m}_{i(k)}}$ values and $\hat{\Sigma}_{\hat{\beta}}$ = estimated covariance

matrix for the beta parameters estimated using my formulation. Then equation (8) is rewritten as follows:

$$s_t^2 = \sum_k^l \frac{1 - p_k}{p_k^2} \hat{M}_k^2 + \sum_{k \neq k'}^{l} \sum^{l'} \frac{p_{kk'} - p_k p_k}{p_{kk'} p_k p_{k'}} \hat{M}_k \hat{M}_{k'} + \sum_k^l \frac{1}{p_k} \sum_i^{n_k} \left(1 - \frac{1}{\hat{\Theta}_{i(k)}}\right) \left(\hat{m}_{i(k)} \hat{\Theta}_{i(k)}\right)^2$$
$$+ \boldsymbol{\delta}' \Sigma \boldsymbol{\delta} + \sum_{i(k) \neq i'(k')} \left[\frac{1}{p_k p_{k'}} \hat{m}_{i(k)} \hat{m}_{i'(k')} s_{\hat{\Theta}_{i(k)}, \hat{\Theta}_{i'(k')}}\right]. \tag{9}$$

Sampling Simulations

To investigate the effects of surveying only a portion of the range on precision of the estimate, I examined if our stratification of quadrats into expected elk densities for the 2006 survey was accurate based on the sum of the maximum counts of elk groups in each quadrat. I also simulated all combinations of sampling rates between 50–100% at 10% intervals for the different density strata. For each sampling rate and each stratum, I generated 1,000 datasets from the survey data collected in 2006, and examined the average variance of population estimates calculated using GS. Lastly, I examined the optimal sampling rates based on the criteria of minimizing cost and maximizing precision for sample sizes ranging from 45–91 quadrats. Lohr (1999) provided the following equation for determining the optimal number of samples in each stratum to minimize the variance of the population estimate:

$$n_h = \left(\frac{\dfrac{N_h S_h}{\sqrt{c_h}}}{\displaystyle\sum_{l=1}^{H} \frac{N_l S_l}{\sqrt{c_l}}} \right), \tag{10}$$

where n_h = the number quadrats to sample from stratum h, N_h = the total number of quadrats in stratum h, S_h = the within stratum standard deviation of number of elk in each quadrat, and c_h = the cost of sampling a quadrat in stratum h. I used the within stratum standard deviation of the sum of the maximum counts for each quadrat to estimate S_h. For a given sample size, I calculated average variance of population estimates based on the optimal sample allocation as determined above using the GS estimation procedure, and a Monte-Carlo resampling procedure of the 2006 survey data with 1,000 repetitions.

Cost

To evaluate the cost effectiveness of the sightability model estimation procedure, I compared the costs associated with this technique with the costs associated with the current estimation procedure.

Results

Sightability Model Development–Estimating Detection Probability Estimation

During the winters of 2004 and 2005, we collected information on 105 elk groups in 2004 and 125 elk groups in 2005 for sightability model development. Fourteen observations were censored due to lack of information about independent variables. We counted a total of 1,435 elk in 216 groups based on the maximum of observer counts. The mean group size was 6.6 elk, and the median group size was 4 elk. Group sizes ranged from 1 to 53 elk. Of the 216 groups, observers saw 1028 elk in 110 groups (9.3 elk/group) without the aid of telemetry equipment (i.e., groups were classified as seen). Observers used telemetry equipment (i.e., groups were classified as unseen) to locate 407 elk in 106 groups (3.8 elk/group). Wind speed during the survey had an average value of 11.9 km/hr with speeds ranging from 0 to 32.2 km/hr. The mean wind speed for groups that were seen was 12.1 km/hr, and the mean wind speed for elk groups classified as unseen was 11.7 km/hr. Table 2 displays the number of elk groups both seen and unseen for each level of the various class variables. When calculating the sightability models, class 3 of the variable, snow conditions, was eliminated since no elk groups occurred in this class. Also to facilitate calculation of sighting probabilities, class 2 and class 3 of the variable, percent conifer, were combined because no elk groups containing radiomarked individuals were observed without the aid of telemetry equipment in class 3. The top 10 models selected using information-theoretic approaches are shown in Table 3. Model averaged beta parameter estimates and associated unconditional standard errors for GS and the SF sightability models generated during the logistic regression analyses are shown in Table 4. Relative likelihood values for each of the parameters for both the GS and SF are presented in Table 5. Covariance matrices for the model averaged beta parameters for the GS and SF sightability models are presented in Tables 6 and 7 respectively. The 2 most important variables using SF or GS in determining elk

Table 2. Number of elk groups classified as seen and unseen during aerial flights for each level of the following class variables: conifer cover[a], behavior[b], light class[c] and snow conditions[d] for elk in Michigan during the winters of 2004 and 2005. Percentage of groups for a given response within each level of the class variables is shown in parentheses.

	Class Variable												
	Conifer			**Behavior**			**Light Class**				**Snow Age**		
Response	**1**	**2**	**3**	**B**	**B/S**	**S**	**BH**	**BM**	**FL**	**FM**	**1**	**2**	**3**
Seen	94 (85)	16 (15)	0	55 (50)	21 (19)	34 (31)	23 (23)	19 (19)	15 (15)	53 (53)	53 (48)	57 (52)	0
Unseen	53 (50)	29 (27)	24 (23)	70 (66)	8 (8)	28 (25)	28 (24)	15 (13)	8 (7)	55 (47)	47 (44)	59 (56)	0

[a] Conifer cover has 3 classes: 1 (0–33%), 2 (34–66%) and 3 (67–100%).

[b] Behavior has 3 classes: B (bedded), B/S (bedded/standing) and S (standing)

[c] Light class has 4 classes: BH (bright light with high intensity), BM (bright light with medium intensity, FL (flat light with low intensity) and FM (flat light with medium intensity).

[d] Snow conditions has 3 classes: 1 (complete snow cover), 2 (some low vegetations showing) or 3 (bare ground showing).

Table 3. Top 10 elk sightability models, AIC_c values, Δ AIC_c values, relative model likelihoods (RML) and associated Akaike weights (AW) in Michigan, 2004 and 2005.

Model	AIC_c Value	Δ AIC_c	RML	AW
conifer, lngsize, snow	254.12	0.00	1.00	0.36
conifer, lngsize	255.76	1.64	0.44	0.16
conifer, lngsize, snow, windcont	255.97	1.84	0.40	0.14
behave, conifer, lngsize, snow	257.31	3.19	0.20	0.07
conifer, lngsize, windcont	257.44	3.31	0.19	0.07
conifer, lightclass, lngsize, snow	258.12	3.99	0.14	0.05
behave, conifer, lngsize	258.96	4.84	0.09	0.03
behave, conifer, lngsize, snow, windcont	259.19	5.07	0.08	0.03
conifer, lightclass, lngsize	259.20	5.07	0.08	0.03
conifer, lightclass, lngsize, snow, windcont	260.27	6.14	0.05	0.02

Table 4. Model averaged parameter estimates of group size[a], wind speed, behavior[b], percent conifer cover[c], snow conditions[d] and light class[e] for my formulation which estimates group size (GS) and the Samuel et al. (1987) sightability model (SF) constructed for elk in Michigan during winters of 2004–2005. Unconditional standard errors of estimates are presented in parentheses.

				Class Variables											
				Behavior			Percent Conifer		Snow Conditions		Light Class				
Model	Intercept	Group Size	Wind	B	B/S	S	1	2	1	2	BH	BM	FL	FM
GS	-2.68	0.86	0.01	-0.06	-0.01	0	1.59	0	0.41	0	-0.05	0.04	0.07	0
	(0.72)	(0.26)	(0.34)	(0.32)	(0.58)	(0)	(0.40)	(0)	(0.40)	(0)	(0.34)	(0.37)	(0.51)	(0)
SF	-2.74	0.93	0.01	-0.06	-0.01	0	1.52	0	0.48	0	-0.06	0.04	0.09	0
	(0.59)	(0.22)	(0.02)	(0.08)	(0.11)	(0)	(0.35)	(0)	(0.26)	(0)	(0.07)	(0.07)	(0.09)	(0)

[a] Group size variable represents the ln of estimated group size (GS) or maximum count (SF).

[b] Behavior has 3 classes: B (bedded), B/S (bedded/standing) and S (standing).

[c] Conifer cover has 3 classes: 1 (0–33%) and 2 (34–100%).

[d] Snow conditions has 3 classes: 1 (complete snow cover) or 2 (some low vegetations showing).

[e] Light class has 4 classes: BH (bright light with high intensity), BM (bright light with medium intensity, FL (flat light with low intensity) and FM (flat light with medium intensity).

Table 5. Relative likelihood values for independent variables used in GS and SF sightability model calculations for elk in Michigan during winters of 2004–2005.

Model	Group Size	Wind	Behavior	Conifer	Snow	Light Class
GS	0.99945	0.28578	0.17534	0.99997	0.66933	0.13381
SF	0.99978	0.28741	0.17548	0.99989	0.72540	0.15202

Table 6. Covariance matrix for model averaged beta parameter estimates of group size[a], wind speed, behavior[b], percent conifer cover[c], snow conditions[d] and light class[e] calculated using the sightability model, which allows for estimates of group size (GS).

					Class Variable											
					Behavior			Percent conifer		Snow conditions		Light class			
Variable	Class	Intercept	Group size	Wind	B	B/S	S	1	2	1	2	BH	BM	FL	FM
Intercept		0.513	-0.114	-0.009	-0.092	0.016	0	-0.139	0	-0.126	0	-0.072	-0.021	-0.004	0
Group size		-0.114	0.068	0.000	0.002	-0.048	0	-0.001	0	0.025	0	0.012	-0.007	-0.009	0
Wind		-0.009	0.000	0.001	0.001	-0.001	0	0.001	0	-0.001	0	0.002	-0.001	-0.002	0
	B	-0.092	0.002	0.001	0.104	0.038	0	0.019	0	0.003	0	0.009	-0.008	-0.018	0
Behavior	B/S	0.016	-0.048	-0.001	0.038	0.338	0	0.008	0	0.035	0	-0.044	0.030	0.037	0
	S	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Percent conifer	1	-0.139	-0.001	0.001	0.019	0.008	0	0.158	0	0.008	0	0.002	0.009	-0.001	0
	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Snow conditions	1	-0.126	0.025	-0.001	0.003	0.035	0	0.008	0	0.158	0	0.021	0.018	0.021	0
	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	BH	-0.072	0.012	0.002	0.009	-0.044	0	0.002	0	0.021	0	0.117	-0.001	-0.026	0
Light class	BM	-0.021	-0.007	-0.001	-0.008	0.030	0	0.009	0	0.018	0	-0.001	0.139	0.078	0
	FL	-0.004	-0.009	-0.002	-0.018	0.037	0	-0.001	0	0.021	0	-0.026	0.078	0.256	0
	FM	0	0	0	0	0	0	0	0	0	0	0	0	0	0

[a] Group size variable represents the ln of estimated group size (GS) or maximum count (SF).

[b] Behavior has 3 classes: B (bedded), B/S (bedded/standing) and S (standing).

[c] Conifer cover has 3 classes: 1 (0–33%), 2 (34–66%) and 3 (67–100%).

[d] Snow conditions has 3 classes: 1 (complete snow cover), 2 (some low vegetations showing) or 3 (bare ground showing).

[e] Light class has 4 classes: BH (bright light with high intensity), BM (bright light with medium intensity, FL (flat light with low intensity) and FM (flat light with medium intensity).

Table 7. Covariance matrix for model averaged beta parameter estimates of group size[a], wind speed, behavior[b], percent conifer cover[c], snow conditions[d] and light class[e] calculated using the sightability model, which allows for estimates of group size (SF).

					Class Variable										
					Behavior			Percent conifer		Snow conditions		Light class			
Variable	**Class**	**Intercept**	**Group size**	**Wind**	**B**	**B/S**	**S**	**1**	**2**	**1**	**2**	**BH**	**BM**	**FL**	**FM**
Intercept		0.352	-0.090	-0.001	-0.003	-0.001	0	-0.098	0	-0.055	0	-0.001	-0.001	-0.001	0
Group size		-0.090	0.050	0.000	0.000	-0.002	0	-0.003	0	0.013	0	0.000	0.000	0.000	0
Wind		-0.001	0.000	0.000	0.000	0.000	0	0.000	0	0.000	0	0.000	0.000	0.000	0
	B	-0.003	0.000	0.000	0.006	0.001	0	0.001	0	0.000	0	0.000	0.000	0.000	0
Behavior	B/S	-0.001	-0.002	0.000	0.001	0.012	0	0.000	0	0.001	0	0.000	0.000	0.000	0
	S	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Percent conifer	1	-0.098	-0.003	0.000	0.001	0.000	0	0.122	0	0.001	0	0.000	0.000	0.000	0
	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Snow conditions	1	-0.055	0.013	0.000	0.000	0.001	0	0.001	0	0.067	0	0.000	0.000	0.000	0
	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	BH	-0.001	0.000	0.000	0.000	0.000	0	0.000	0	0.000	0	0.005	0.000	0.000	0
Light class	BM	-0.001	0.000	0.000	0.000	0.000	0	0.000	0	0.000	0	0.000	0.005	0.000	0
	FL	-0.001	0.000	0.000	0.000	0.000	0	0.000	0	0.000	0	0.000	0.000	0.008	0
	FM	0	0	0	0	0	0	0	0	0	0	0	0	0	0

[a] Group size variable represents the ln of estimated group size (GS) or maximum count (SF).

[b] Behavior has 3 classes: B (bedded), B/S (bedded/standing) and S (standing).

[c] Conifer cover has 3 classes: 1 (0–33%), 2 (34–66%) and 3 (67–100%).

[d] Snow conditions has 3 classes: 1 (complete snow cover), 2 (some low vegetations showing) or 3 (bare ground showing).

[e] Light class has 4 classes: BH (bright light with high intensity), BM (bright light with medium intensity, FL (flat light with low intensity) and FM (flat light with medium intensity).

sightability were conifer cover and group size based on the RI values. Snow conditions were of lesser importance, and the remaining predictor variables were of little influence.

Survey–Population Size Estimation

In the winter of 2006, we completed the first elk survey. The entire range was surveyed with the exception of quadrat C1, which was not surveyed as it fell in air space restricted by the United States Air Force. The survey was completed in 9 days and required 85 hrs of total flight time. We flew 4,368 mile of transects. During the flights, observers saw 72 unique groups of elk containing 559 individuals based on maximum of observer counts. Of the 559 individuals observed, 190 were identified as bulls, 176 as cows, 64 as calves, and 129 were unable to be classified. The locations of groups observed during the survey are shown in Figure 13. Average group size was 7.8 elk/group (SD = 10.4), and ranged in size from 1–50 elk. The mean difference between observer counts of elk in groups was 0.32 elk (SE = 0.071), and ranged from 0–5 elk with difference increasing with group size.

Using the GS sightability model, I estimated the size of the late winter Michigan elk herd in 2006 at 905 elk (SE = 125) with a CV = 13.8% and standard normal 95% confidence interval of 660–1150 elk. The total variance was 15617.2. The largest component of the total variance was variability due to estimating group size and sighting probability (10083.8). The remaining error was a result of sightability error (5533.4). Since we surveyed the entire range there was no variability due to sampling portions of the range.

I estimated the size of the late winter Michigan elk herd in 2006, using the SF sightability model, as 872 elk (SE = 107) with a CV of 12.3% and standard normal 95%

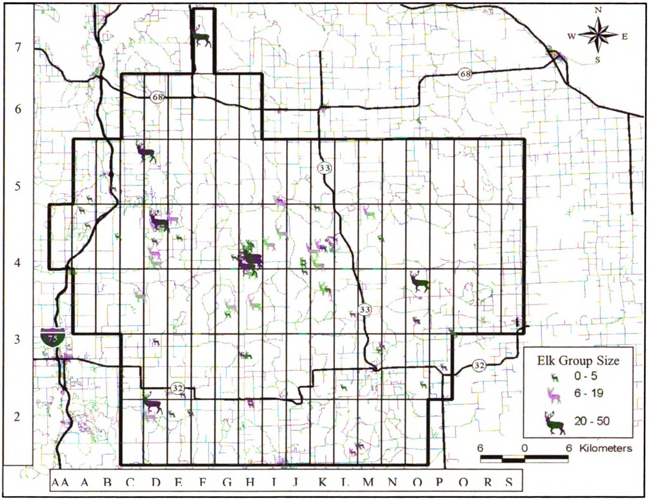


Figure 13. Location and relative size of elk groups observed during aerial survey in late winter in Michigan, 2006 (identifying labels are along the margins).

confidence interval of 658–1086 elk. The total variance was 11495, with the smallest component due to sightability error (4919.1). The remaining error was due to estimating the sighting probability (6575.9).

Sampling Simulations

The results of the accuracy assessment of stratification of quadrats into expected elk densities are shown in Table 8 by stratum. Fifty–one quadrats were classified correctly, and 40 were misclassified. Of those correctly classified, the majority (46) were in the low density strata. Figure 14 displays the location of correctly and incorrectly classified quadrats. The medium density stratum had the greatest error in classification with only 1 quadrat correctly classified. The low density stratum was the least variable with regards to the number of elk in each quadrat, 48.17. The medium density was more variable, 114.14, and the high density stratum had the largest within stratum variability, 1505.99.

The effects of varying sampling rates on the average variance of population estimates based on the GS procedure are displayed in Figures 15–20. These analyses demonstrate a continuously decreasing average variance as sampling rate increases in all 3 density strata. However, it appears sampling rate has the most effect on the average variance in the high density stratum.

The results of the Monte-Carlo simulations based on the optimal sampling rates for each density stratum demonstrated the high density stratum should be sampled in its entirety for all sample sizes of quadrats. The medium density stratum should be sampled at a lesser sampling rate, and the low density stratum should be sampled at the lowest sampling rate when all quadrats are not surveyed. The optimal number of quadrats from each density strata for a given sample size and the average variance of the estimated

Table 8. Accuracy assessment of assignment of quadrats to low (0–15 elk), medium (16–30 elk) and high (31+ elk) density strata in Michigan, 2006.

	Correct stratum		
Assigned Stratum	High	Medium	Low
High	4	1	11
Medium	2	1	25
Low	1	0	46

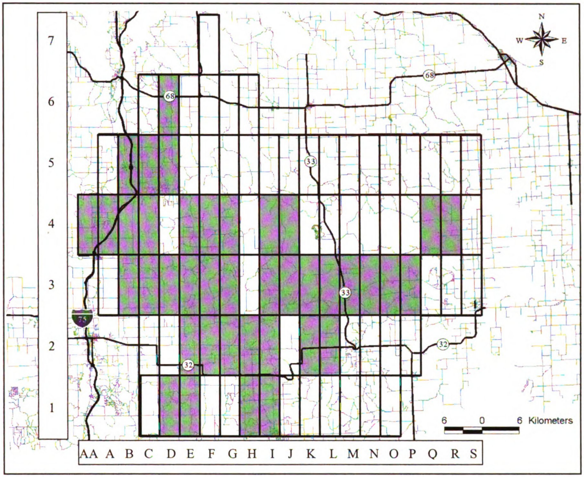


Figure 14. Location of quadrats correctly (white) and incorrectly (gray) assigned to expected elk density strata in Michigan, 2006(identifying labels are along the margins).

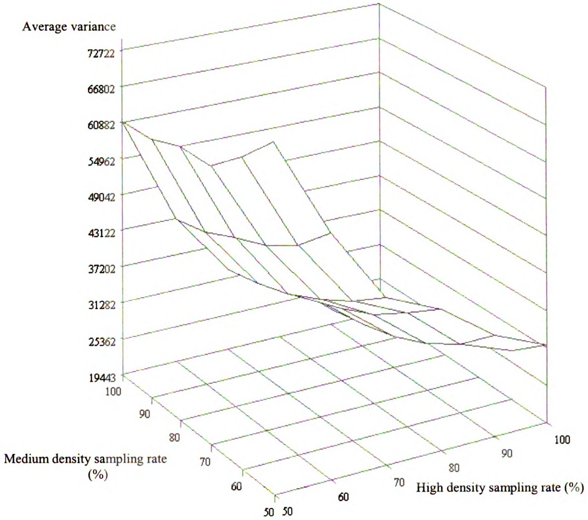


Figure 15. Effects on average variance of the population estimate of varying the sampling rate in the high (31+ elk) elk density and the medium (16–30 elk) density strata with a low density stratum (1-15 elk) sampling rate of 50%.

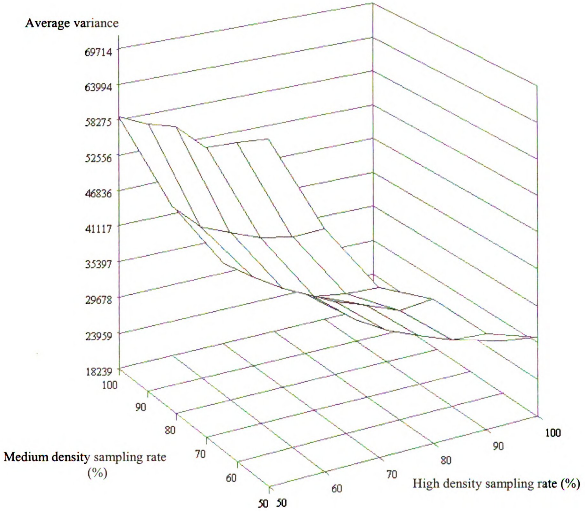


Figure 16. Effects on average variance of the population estimate of varying the sampling rate in the high (31+ elk) elk density and the medium (16–30 elk) density strata with a low density stratum (1-15 elk) sampling rate of 60%.

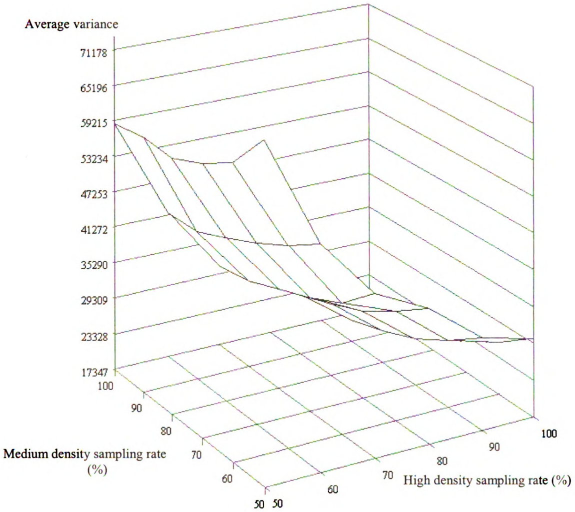


Figure 17. Effects on average variance of the population estimate of varying the sampling rate in the high (31+ elk) elk density and the medium (16–30 elk) density strata with a low density stratum (1-15 elk) sampling rate of 70%.

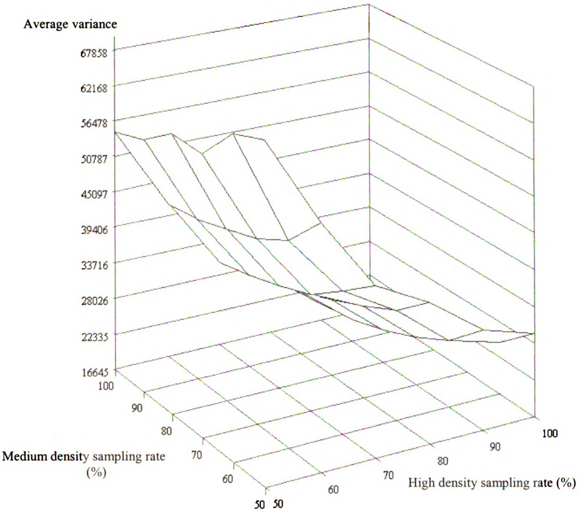


Figure 18. Effects on average variance of the population estimate of varying the sampling rate in the high (31+ elk) elk density and the medium (16–30 elk) density strata with a low density stratum (1-15 elk) sampling rate of 80%.

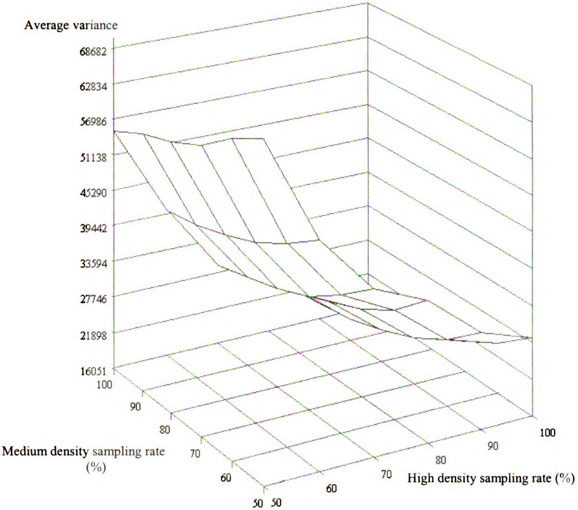


Figure 19. Effects on average variance of the population estimate of varying the sampling rate in the high (31+ elk) elk density and the medium (16–30 elk) density strata with a low density stratum (1-15 elk) sampling rate of 90%.

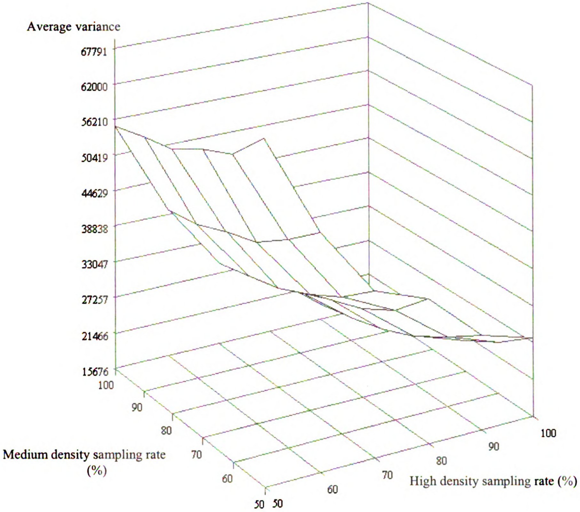


Figure 20. Effects on average variance of the population estimate of varying the sampling rate in the high (31+ elk) elk density and the medium (16–30 elk) density strata with a low density stratum (1-15 elk) sampling rate of 100%.

population is shown in Table 9.

Cost

The total cost estimate and individual expenditures for the 2006 elk survey (Table 10) are based on 85 hours of total flight time, and it assumed each plane and pilot flew 42.5 hours. I also assumed each plane had a wildlife technician and biologist as observers.

Costs associated with the historical population estimation procedure using a helicopter with current prices were much higher than those with the sightability technique (Table 11). Total estimates of individual expenditures are based on values provided by Otten (1989). Costs of the same procedure using a MDNR fixed-wing aircraft are more reasonable (Table 12).

Discussion

Sightability Model Development–Detection Probability Estimation

We observed lower mean elk group sizes for elk groups seen by observers and elk groups missed by observers as well as across all elk groups compared to the values reported by Otten (1989) for elk in Michigan. He found across all elk groups, a mean elk group size of 9.8 elk/group. For elk groups seen by observers, he estimated a mean elk group size of 12.3 elk/group, and for elk groups missed 5.1 elk/group. These smaller group sizes are not surprising given the ban on winter feeding and baiting in this area, which during Otten's study created artificially large groups concentrated at winter feeding sites (Otten et al. 1993). Also some discrepancy is due to my attempts to ensure an even distribution of observations throughout the various levels of the class variables when possible. Thus

Table 9. The sample size of quadrats surveyed, the average variance of 1,000 elk population estimates generated using the optimal number of samples from each density strata, and the optimal number of quadrats sampled from each density stratum based on the elk survey in Michigan, 2006.

		Density Stratum		
Sample Size	Average Variance	High	Medium	Low
45	36,146.65	16	14	15
46	36,312.62	16	14	16
47	34,216.96	16	15	16
48	33,804.08	16	15	17
49	31,700.95	16	16	17
50	31,476.74	16	16	18
51	29,696.22	16	17	18
52	29,919.18	16	17	19
53	28,539.81	16	18	19
54	28,023.74	16	18	20
55	27,004.65	16	19	20
56	26,650.14	16	19	21
57	25,358.54	16	20	21
58	25,152.73	16	20	22
59	24,364.09	16	21	22
60	23,822.63	16	21	23
61	23,016.19	16	22	23
62	22,818.90	16	22	24
63	22,870.17	16	22	25
64	21,772.38	16	23	25
65	21,543.66	16	23	26
66	20,774.76	16	24	26
67	20,542.25	16	24	27
68	19,981.18	16	25	27
69	19,833.83	16	25	28
70	19,276.88	16	26	28
71	19,112.97	16	26	29
72	18,533.04	16	27	29
73	18,284.24	16	27	30

Table 9. (cont'd)

Sample Size	Average Variance	Density Stratum		
		High	Medium	Low
74	17,877.18	16	28	30
75	17,702.27	16	28	31
76	17,480.44	16	28	32
77	17,301.66	16	28	33
78	17,129.11	16	28	34
79	16,886.33	16	28	35
80	16,872.79	16	28	36
81	16,689.94	16	28	37
82	16,532.07	16	28	38
83	16,414.07	16	28	39
84	16,312.12	16	28	40
85	16,227.14	16	28	41
86	16,153.53	16	28	42
87	16,000.35	16	28	43
88	15,871.65	16	28	44
89	15,797.02	16	28	45
90	15,706.70	16	28	46
91	15,617.15	16	28	47

Table 10. Costs associated with conducting the elk survey of the entire range in northern Michigan, 2006.

Cost component	Per unit cost ($)	Total component cost ($)
Plane	100/hr	8,500
Pilot	28/hr - lead pilot	1,190
	26/hr - pilot	1,105
Personnel	23/hr - technician	978
	29/hr - biologist	1,233
Total cost ($)		13,005

Table 11. Projected costs for conducting the historical elk survey procedure using a helicopter in northern Michigan, 2006.

		Length of Survey		
Cost component	Per unit cost ($)	2 days	3 days	4 days
Helicopter rental	1275/day	2,550	3,600	4,650
Helicopter fuel	4.00/gal	1,200	1,800	2,400
Pilot lodging	65.00/night	65	130	195
Personnel	23/hr - technician	5,888	8,832	11,776
	29/hr - biologist	1,856	2,784	3,712
Snowmobile rental	125.00/day	1,750	2,625	3,500
Total Cost ($)		13,309	19,771	26,233

Table 12. Projected costs for conducting the historical elk survey procedure using a fixed-wing aircraft in northern Michigan, 2006.

		Length of Survey		
Cost component	Per unit cost ($)	2 days	3 days	4 days
DNR fixed-wing	700/day	1,400	2,100	2,800
Airplane fuel	4.00/gal	1,200	1,800	2,400
Pilot lodging	65.00/night	65	130	195
Personnel	23/hr - technician	5,888	8,832	11,776
	29/hr - biologist	1,856	2,784	3,712
Snowmobile rental	125.00/day	1,750	2,625	3,500
Total Cost ($)		12,159	18,271	24,383

in 2005, we surveyed more groups in the heavier conifer classes where elk groups tended to be smaller, and thereby reduced my mean group size.

We collected a large number of observations for development of the sightability models (216) compared to other studies calculating elk sightability. For example, Samuel et al. (1987) used observations of 111 elk groups for their model development, Otten (1989) used observations of 79 elk groups and Anderson et al. (1998) used observations of 55 elk groups.

The sightability model parameter estimates indicate the following about elk sightability: larger elk groups have a higher sightability than smaller groups; increasing wind speed increases sightability of elk groups; elk groups which were standing have an increased probability of being observed over groups which were classified as bedded or bedded and standing; groups which were located in conifer cover class 1 were more likely to be observed as opposed to groups in the heavier conifer cover class; elk groups in areas of complete snow cover had a higher probability of being observed than elk groups where some vegetation was showing; and elk groups located in flat light with low intensity, bright light with medium intensity, flat light with medium intensity and bright light with high intensity had a decreasing probability of being observed, respectively. However, conifer cover class and group size are the most important variables influencing elk sightability based on RI values and standard errors of parameter estimates. Snow conditions are of lesser influence, and the remaining variables have insignificant impact on elk sightability.

My sightability model results are comparable with those of other studies. Samuel et al. (1987) made similar findings in Idaho. They found that group size and percent vegetation cover were the 2 most influential variables affecting elk sightability, while behavior and snow conditions were of lesser importance. Otten et al. (1993) determined conifer cover influenced elk sightability in Michigan from a helicopter; however, group size was not determined to be influential. McCorquodale (2001) also determined canopy cover and group size were influential variables in the elk sightability models developed for Washington.

Survey–Population Size Estimation

The comparison between the SF and GS estimators demonstrated, as expected, the GS increased both point estimates of population size as well as variance estimates relative to the SF. However, we believe that higher estimates produced by the GS estimator are less biased. Cogan and Diefenbach (1998) demonstrated the SF estimator, in the presence of undercounting, produced negatively biased population estimates and underestimated the variance of those point estimates. Given the differences in counts of the same elk group by multiple observers shown in this study, we believe there is little doubt undercounting of elk groups is occurring. The GS procedure relaxes the assumption that the size of elk groups be known constants, and allows for estimation of group size. This estimation reduces the bias resulting from the violation of the above assumption, and increases the variance estimates accordingly which produces confidence intervals with closer to nominal coverage (see Chapter 3). Interestingly, when group size is estimated the largest component of the variance in the GS model is due to estimating group size and sighting probability, whereas in the SF the largest component of variability is due to sightability error. Thus, the findings of Cogan and Diefenbach (1998) of below nominal confidence interval coverage for the SF are not surprising as the SF formulation does not include a critical component of variability—the variability associated with estimating group size.

Sampling Simulations

The resulting increases in average variance of population estimates, as a result of reducing the number of quadrats surveyed, were clearly demonstrated in the analyses examining the effects of varying sampling rates in each stratum (Figures 15–20). Reduction in sampling effort, particularly in the high density stratum, resulted in marked increases in the average variance of population estimates. The surfaces showed that the average variance continued to decrease as sampling effort increased with no obvious asymptote for this stratum. In the medium and low density strata there was a continued reduction in average variance with increasing sampling effort, however, the effects lessened as sampling rates approach 100%. Thus, effects of sampling on average variance were less dramatic in these 2 strata. This was not surprising given that the high density stratum was considerably more variable with regards to total number of elk within quadrats than the low or medium density strata.

The effect of increasing variance was also demonstrated in the analysis examining optimal sample sizes per stratum given a fixed sample size. The number of samples, determined to be optimal in each stratum for a given sample size, were a reflection of the variability associated within each stratum. Thus the high, medium and low density strata showed decreasing variability in the number of elk groups within quadrats and consequently decreasing recommended sampling rates, respectively. From these simulations it was clear that for the most precise population estimates, the high density stratum should always be completely surveyed, the medium density stratum should be surveyed at the next highest rate, and the low density stratum should be the focus of the reduction in sampling effort if the range cannot be completely surveyed. Also even minor reductions in sampling effort can have significant impacts on the length of 95% confidence intervals. For example, if only 41 of the 47 low density quadrats and all of the quadrats in the other 2 strata were sampled, the length of the confidence interval increased by 10 elk. If 35 of the 47 low density quadrats and all of the quadrats in the other 2 strata were sampled, the length of the confidence interval increased by 20 elk.

Given these results and the inability to correctly classify quadrats into density strata (Table 8), we strongly recommend surveying the entire range if precise population estimates are desired. At a minimum the range should be surveyed in its entirety for several years (i.e., 3–5) to examine the temporal variability of the number of elk groups in each quadrat during the survey and contributing factors (e.g., snow depths, mast production, recreational pressure, etc.). Such an analysis will likely produce more accurate assignment of quadrats to density strata. If the range cannot be surveyed completely, sample sizes for each stratum should be based on Table 9 and drawn using a probabilistic sampling scheme (e.g., simple random sample from each stratum); however, precision of population estimates will suffer accordingly. It is also important to note the sample sizes recommended in Table 9 are based on the 2006 elk survey data and, therefore, the within stratum variability may change in subsequent surveys. These changes will alter the optimal sample sizes, and therefore, the within stratum variability should be assessed over multiple years and the average should be used to calculate optimal sample sizes.

Thus, when determining whether to survey the entire range or sample a portion of it, the question to ask is: what is an acceptable level of precision associated with the elk population estimate relative to cost? Given the relatively low cost of the 2006 survey, the consideration ultimately is only of the desired level of precision of the population estimate. When the entire range was sampled the SE = 125 elk, which resulted in a CV = 13.8%. The precision of the 2006 elk population estimate is comparable to other elk surveys across the country (Otten 1989, Steinhorst and Samuel 1989, Anderson et al. 1998, Noyes et al. 2000). However, decreasing the level of precision through sampling dictates that changes in population size will need to be larger before differences in population size are designated as statistically different. Thus, as the variance increases the usefulness of the estimate for management purposes decreases.

Costs

One of my objectives was to create an economical elk population estimation technique for the MDNR biologists. The technique described above achieved this objective. The cost of the 2006 elk survey was inexpensive relative to the historical technique with the exception of 2 days of surveying using MDNR fixed-wing aircraft. However, 2 days of surveying using the historical technique would only allow for a small portion of the range to be surveyed and given the range expansion in the last 10 yrs (Figure 1: Chapter 1) the use of this technique becomes impractical. Also this technique only generated an index to population size, whereas the 2006 elk survey, which was conducted over the entire range, allowed for estimation of population size and an associated measure of precision.

Management Implications

The population estimation technique developed met all the project objectives: it incorporated sightability model correction factors, allowed for estimation of group sizes, utilized a probabilistic sampling scheme for surveying the range, provided statistically defensible population estimates, and was economically feasible to conduct. It represents a considerable improvement over the historical aerial/snowmobile technique as it addresses the shortcomings of this procedure and allows for rigorous population estimation. Thus, this estimation procedure is a useful tool that MDNR elk biologists can employ to monitor population size, set harvest objectives, and meet the various demands of a diverse array of stakeholders utilizing Michigan's elk herd.

Availability of Estimation Program

The program that I used to estimate population size and associated variances is available as SAS code. The code has been archived in several locations, and is available upon request. I have used the code extensively, and I am not aware of any "bugs", however, I make no guarantees about the accuracy of the program or the resulting output. Dr. Henry Campa III and Dr. Scott Winterstein in the Department of Fisheries and Wildlife at Michigan State University have several archived copies of the program. Also Dr. Dean Beyer, Michigan Department of Natural Resources, and I, Colorado Division of Wildlife, have copies available for distribution.

CHAPTER 3: DERIVATION OF ELK POPULATION ESTIMATOR ALLOWING FOR GROUP SIZE ESTIMATION

Introduction

Sightability models have been widely used to estimate population size for a wide array of wildlife species, particularly large cervids (Samuel et al. 1987, Bodie et al. 1995, Anderson and Lindzey 1996, Ayers and Anderson 1999). Sightability models are used to estimate the detection probability of groups of the species of interest, thereby correcting for groups that are missed by observers. Generally, sightability models are logistic regression models with various group-specific as well as environmental covariates used as predictor variables (Samuel et al. 1987). Estimates of population size are calculated by summing the quotients of complete counts of groups counted during a survey divided by their detection probability as determined from the sightability model. The technique was first put forth by Samuel et al. (1987), and Steinhorst and Samuel (1989) provided the statistical theory behind the estimation procedure. Unsworth et al. (1990) validated the Samuel et al. (1987) model for elk in Idaho showing the merit of the technique.

Although this estimation procedure has proven useful, a limitation is the assumption that group sizes of the species of interest are known. Typically, the maximum of observer counts is used as the estimate of group size, although the maximum as an estimator of true group size is known to be negatively biased (Olkin et al. 1981, DasGupta and Rubin 2005). Cogan and Diefenbach (1998) confirmed this bias and the violation of the above assumption using counts of elk groups of known size by observers from helicopters in Pennsylvania. Findings in Chapter 2 also demonstrated this assumption was violated when counting elk groups from fixed-wing aircraft in Michigan by examining multiple counts of groups by independent observers (see Chapter 2).

Through simulation, Cogan and Diefenbach (1998) showed when group sizes were undercounted population estimates based on these estimates of group size showed severe, negative bias and confidence interval coverage was below nominal.

I developed a bias correction procedure based on estimating group sizes, and incorporated the variability resulting from this estimation into the approximate variance estimates. This correction reduces bias and increases variance estimates since group size is treated as a random variable rather than a known value. The modified Horvitz-Thompson estimator (Steinhorst and Samuel 1989) for estimating population size is shown below:

$$T = \sum_{k}^{L} \frac{D_k}{p_k} \sum_{i}^{N_k} R_{i(k)} m_{i(k)} \Theta_{i(k)} \qquad (1)$$

where D_k= 1 if the k^{th} land unit is sampled and D_k= 0 otherwise, p_k = the known probability that the k^{th} land unit is selected as part of the sample, $R_{i(k)}$ = 1 if the i^{th} group in the k^{th} land unit is observed and $R_{i(k)}$ = 0 otherwise, $m_{i(k)}$ = size of the i^{th} group in the k^{th} land unit, $\Theta_{i(k)}$ = is the inverse of the sighting probability or detection probability for the i^{th} group in the k^{th} land unit obtained from a sightability model, L = total number of land units, and N_k = the total number of elk groups in the study area. The realization of this estimator correction for unknown group sizes is:

$$t = \sum_{k}^{l} \frac{1}{p_k} \sum_{i}^{n_k} \hat{m}_{i(k)} \hat{\Theta}_{i(k)}, \qquad (2)$$

where $\hat{m}_{i(k)}$ = estimated group size of the i^{th} group in the k^{th} land unit, $\hat{\Theta}_{i(k)}$ = is the inverse of the estimated sighting probability or detection probability for the i^{th} group in the k^{th} land unit obtained from a sightability model l = the number of quadrats in the sample and n_k = the number of groups observed during the survey. This chapter is about estimation of T and its approximate variance, and the examination of the performance of this estimator.

It is assumed throughout that a logistic regression model for estimating detection probability of groups has been previously developed, and in this logistic regression model, the natural log transformation of group size is used as a predictor variable (Samuel et al. 1987) as in Chapter 2. Group size is a common and often significant predictor variable in sightability models (Samuel et al. 1987, Otten et al. 1993, Anderson et al. 1998, Walsh 2007). Elk surveys conducted in 2006 in Michigan will serve as an example for this estimator, and all analysis and discussion will be based on data collected during these surveys.

In Section 2, I describe an example of how estimates of $\hat{m}_{i(k)}$ can be calculated using multiple, independent observer counts of group size, and I compare a method-of-moments estimator (DasGupta and Rubin 2005) to a joint-binomial-maximum-likelihood estimator. However, $\hat{m}_{i(k)}$ can be estimated using any statistically valid means beyond those explored here, and estimation of T is still possible. In Section 3, I derive the approximate variance for the estimate of T using the conditional variance formula, assumptions of log normality and the delta method. In Section 4, I examine the performance of the estimator including bias, coefficient of variation (CV), mean-squared error (MSE), and asymptotic confidence interval coverage through Monte-Carlo simulations based on 2006 Michigan elk survey data, and Section 5 is a discussion of the results.

Estimation of Group Sizes Using Multiple Independent Observer Counts

Multiple independent counts of groups of the species of interest can often be obtained quickly and economically during wildlife surveys when multiple observers are used. For example, when conducting aerial elk surveys in Michigan, 3 independent counts of groups can be obtained by using counts from the pilot and the 2 observers attempting to locate elk groups out each side of the plane. These counts can then be used to estimate the true group size.

One means of estimating group size, based on the Binomial distribution assumptions, and assuming a constant probability of detecting individuals within a group across observers, is the joint binomial likelihood that generates maximum likelihood estimates (MLE) of true group size. The likelihood is as follows:

$$L(N|X_1, X_2, X_3) = \prod_{i=1}^{3} \binom{N}{X_i} p^{X_i} (1-p)^{N-X_i}. \tag{3}$$

with N = true group size, X_i = count of group size by the i^{th} observer and p = the probability of observers detecting an individual within a group from the air. However, no closed form estimator for N exists and numerical techniques must be employed. Olkin et al. (1981) and Carroll and Lombard (1985) provide 2 estimators of N based on the likelihood which improve stability through use of a jack-knife procedure and integrating the likelihood over a beta density for p.

A second estimator is the method-of-moments estimator (MME) proposed by DasGupta and Rubin (2005):

$$\hat{m}_{i(k)} = \frac{X_{(w)}^{\alpha+1} \left(S^2\right)^{\alpha}}{\bar{X}^{\alpha} \left(X_{(w)} - \bar{X}\right)^{\alpha}}, \tag{4}$$

where $X_{(w)}$ = maximum of w observer counts of group size, $\overline{X}$ = mean these counts, S^2 = sample variance of these counts, and α = constant. The approximate estimate of the asymptotic variance is as follows:

$$\hat{\text{var}}(\hat{m}_{i(k)}) \approx \frac{2\alpha^2 \hat{m}_{i(k)}(\hat{m}_{i(k)} - 1)}{w}. \tag{5}$$

This MME requires a fixed α value. DasGupta and Rubin (2005) recommended $\alpha = 1$; however, they only examined scenarios of large N values and small p values where N = group size and p = probability of detecting an individual within the group. Generally, once a group is detected during a wildlife surveys p is large, and depending on the species, N may be small. Thus, to determine the optimal value of α, I simulated 3 random counts from a binomial distribution based on values of N ranging from 1–50 and values of p ranging from (0.70–0.99). These values were chosen as they were the range of elk group sizes reported during elk surveys in Michigan and probability of success values reported by Cogan and Diefenbach (1998) for elk in Pennsylvania. For each combination of N and p values, I varied α from 0.00–1.00, and generated estimates of N using the MME, associated variance estimates calculated using equation (5), and calculated MSE values over 10,000 repetitions. I summed the MSE values across all N and p values for each α, and determined that $\alpha = 0.10$ minimized this sum (Table 13). This value of α was used in all subsequent calculations since it minimized MSE across the expected range of N and p values for elk surveys in Michigan.

Since estimators of N in the binomial often exhibit erratic behavior including the MLE and other MMEs (Olkin et al. 1981, Hall 1994), I evaluated the stability of this MME. I generated 3 random counts from a binomial distribution with true group sizes

Table 13. Top 5 values of α that minimized MSE values of method-of-moments estimates of N across all values of N (1–50) and p (0.50–0.99)

α	MSE
0.10	15,493
0.09	15,571
0.11	15,621
0.08	15,841
0.12	15,965

ranging from 1–75 and probability of success (p) ranging from 0.50–0.99, and calculated the MME of N at $\alpha = 0.10$. I then added a value of 1 to one of the random counts and recalculated the MME of N. Stability was evaluated by examining the differences between the 2 estimates of Nover 1,000 repetitions for all N and p combinations. The stability of the estimator was good with the mean difference of 2.51 (SD = 1.94) and a range of 0.50–17.10 between the 2 estimates across all values of true group size and p.

To determine which estimation procedure, MLE or MME, was better for estimation of true elk group size given 3 independent counts of group size, I once again generated 3 random counts from a binomial distribution with N ranging from 1–50 (i.e., range of elk group sizes seen in Michigan) and values of p ranging from (0.70–0.99). I then estimated N using the MLE and MME with $\alpha = 0.10$, calculated associated variances, and estimated MSE values for 1,000 repetitions of each N and p combination. I determined the MME yielded the minimum MSE values, summed across all N and p values over the 1,000 repetitions, with a sum of 3,7933.99 compared to the MLE, which had a sum of 7,001.69. Thus the MME was used to estimate group sizes for all further analyses.

Estimation of the Approximate Variance of *T*

The variance of the estimator of population size T in equation (1) is complicated as the estimate of group size, $\hat{m}_{i(k)}$ occurs both in the numerator as well as in the denominator of equation (1), since it is a predictor variable in the logistic regression model that produces $\hat{\Theta}_{i(k)}$. However, an approximate variance estimate can be derived using the following lemma (Ross 2003) and the delta method. Notation follows that of Steinhorst and Samuel (1989).

Lemma. The variance of the scalar function, $T(\mathbf{D}, \mathbf{R}, \mathbf{B})$, of 3 random vectors, is

$$\mathrm{var}[T(\mathbf{D},\mathbf{R},\mathbf{B})] = \mathrm{E}_D[\mathrm{var}_{R|D}(\mathrm{E}_{B|R,D}[T])] + \mathrm{var}_D(\mathrm{E}_{R,B|D}[T]) + \mathrm{E}_D[\mathrm{E}_{R|D}[\mathrm{var}_{B|R,D}(T)]],$$

where $\mathbf{D}$ is a random vector with k^{th} element = D_k, which is 1 if the k^{th} land unit is sampled and 0 otherwise, $\mathbf{R}' = (\mathbf{R}'_1, \ldots, \mathbf{R}'_L)$ with $\mathbf{R}'_k$ being a random vector whose i^{th} element = $R_{i(k)}$, which is 1 if the i^{th} group in the k^{th} land unit is observed and 0 otherwise, and $\mathbf{B}'_k = (\mathbf{B}'_1, \ldots, \mathbf{B}'_L)$ with $\mathbf{B}'_k$ being a random vector whose i^{th} element $= \hat{m}_{i(k)}\hat{\Theta}_{i(k)}$.

Using this lemma and the $\mathrm{E}[\hat{m}_{i(k)}\hat{\Theta}_{i(k)}] \approx m_{i(k)}\Theta_{i(k)}$ (Appendix C), the first 2 variance components are identical to the variance components given in *Theorem 1* in Steinhorst and Samuel (1989) with $m_{i(k)}$ replaced by $\hat{m}_{i(k)}$. They are identical since the expectation of the first 2 terms is taken with respect to $\hat{m}_{i(k)}\hat{\Theta}_{i(k)}$ first. The third variance component can be approximated using the delta method, the above lemma and assuming log normality of $\Theta_{i(k)}$ (Appendix D). The resulting estimate of approximate variance is as follows:

$$s_t^2 = \sum_k^l \frac{1-p_k}{p_k^2}\hat{M}_k^2 + \sum_{k\neq k'}^{l}\sum^{l'} \frac{p_{kk'} - p_k p_{k'}}{p_{kk'} p_k p_{k'}}\hat{M}_k \hat{M}_{k'} + \sum_k^l \frac{1}{p_k}\sum_i^{n_k}\left(1 - \frac{1}{\hat{\Theta}_{i(k)}}\right)\left(\hat{m}_{i(k)}\hat{\Theta}_{i(k)}\right)^2$$
$$+ \boldsymbol{\delta}'\Sigma\boldsymbol{\delta} + \sum_{i(k)\neq i'(k')} \mathrm{E}_{m_j m_{j'}}\left[\frac{1}{p_k p_{k'}}\hat{m}_{i(k)}\hat{m}_{i'(k')}\mathrm{cov}\left(\hat{\Theta}_{i(k)}, \hat{\Theta}_{i'(k')}\right)\right], \tag{6}$$

where $\hat{M}_k = \sum_i^{n_k}\hat{m}_{i(k)}\hat{\Theta}_{i(k)}$, $\boldsymbol{\delta}$ = vector of partial derivatives of $\sum_k^l\sum_i^{n_k}\frac{\hat{m}_{i(k)}\hat{\Theta}_{i(k)}}{p_k}$ with respect to each of $\hat{m}_{i(k)}$ and to each of the $\hat{\beta}$'s from the sightability model (i.e.,

$\delta_{\hat{m}_{i(k)}} = \frac{1}{p_k}\left(1 + e^{-\mathbf{X}_{i(k)}\hat{\boldsymbol{\beta}}}\left(1 - \hat{\beta}_1\right)\right)$ and $\delta_{\hat{\beta}_h} = \sum_{k}^{l}\sum_{i(k)}^{n_k} \frac{\hat{m}_{i(k)} e^{-\mathbf{X}_{i(k)}\hat{\boldsymbol{\beta}}} x_{hi(k)}}{p_k}$ with $X_{i(k)}$ = the

vector of predictor variables used in the sightability model for the $i(k)^{\text{th}}$ group, $\hat{\beta}_1$ = the beta associated with the ln($\hat{m}_{i(k)}$) as a predictor in the sightability model, and $x_{hi(k)}$ is the h^{th} predictor for the $i(k)^{\text{th}}$ observation), $\Sigma = \begin{bmatrix} \hat{\sigma}^2_{\hat{m}_1} & 0 & 0 & 0 \\ 0 & \ddots & 0 & 0 \\ 0 & 0 & \hat{\sigma}^2_{\hat{m}_{i(k)}} & 0 \\ 0 & 0 & 0 & \hat{\Sigma}_{beta} \end{bmatrix}$ with $\hat{\sigma}^2_{\hat{m}_{i(k)}}$

derived from equation (5), or $\hat{\sigma}^2_{\hat{m}_{i(k)}} = 0$ if all counts of group size are equal,

$\hat{\Sigma}_{beta}$ = estimated variance-covariance matrix for the $\hat{\beta}$'s from the sightability model. The final term in equation (6) is a summation of expectations, which can be approximated using the average value of N simulated values of $\hat{m}_{i(k)}$ and $\hat{m}_{i'(k')}$, which are generated from a Normal distribution with mean = $\hat{m}_{i(k)}$ and variance =

$\frac{2\alpha^2 \hat{m}_{i(k)}(\hat{m}_{i(k)} - 1)}{w}$, and the $\hat{\text{cov}}(\hat{\Theta}_{i(k)}\hat{\Theta}_{i'(k')})$ =

$$e^{-(\mathbf{X}_{i(k)}+\mathbf{X}_{i'(k')})'\hat{\boldsymbol{\beta}}-(\mathbf{X}_{i(k)}+\mathbf{X}_{i'(k')})'\hat{\boldsymbol{\Sigma}}_{beta}(\mathbf{X}_{i(k)}+\mathbf{X}_{i'(k')})/2}\left(e^{\mathbf{X}_{i(k)}{}'\hat{\boldsymbol{\beta}}\mathbf{X}_{i'(k')}} - 1\right).$$

This covariance term is identical to the final term in the variance equation proposed by Steinhorst and Samuel (1989), which is valid using an approximation of asymptotic log normality.

I examined the amount of bias associated with using this approximation of the final term in equation 6, as well as the bias associated with using solely the point estimates as an approximation of the final term of equation (6) (i.e.,

$\sum_{i(k)\neq i'(k')}\left[\frac{1}{p_k p_{k'}}\hat{m}_{i(k)}\hat{m}_{i'(k')}\,\hat{\text{cov}}\left(\hat{\Theta}_{i(k)},\hat{\Theta}_{i'(k')}\right)\right]$). I generated 1,000 datasets with group size being estimated using equation (4) based on 3 random counts generated from a binomial distribution with N = estimated group size, which was assumed the true group size, and p = average probability of success from observer counts of group size from the 2006 Michigan elk survey data. I then calculated the final covariance term in equation (6) using the true group sizes and the 2 approximating methods. Bias was then calculated as the difference between the values of the approximating methods and true group size. The point estimate approximation yielded the largest bias with an average bias of 47.45 (SD = 39.21), and the averaging approximation had an average bias of -18.04 (SD = 14.55). Both of these approximating methods produced little bias relative to the overall variance of the population estimate, 0.30% and 0.12%, respectively. The averaging method appears to produce less biased results, but a considerable amount of computing time is required for this method. Therefore, if large simulations need to be conducted the point estimate approximation will yield reasonable results with slightly liberal variance estimates.

Performance of estimator

To assess the performance of the proposed estimator for estimating elk population size, I followed the technique used by Cogan and Diefenbach (1998). I first created 1,000 elk sightability models using Monte Carlo simulation techniques based on 2004 and 2005 Michigan elk sightability model datasets (Chapter 2). Each sightability model was created following the technique outlined in Chapter 2 for generating model-averaged parameter estimates (Burnham and Anderson 2002), and their associated unconditional variance-covariance matrix, which incorporates the measurement error associated with estimating group size.

Secondly, I created 20 elk survey datasets by sampling observation of elk groups with replacement from the 2006 Michigan elk survey until the total number of elk sampled reached the desired population size. I examined population sizes of 250, 500, 750 and 1,000 elk, which span the range of elk sizes historically seen in Michigan. I generated 3 random counts from a binomial distribution with N = estimated group size for each observation, and p = average probability of success across observer counts of group size from each observation given N. Then group size was estimated using these 3 random counts and equation (4). Each group was classified as seen by observers if a Uniform (0, 1) random variable was less than or equal to the "true" detection probability, otherwise it was considered as missed by observers. Logistic regression was used to calculate the "true" detection probability using the parameter estimates from Michigan's current sightability model (Chapter 2), and the values of the predictor variables associated with each observation from the survey datasets. Once all elk groups were classified as seen or missed, total population size was estimated for each survey dataset across all population sizes using equation (2) and each of the 1,000 sightability models. Thus 20,000 population estimates were generated for each population size. Variances were calculated using equation (6), where the last term was estimated using the point estimate approximation to minimize computing time.

Performance of the estimator was then assessed by calculating the average bias, 95% confidence interval coverage, average CV, and average MSE for each population size. Confidence intervals were 95% asymptotic normal confidence intervals.

I also examined the performance of the Steinhorst and Samuel (1989) estimator, using the same 1,000 sightability models and 20 survey datasets for each population size for comparison. However, group size was estimated as the maximum of the 3 random counts generated previously. I examined the same performance measures as described previously (Table 14). From these results it is apparent that the proposed estimator outperforms the traditional sightability model estimator, and bias is reduced substantially when group sizes are estimated. The proposed estimator has increased MSE values due to increased variances as evidenced by the larger CV values, but confidence interval coverage is closer to the 95% nominal level compared to the traditional estimator.

These results also demonstrate the approximate variance formula presented in equation (6) generates acceptable variance estimates based on the confidence interval coverage reported.

Conclusion

Any statistically valid method (e.g., mark-recapture, distance-sampling, etc.) can be used to estimate group size for use with this estimator. We chose to use the method-of-moments estimator based on multiple independent counts to estimate group size, since it performs reasonably well given the limited number of independent counts used in this study. Also it provides an effective way for wildlife managers to estimate the size of each group. It is important to note that the α value used in this study for estimating Michigan elk group sizes may not be appropriate for other regions or other species, and it

Table 14. Average of performance measures for the population estimator that includes estimates of group size (GS) and for the traditional sightability model estimator (SF) based on Monte-Carlo simulations with 20,000 repetitions for each population size from Michigan elk survey data (2006).

Estimator	Population Size	Bias	CV	MSE	Confidence Interval Coverage (%)
GS	250	2.90	0.20	7,280.87	90.90
GS	500	-4.04	0.16	16,159.60	92.40
GS	750	3.36	0.15	31,092.33	94.70
GS	1,000	1.93	0.14	50,892.76	93.50
SF	250	-7.40	0.16	3,969.98	86.20
SF	500	-20.19	0.12	8,445.35	87.30
SF	750	-19.92	0.11	14,508.76	88.90
SF	1,000	-30.33	0.10	22,981.58	85.60

should be independently determined for each study area and species using simulations as described.

The inclusion of the estimation of the size of individual groups in the traditional sightability model population estimator allows for less biased population estimates. It also increases the variance of these point estimates allowing confidence interval coverage to approach the nominal level, which is desirable given the findings of Cogan and Diefenbach (1998) and my findings of below nominal coverage of the traditional estimator as a result of undercounting of group sizes.

Thus this new estimator is an important tool for wildlife managers attempting to derive accurate population estimates for wildlife species using aerial surveys, and can aid managers in achieving a wide array of management objectives.

CHAPTER 4: EXAMINATION OF ELK HOME RANGES AND RANGE UTILIZATION

Introduction

Notable changes in the movements and distribution of elk (*Cervus elaphus*) in Michigan have occurred in the last 2 decades based on the increase in the number of elk harvested, observed and reported beyond the boundaries of the historic range as originally defined in the Elk Management Plan (Michigan Department of Natural Resources 1984). The causative factors for these changes are not well understood. But undoubtedly, the discovery of bovine tuberculosis (TB) in free-ranging white-tailed deer (*Odocoileus virginianus*) inhabiting areas within and adjacent to the elk range, and the sweeping management actions aimed at preventing the spread of the disease played a role. In particular, the ban on winter-feeding of ungulates instituted in 1998, which occurred historically throughout the elk range, has changed how elk utilize the range (D. Smith, Michigan Department of Natural Resources, personal communication).

Using historical elk harvest and survey data it was estimated the elk range had expanded by over 50% since 1984 (D. E. Beyer, Michigan Department of Natural Resources, unpublished report). This range expansion created concern among biologists that agricultural depredations will increase, as many areas of expansion have been in privately owned agricultural lands. Also, this expansion has increased the number of elk in areas with higher apparent TB prevalence (Hickling 2002, O'Brien et al. 2002), providing more opportunity for interspecies transmission of the disease. Given these concerns, developing an understanding of current elk movement patterns and distribution is critical for determining harvest strategies, habitat management practices, and minimizing elk-human conflicts.

Problems with the distribution and browsing pressure exerted by elk on 2 large private hunt clubs, Black River Ranch and Canada Creek Ranch, in the central portion of core elk area have also become an increasing concern in recent years (D. Smith, Michigan Department of Natural Resources, personal communication). These problems, however, are not new since Moran (1973) described elk issues associated with these clubs. Perhaps more recently, the lack of elk harvested on the ranches for several years prior to and during the early portion of this study, combined with deer habitat work, forest management practices, and several good mast years have exacerbated these issues.

The main goal of this portion of the study was to gain valuable information regarding current elk movement patterns and distribution particularly on the eastern portion of the Michigan elk range, which is the region of major range expansion (Figure 1: Chapter1).

The objectives to achieve this goal were as follows:

1. Using elk location data, determine the size of elk home ranges and examine sex-specific differences where home range is defined as "the area traversed by the individual in its normal activities of food gathering, mating and caring for young" (Burt 1943).
2. Determine areas of high elk usage across years.
3. Determine areas of joint space use of elk from various portions of the range.
4. Examine elk use of large hunting clubs within the core elk range where human-elk conflicts have been increasing.
5. Determine the probability of elk using various cover types, particularly managed openings.

Study area

The study site selected for this project includes the current elk range (Figure 2: Chapter 1) in the northern portion of the Lower Peninsula of Michigan (Moran 1973). The range occupies approximately 3,450 km^2 (D. E. Beyer, Michigan Department of Natural Resouces, unpublished report), and is centered on the Pigeon River State Forest near Vanderbilt, Michigan (Bender 1992). We focused our study mainly on the eastern region of the elk range near Atlanta in Montmorency County (Figure 3: Chapter 1). Based on examination of landownership patterns over 33% of the elk range is publicly owned, with another 3% controlled by 2 large private hunting clubs in the center of the elk range (Michigan Department of Natural Resources 2000).

The region consists of flat-topped ridges interspersed with headwater swamps, the product of glacial action. Elevation ranges across the area range from 170–460 m above sea level.

Mean annual temperature is 6.3° C with January having the lowest mean monthly temperature (-7.7° C) and the highest (19.7° C) occurring in July (NOAA 2006). Mean annual rainfall is 67.3 cm, and mean annual snowfall is 189 cm (NOAA 2006) with precipitation being generally well distributed throughout the year.

Vegetation types throughout the region are diverse and intermixed due to variations in topography, soil types and human activities. Deciduous forests are the dominant component of the landscape and represent 30.53% of the area. Woody wetlands represent the second largest land cover type encompassing 28.26% of the area. Evergreen forests and mixed forests compose the next largest proportion of the land area representing 7.64% and 8.29%, respectively (United States Geological Survey 1999). Moran (1973) provides a detailed description of vegetation types throughout the region.

Methods

Capture

Michigan Department of Natural Resources (MDNR) personnel captured elk using helicopter net-gunning techniques (Carpenter and Innes 1995) in early February of 2003 and of 2005. In the summer of 2004, several elk were darted using chemical immobilization procedures (Roffe et al. 2005). Michigan State University All University Committee on Animal Use and Care exempted this project (D. L. Garling, AUCAUC, written communication, 12 27 2003).

Most elk were collared with a 550 g, MOD-600HC radiocollar from Telonics (Mesa, Arizona, USA). Five individuals captured in 2006 were collared with G2000 GPS Collars from Advanced Telemtry Systems (Isanti, Minnesota, USA). These collars were programmed to take fixes every 7 hours.

Elk Locations

Project personnel attempted to locate every surviving animal captured in 2003, a minimum of 3 times a week, and elk collared in 2005 a minimum of 2 times a week throughout the study. A less intense sampling regime was used for elk collared in 2005 as a result of limited resources. This amount of effort ensured collection of greater than 50 relocations/animal/year, the minimum sampling intensity suggested to obtain unbiased annual home range estimates (Otis and White 1999, Seaman et al. 1999 and Garton et al. 2001). Also this level of effort conforms to the recommendations of Borger et al. (2006)

of 10 locations/month, which they found was adequate to generate unbiased home range estimates using kernel methods based on home ranges of roe deer (*Capreolus capreolus*) in Italy. Lastly, this sampling design likely allowed elk the opportunity to move throughout their annual home range within the sampling period, and allowed for unbiased temporal coverage with ample time for movement between subsequent locations to minimize issues of autocorrelation (De Solla et al. 1999, Otis and White 1999).

Radiocollared animals were located using the loudest point method (Springer 1979, White and Garrott 1990) with portable Model R1000 receivers (Communication Specialists, Orange, California, USA), hand-held, 2 and 3-element yagi antennas (Telonics, Mesa, Arizona, USA), GPS units (Garmin, Olathe, Kansas, USA) and compasses to determine receiver location and bearing to each radiocollared animal. Personnel collected a minimum of 3 bearings to estimate each point location, and bearings were collected in the shortest amount of time possible to minimize errors associated with a moving animal (White and Garrott 1990). Every attempt was made to obtain bearings with a minimum difference of 25° to promote location accuracy and precision.

Personnel conducted relocations of marked individuals in 2 shifts, a morning shift (5:30–14:00) and an afternoon shift (15:00–22:00). Order of relocations of individual animals within each shift followed a cluster sampling technique. Animals were placed into 3 primary sampling units (psu) based on their geographic distribution to maximize efficiency in relocating animals, and I created a sampling route for each psu based on locations of marked individuals. Personnel sampled 1 psu each shift with order of relocations of elk within a psu being selected based on a simple random sample without replacement of marked animals. The selected animal was the individual initially located. Personnel subsequently located all marked individuals in the vicinity based on scanning of all radio frequencies. Once animals in the cluster were sampled, personnel proceeded to follow the sampling route for the psu in the direction that was most temporally efficient. This procedure was designed to ensure unbiased temporal coverage of relocations, avoid clumping of observations and alleviate concern over autocorrelation issues as well as maintain statistical efficiency (Otis and White 1999). If marked individuals were together, these aggregations were treated as a single unit when selecting an initial animal to relocate until such time as groups dissolved.

Elk have been shown to exhibit differences in habitat selection and space use between diurnal (800–2000 hours) and nocturnal periods (2000–800 hours) (Beyer and Haufler 1994). Thus, we attempted to obtain elk locations throughout a portion of both periods.

We also attempted to obtain a minimum of 2 visual locations on randomly selected radiocollared elk each week. We used homing techniques to acquire visual locations (White and Garrott 1990), and locations were determined using a hand-held GPS unit.

Analysis

Error assessment.–An important component of any radio telemetry study where animals are not directly located is estimation of both precision and accuracy of the triangulation system (White and Garrott 1990, Withey et al. 2001). I estimated precision of bearings for each observer by placing transmitters in various cover types and topography to incorporate the range of variability within the region of our study (White and Garrott 1990). Every transmitter was attached to a plastic bottle filled with saline solution to simulate the absorption of the radio signal by an elk's body (Hupp and Ratti 1983). Observers then using triangulation techniques (White and Garrott 1990) took bearings from known locations to the test transmitters. Bias and precision for each observer were calculated based on differences between estimated bearings and true bearings using the formula presented by White and Garrott (1990). Bias, averaged across observers, was tested to determine if it was significantly different from zero using a standard *t*-test. I lastly calculated average SD of bearings to the test transmitters to test precision of the loudest point method.

By placing them at a fixed location for approximately 1 week prior to deployment and examining the variability in estimated locations, I investigated the SD of GPS collar fixes. It was assumed the fixes were unbiased.

Location estimation.–Prior to location estimation, I visually inspected the point locations from which bearings were taken in ArcView Version 3.2 (ESRI, Redlands, California, USA), and corrected data entry errors and removed erroneous data. Next, I used Lenth's maximum likelihood estimation (MLE) procedures in Locate III (Nams 2006) to calculate all location estimates based on the bearing data. The standard deviation of the bearings was fixed as the standard deviation calculated during the error assessment. I examined the accuracy of all estimated locations using ArcView, and removed points that were estimated incorrectly based on visual inspection.

Home range estimation. – I estimated home ranges of individual animals using multivariate Gaussian fixed kernel estimators (Worton 1987, 1989; Wand and Jones 1995) in R Version 2.4.1 (2006). I placed a grid over the entire study area with 160.9344 m spacing, and estimated the probability density at each grid point using the fixed kernel estimators. Fixed kernel estimators provide several advantages over other types of estimators. For example, they do not make any assumptions about the underlying distribution and handle complex multi-modal distributions with multiple centers of activity well (Kernhonan et al. 2001). These estimators also create a utilization distribution (UD), which can be a useful metric for analyzing animal space use (Marzluff et al. 2001, 2004; Millspaugh et al. 2006). They also tend to perform better, have less bias especially in the outer contours of the UD, are robust to outliers, and require a smaller sample size (i.e., number of locations) compared to other estimators including the adaptive kernel estimators (Seaman and Powell 1996, Seamann et al. 1999, Borger et al. 2006). The smoothing parameter or bandwidth was determined for each elk using a 2-stage, direct plug-in (DPI) bandwidth selector (Wand and Jones 1995, Kernohan et al. 2001). The smoothing parameter represents the standard deviation for each of the individual kernels in the kernel function, and therefore determines the distance from a particular elk location for which that elk location will have influence on the density estimate of surrounding grid points. I chose the DPI method over the more commonly used least squares cross-validation (LSCV) bandwidth selector, as research based on simulations suggests that the DPI selector is a better bandwidth selector in the sense it provides less variable, unbiased estimates of the bandwidth compared to LSCV (Wand and Jones 1995). Also the rate of convergence to theoretical optimal bandwidth is greater for the DPI selector compared to LSCV.

Wand and Jones (1995) provide a detailed description of each of these techniques, which I summarize below for the univariate case. Extensions to the 2-dimensional case are straightforward as h is replaced with **H** a 2 X 2 bandwidth matrix, and replacing x by a matrix of (x, y) locations.

LSCV is a bandwidth selector which attempts to choose a bandwidth size that minimizes mean integrated squared error (MISE). MISE can be calculated as follows:

$$MISE\{\hat{f}(.;h)\} = E\int \hat{f}(x;h)^2\,dx - 2E\int \hat{f}(x;h)f(x)dx + \int f(x)^2 dx\,,$$

where $\hat{f}(x,h)$ is the kernel estimate of the density at point x given bandwidth h, and $f(x)$ is the true density estimate at point x. However, this expression can be formulated in the following manner since the final term is not dependent on h:

$$MISE\{\hat{f}(.;h)\} - \int f(x)^2 dx = E[\int \hat{f}(x;h)^2\,dx - 2\int \hat{f}(x;h)f(x)dx]\,.$$

LSCV(h) is an unbiased estimator of the right hand side of this formulation and is calculated as follows:

$$LSCV(h) = \int \hat{f}(x;h)^2 dx - 2n^{-1}\sum_{i=1}^{n}\hat{f}_{-i}(X_i;h)$$

where $f_{-i}(x;h) = (n-1)^{-1}\sum_{j \neq i}^{n} K_h(x - X_j)$ is the leave-one-out kernel density estimator. Thus the optimal bandwidth under the LSCV technique is the bandwidth that minimizes LSCV (h).

The DPI selector is based on the notion of using estimates for unknown quantities in the formula for the *AMISE*-optimal bandwidth: $h_{AMISE} = \left[\frac{R(K)}{\mu_2(K)^2\varphi_4 n}\right]^{\frac{1}{5}}$, where K represents the chosen kernel, $R(K) = \int K(x)^2\,dx$, $\mu_2(K) = \int x^2 K(x)dx$,

$\varphi_4 = \int f''''(x) f(x) dx$, and n = the number of observations. The only unknown quantity in the *AMISE*-optimal bandwidth is φ_4 as it is dependent on $f(x)$. The DPI selector replaces this quantity in the following estimator:

$$\hat{h}_{DPI} = \left[\frac{R(K)}{\mu_2(K)^2 \hat{\varphi}_4(g) n} \right]^{\frac{1}{5}}, \text{ where}$$

$\hat{\varphi}_4(g) = n^{-1} \sum_{i=1}^{n} \hat{f}^{(4)}(X_i; g) = n^{-2} \sum_{i=1}^{n} \sum_{j=1}^{n} L_g^{(4)}(X_i - X_j)$, and L may be a different kernel

than K with bandwidth $g = \left[\frac{2K^{(4)}(0)}{-\mu_2(K)\varphi_6 n} \right]^{\frac{1}{7}}$, and the sample of locations, X, is given.

However, in this formula g must also be estimated since φ_6 is a function of $f(x)$—this problem does not go away. At each stage this same problem arises since the φ needs to be estimated (e.g., at the next stage φ_6 is estimated as a function of φ_8). DPI selectors address this problem by using a normal scale rule as a plug-in at some stage, l, to estimate φ_r. Such a band-width selector is called an l-stage DPI bandwidth selector. The normal scale rule is used since it is easy to calculate and is available in following form:

$\varphi_r = \frac{(-1)^{\frac{r}{2}} r!}{(2\hat{\sigma})^{r+1} \left(\frac{r}{2}\right)! \pi^{\frac{1}{2}}}$, where $\hat{\sigma}$ is estimated from X and r^{th} derivative is even. For this analyses $l = 2$, and we used the same normal kernel for L and K.

Using the fixed kernel estimates, I calculated annual home range sizes at the 95% and 50% probability contours for individuals in the study for at least 2 years, and overall home range areas averaged across all study years at the 95% and 50% probability contours for each individual. These probability contours have been commonly used in wildlife studies (Seaman and Powell 1996, Hooge and Eichenlaub 1997, Anderson et al. 2005). I calculated the variance of these home range areas empirically using bootstrapping procedures (Efron and Tibshirani 1993) outlined by Kernhonan et al. (2001) with 1,000 repetitions. In addition, I incorporated radiotelemetry sampling error into the bootstrapping procedures to account for the uncertainty associated with the location estimates based on the assumption of asymptotic normality of MLE estimates. This error was incorporated during each iteration of the bootstrap procedure by taking each estimated location selected in the bootstrap dataset, and replacing it with a location generated from a multivariate normal distribution with a mean = the estimated location and variance-covariance matrix generated from the estimated standard errors for X and Y, and their correlation, which was produced for each estimated point location in Locate III. Elk locations selected in the bootstrap datasets, which were confirmed visually on the ground or from the air, and locations from GPS collars were assumed to have no location error, as error in these cases is trivial compared to the error associated with triangulation. Given the 1,000 bootstrap estimates of the probability density function and their associated area at each probability contour, the quantile method was used to generate 95% confidence intervals for each home range area (Efron and Tibshirani 1993).

Two bulls collared in 2003 with VHF collars were recollared in 2005 with GPS collars. However, due to design problems these collars malfunctioned within 3 months post-deployment. Locations were then acquired using triangulation techniques for the remainder of the season until collar removal. This created a large amount of data while the GPS receivers were functioning, relative to the amount of data collected during the rest of the year. To avoid biasing kernel estimates as a result of this wealth of data, I weighted the locations obtained from the GPS collars using a normal density kernel, based on the following equation suggested by Katajisto and Moilanen (2006):

$$D(t_i) = \sum_{i=1}^{n} \exp\left(-\frac{(t - t_i)^2}{2h_t^2} \right),$$

where t represents time a location was taken, and h_t = bandwidth. For this analysis, t represented the time since the initial location in decimal days, and $h_t = 1.12$ which is approximately half of the mean time between subsequent locations for the 2 elk of interest. This bandwidth size was subjectively selected as it represents the standard deviation of the kernel function, and thus creates a weighting of approximately 1 for GPS fixes that are the average time apart based on the sampling regime for the VHF collars. Weights for the i^{th} GPS fix were the inverse of $D(t_i)$. All locations collected using triangulation techniques were given a weight of 1, assuming temporal independence. These weights were then used to weight locations in the kernel and variance estimation procedures described above. However, the kernel had to be modified to ensure normalization to unity. This was achieved by dividing by the effective population size rather than the total number of locations used in the kernel estimator. I calculated the effective population size by summing the weights of all locations. The following equation was the result of this procedure:

$$\hat{f}(\boldsymbol{x}) = \frac{1}{\sum_{i=1}^{n} w_i} \sum_{i=1}^{n} \frac{w_i}{\boldsymbol{h}^2} K\left(\frac{\boldsymbol{x} - \boldsymbol{X}_i}{\boldsymbol{h}} \right),$$

where $\boldsymbol{x}$ is the location at which density is to be estimated, w_i is the weights for the i^{th} observed location, $\boldsymbol{h}$ is the bandwidth matrix, and $\boldsymbol{X}_i$ is the i^{th} observed location. Using this procedure, allows for better estimation of the kernel density function as all information is being used. Using simulations and a similar technique, Katajisto and Moilanen (2006) demonstrated that estimates of the kernel density function were considerably better using this type of approach compared to resampling the data with an appropriate time interval, which results in the loss of information.

I compared sex-specific differences between mean home range areas for both overall, and annual home range areas using two-tailed Mann-Whitney tests, as well as comparison of standard normal confidence intervals between means of interest. Variances of means were calculated by summing the individual variances for each home range area and dividing by the square of the total number of individual home range areas used to calculate the mean (i.e., I assumed each individual was independent). Using the same procedures I examined year-specific differences within and between each sex class.

Overall range use.–To allow for population level inference concerning the probability of use of the study area, I combined individual kernel estimates to generate an overall kernel density for the sample of radiocollared individuals. As individuals vary in the number of years collared and, therefore, the number of locations acquired, combining all the locations for all elk would bias the population density function, as those with more locations would be weighted heavier than those with fewer. This data manipulation would effectively create spikes in the density surface where home ranges of elk collared and alive all 3 years of the study were located. To address this problem, I created kernel density estimates for each individual using the techniques described above with probability density estimated at points on a common grid with spacing of 160.9344 m. The grid was created in Arcview to ensure coverage of the estimated home ranges of all radiocollared elk. I created the population level density function by averaging across all individual density estimates at each point on the grid in SAS Version 9.1 (2003) (Wand and Jones 1995). The following equation summarizes the above procedure:

$$\bar{f}_{pop}(\boldsymbol{x}) = \frac{1}{n}\sum_{i=1}^{n}\hat{f}_i(\boldsymbol{x}),$$

where $\bar{f}_{pop}(\boldsymbol{x})$ is the averaged kernel density estimate for the sample of radiocollared elk at location $\boldsymbol{x}$, and $\hat{f}_i(\boldsymbol{x})$ is kernel density estimate at location $\boldsymbol{x}$ for the i^{th} individual elk. Variances for each point of the averaged surface were calculated by summing the individual variances, generated using the bootstrap procedure previously described, and dividing this summation by the square of the total number of individuals used to calculate the mean (i.e., 58). This surface and the variance surface were graphically displayed in ARCGIS 9.0 (ESRI, Redlands, California, USA) using interpolated distance weighting (IDW) with parameters of K = 2 and 12 nearest neighbors. Areas of high elk use were noted, and the amount of area used was calculated for the 95% probability contour using Hawth's Analysis Tools (Beyer 2006). This process was repeated for each year of the study to look at annual range use based on average kernel density estimates. However, for the annual, averaged kernel densities, only animals that had at least 2 years of data were used, to allow for qualitative comparison of range use across years. These kernel averaging analyses require the following assumptions to allow population level inference: 1) Individuals collared represent a random sample of the population, and therefore their range use reflects that of the population. 2) Collared elk are independent. 3) Individual kernel density estimates adequately describe range use.

Joint space use between elk groups.–To examine joint space use between groups of elk from various portions of the range, the study area was subjectively broken into distinct summering areas based on summer distribution of radiocollared elk. Summer locations were used to segregate elk into groups, since radiocollared individuals tended to be in discrete groups and widely distributed during this time of year before rut and wintering activities. Movements of radiocollared elk among areas were then qualitatively characterized. To quantitatively assess and delineate areas of joint space use I created population level kernels for each summering area, using the same kernel averaging procedure described above, (i.e., I averaged the kernel density estimates for all radiocollared elk assigned to a specific summering area). I then multiplied the density estimates from each summering area's population level kernel for each point on the common grid, with the density estimates for the same grid points from the population level kernels for all other summering areas between which interchange occurred. This analysis created joint density functions, and delineated areas of interchange and intensity of joint space use within these areas (Wand and Jones 1995). Variance estimates for the density function were approximated using the delta method and the bootstrap estimated variances for each grid point. The following is the approximate variance equation:

$$\hat{\mathrm{var}}(\hat{f}_i(\boldsymbol{x}) * \hat{f}_j(\boldsymbol{x})) \approx \hat{f}_i(\boldsymbol{x})^2 \hat{\sigma}_i^2 + \hat{f}_j(\boldsymbol{x})^2 \hat{\sigma}_j^2,$$

where $\hat{f}_i(\boldsymbol{x})$ is the density estimate of the i^{th} kernel at a common grid point, $\boldsymbol{x}$, and $\hat{\sigma}_i^2$ is the estimated bootstrap variance of the density estimate at the common grid point from the i^{th} kernel. This process assumes that individuals or groups for which joint space use was examined were independent.

However, these joint space use analyses only examine space sharing, and do not examine temporal aspects of that sharing (i.e., animals may intersect in space, but not in time). For evidence of intermingling of elk groups from across the range, I examined the movement patterns and distribution of radiocollared elk from the few isolated locations where they were initially collared (i.e., they were in the same space at the same time when they were collared) to summering areas. I assessed the number of summering areas elk captured in the same location used, as a simple metric of the amount of interchange between elk from different summering areas.

Elk use of club lands in the core elk range.–Immigration and emigration of elk associated with Black River and Canada Creek Ranches was addressed through the evaluation of the joint space use of elk groups previously described. Additionally, I examined the movements of collared bulls from Canada Creek during the rutting season (i.e., August through November). No radiocollared bulls were on Black River Ranch prior to the rut. I determined the number of locations of radiocollared elk, radiocollared bulls and radiocollared cows on each of the ranches annually and for the entire study period for each month. This allowed for a rough examination of elk use of these 2 ranches, and the distribution of use within a year. Fixed kernel density estimates were generated for each club using only elk locations that fell within their boundaries. Four surfaces were developed, 3 annual surfaces and 1 surface using all the locations on the clubs during the entire study.

Probability of use of various cover types.–Cover types of interest were determined from IFMAP land classification system (Michigan Department of Natural Resources 2001). I examined 11 different cover types: agricultural (IFMAP code = 5, 6, 7 and 9), aspen association (IFMAP code = 16), upland conifers (IFMAP code = 19–21), lowland forest (IFMAP code = 24–26), mixed conifer/deciduous (IFMAP code = 22), mixed upland deciduous (IFMAP code = 18), northern hardwood association (IFMAP code = 14), oak association (IFMAP code = 15), openings (IFMAP code = 10–13), water (IFMAP code = 23) and other (IFMAP code = 1–4 and 27–35). I also examined the probability of use of openings managed by the MDNR based on ARCVIEW shapefiles of managed openings provided by local MDNR biologists (B. Mastenbrook and D. Smith, Michigan Department of Natural Resources, personal communication).

Probability of use for a particular cover type was determined using Spatial Analyst and 3D Analyst extensions in ARCGIS. I reclassified all grid cells of that cover type with a 1 value, and all other cover types were reclassified with a 0 value. Then using Raster Calculator this reclassified raster was multiplied against the IDW raster for the averaged kernel density estimates for all elk and for all years. This produced a raster containing only pixels, from the averaged kernel density surface, that were associated with the cover type of interest. I then calculated the probability of use by integrating/calculating the volume under this surface. This was repeated for each cover type previously described.

I estimated variances of these probability estimates by intersecting the point locations at which averaged kernel density estimates were generated with the reclassified raster for each cover type using Hawth's Analysis Tools. This created a field for each cover type in the shapefile attribute table containing an indicator of whether a point was contained in the cover type of interest. If the point was contained within the cover type, I calculated the sum of the variances by summing the bootstrap variance estimates associated with each point multiplied by the square of the grid cell area using R. To account for spatial autocorrelation of density estimates created by the kernel function, I generated a correlation structure for the estimates based on distance using a Matern covariance function (Handcock and Stein 1993, Marzluff et al. 2004). The smoothing parameter (Θ) was set at 0.5, which equates to an exponential function. The range or scale parameter (ρ) was determined by the averaging the bandwidth matrices, determined as described previously, across all radiocollared individuals. I calculated covariances between 2 points by multiplying their correlation by the bootstrapped standard errors for each point. Total covariance, for the probability of use of the cover type of interest, I estimated by multiplying each individual covariance estimate for each pair of grid points by 2 times the square of grid cell area (i.e., 25,900 m^2), and summing across all point combinations. Finally, the total variance for each probability of use estimate was calculated by adding the sum of variances and sum of the covariance.

I tested if the probability of using managed openings was greater than expected, by determining if the expected probability of using managed openings was within the normal confidence intervals for the estimated probability for managed openings. The expected probability was calculated by taking the percentage of the total area of all openings (i.e., managed and unmanaged) contained in the study region, occupied by managed openings, and multiplying this percentage by the probability of use calculated for all openings. This analysis is based on the assumption that if there is no effect of management activities on elk use of openings, elk will use all openings with an equal probability.

Results

Capture

Helicopter net gunning in 2003 resulted in 20 adult bulls and 20 adult cows being captured. The same technique in 2005 yielded an additional 16 adult cows. Darting activities in the summer of 2004 resulted in 2 adult cows being radiocollared. Only adult elk were collared, and most bulls were subdominant. No capture related mortalities occurred from any of these collaring activities.

Of the 5 GPS collars placed on elk, only 3 remained functional throughout the deployment period. These 3 collars collected data until all collars were retrieved from the animals in late October 2005.

No mechanical failure of the VHF collars occurred during the duration of the study. All collars functioned the beyond the length of the study.

Elk Locations

Over the 3 years of the study, personnel collected a total of 13,923 triangulated locations on radiocollared elk and an additional 728 visual observations by homing in on collars or incidental sightings. After removal of poorly estimated locations and data entry errors, I used a total of 16,767 locations across all animals and all location techniques (i.e., triangulation, GPS collars, visual sightings and aerial visual sightings) in all subsequent analyses.

The distribution of the times of acquisition of triangulated locations is bimodal with peaks at 1000 and 1600 hours (Figure 21). Approximately 95% of the locations were taken between 0600 and 2100 hours, with 22% of the locations being acquired during the nocturnal time period. All aerial visual sightings were during the diurnal

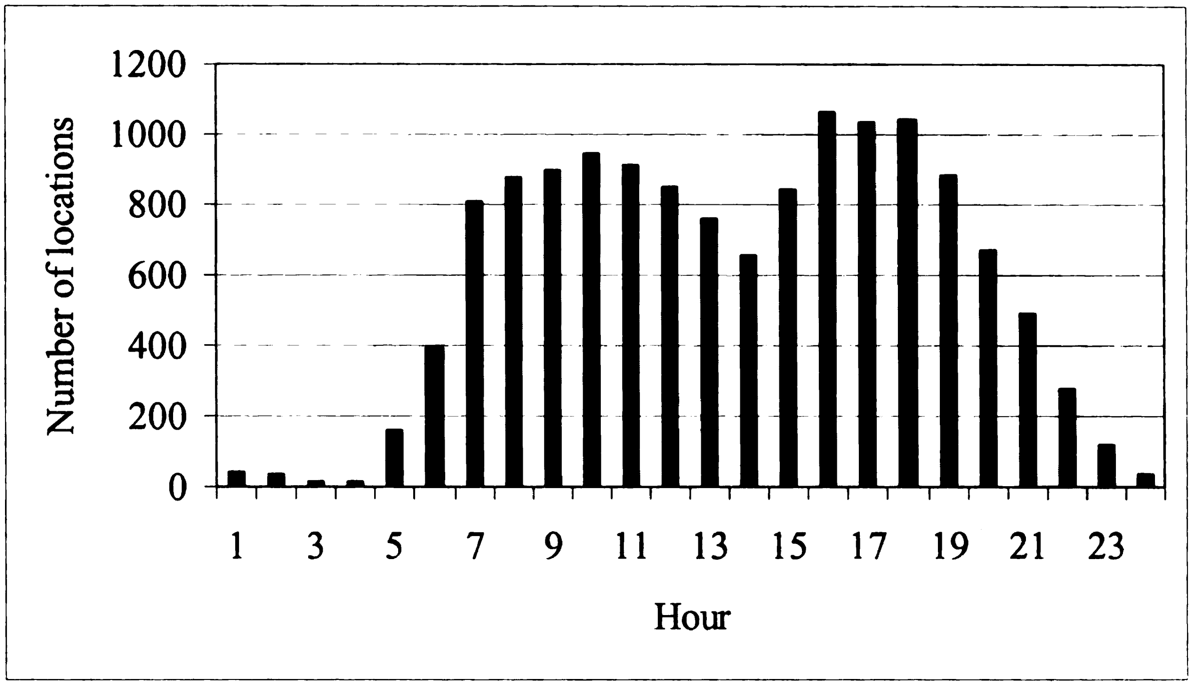


Figure 21. The distribution of acquisition times of triangulated locations for radiocollared elk in Michigan, 2003–2006.

period. GPS fixes from all 5 collared elk were uniformly distributed throughout the day (Figure 22).

Analysis

Error assessment.–Personnel collected 522 useable bearings to collars placed in various locations throughout the study area. The average bias across all observers and collar locations was -1°, however, it was not significantly different from zero (t_{521} = -1.53, $P = 0.126$) at $\alpha = 0.05$. The standard deviation of these bearings was 9.998°, and this value was used in Locate III for all location estimation. Standard deviation of GPS fixes over 148 fixes was 14.23 m with an average difference from the mean location of 10.02 m.

Home range areas.–Mean bull home range size averaged across all study years at the 95% probability contour was 9,587 ha (SE = 143) with a maximum of 17,784 ha and a minimum of 378 ha. Mean cow home range was 6,349 ha (SE = 96) with a maximum of 14,004 ha and a minimum of 2,813 ha. Based on examination of 95% standard normal confidence intervals, the mean bull home range size calculated at the 95% probability contour was significantly larger than the corresponding mean cow home range size. This was confirmed by a Mann–Whitney test (W20,38 = 599, P $\leq$0.001). Mean bull home range size averaged across all study years for the 50% probability contour was 1,764 ha (SE = 39) with a maximum of 3,492 ha and a minimum of 72 ha . Mean cow home range was 1,272 ha (SE = 27) with a maximum of 3,168 ha and a minimum of 368 ha. Based on examination of 95% standard normal confidence intervals, the mean bull home range size calculated at the 50% probability contour was significantly larger than the corresponding mean cow home range size. This was confirmed by a Mann–Whitney test

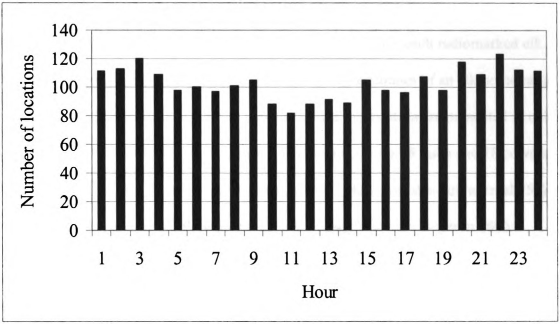


Figure 22. The distribution of acquisition times of GPS fixes for radiocollared elk in Michigan, 2003–2006.

($W_{20,38} = 555$, $P = 0.002$). Estimates of the size of home range areas at the 95% and 50% probability contour, number of locations used in the kernel density functions and associated 95% confidence limits are displayed in Table 15 for each radiomarked elk. Figure 23 depicts a graphical example of kernel density estimates of an elk home range and associated 95% confidence limits. Images in this dissertation are presented in color. I calculated 95% and 50% contour annual home range size for 18 bulls and 18 cows in 2003 and 2004 and for 16 bulls and 14 cows in 2005. Based on standard normal 95% confidence intervals mean bull home range size was significantly larger in 2003 compared to 2004 and 2005 home range size, but there was no statistical difference between 2004 and 2005 (Table 16). Mean cow home range sizes were different across all years with decreasing size from 2003 (Table 16). Within all years, mean bull home range sizes were consistently larger than cow home ranges, and across years they were also larger with the exception of the mean cow home range size in 2003, which was not statistically different from mean bull home range size in 2004 and 2005 (Table 16). The same patterns were generally true for the 50% contour annual home range size. However at this contour, mean annual cow home range size in 2004 was not different from 2003 or from 2005 home range sizes (Table 17). Also mean bull home range size in 2004 is not different from mean cow home ranges in 2003 and 2004 (Table 17). Using the Mann-Whitney test confirmed these relationships (Table 18 and 19). Individual annual home range estimates and upper and lower confidence limits for the 95% and 50% probability contour intervals are shown in Table 20 –23.

Overall range use.–Radiocollared elk used a total area of 58,973 ha over the study period based on the 95% contour of the kernel density surface created by averaging

Table 15. Estimates of home range size (ha) at the 95% and 50% probability contour, associated 95% confidence limits (LCL, UCL), number of locations used in kernel density estimation (n) for radiocollared elk in Michigan, 2003–2005.

ID	Sex	*n*	LCL	95% Contour	UCL	LCL	50% Contour	UCL
3	Bull	352	7,587	8,685	9,288	1,584	1,836	2,061
10	Bull	229	4,860	6,048	6,552	684	837	999
13	Bull	334	13,896	16,020	16,848	2,952	3,492	3,825
14	Bull	352	6,885	8,622	8,757	1,080	1,278	1,449
15	Bull	355	5,220	6,300	6,768	1,071	1,242	1,368
16	Bull	348	12,852	15,732	16,605	1,728	2,070	2,376
17	Bull	361	8,793	10,287	10,665	1,512	1,818	2,052
18	Bull	56	342	378	900	54	72	108
20	Bull	425	4,535	5,307	5,405	1,145	1,311	1,368
22	Bull	232	8,451	10,098	10,548	1,548	1,917	2,187
23	Bull	358	10,953	13,365	13,914	1,359	1,638	1,944
25	Bull	464	6,439	7,659	7,736	1,259	1,489	1,621
29	Bull	345	8,091	9,414	9,837	1,440	1,719	1,935
30	Bull	354	9,675	11,124	11,664	1,800	2,097	2,358
33	Bull	336	9,423	11,421	11,880	1,413	1,773	2,070
34	Bull	363	6,975	7,983	8,460	1,512	1,737	1,881
35	Bull	361	10,989	12,150	12,654	2,772	3,249	3,492
36	Bull	347	5,688	6,948	7,209	981	1,134	1,287
37	Bull	107	5,058	6,408	6,858	882	1,341	1,620
38	Bull	349	15,399	17,784	18,639	2,628	3,231	3,717
1	Cow	365	5,022	5,697	6,201	1,251	1,386	1,539
2	Cow	284	5,148	6,435	6,606	801	945	1,089
4	Cow	368	5,778	6,750	7,164	1,188	1,350	1,503
5	Cow	375	4,833	5,499	5,859	765	900	1,044
6	Cow	356	8,091	9,504	9,972	1,422	1,710	1,926
7	Cow	275	8,271	9,846	10,260	1,431	1,746	1,980
8	Cow	378	4,320	4,959	5,346	648	729	882
9	Cow	310	12,267	14,004	14,598	2,691	3,168	3,465
11	Cow	396	4,707	5,310	5,625	1,098	1,251	1,377
12	Cow	394	4,815	5,364	5,742	1,044	1,170	1,305
19	Cow	282	10,557	12,060	12,681	2,223	2,655	2,970

Table 15. (cont'd).

ID	Sex	*n*	LCL	95% Contour	UCL	LCL	50% Contour	UCL
21	Cow	382	7,650	9,045	9,387	1,278	1,530	1,755
24	Cow	372	4,833	5,589	5,886	1,035	1,179	1,323
26	Cow	375	5,319	6,201	6,606	747	882	1,044
27	Cow	364	7,965	8,541	9,036	1,917	2,205	2,385
28	Cow	365	5,058	5,985	6,300	891	1,071	1,206
31	Cow	378	4,311	5,130	5,481	864	981	1,098
32	Cow	121	6,975	8,856	9,630	1,791	2,340	2,565
39	Cow	376	4,923	5,787	6,156	981	1,107	1,224
40	Cow	96	4,338	5,733	6,489	774	1,107	1,386
41	Cow	171	2,853	3,654	3,834	540	711	819
42	Cow	179	3,816	4,644	4,878	801	1,017	1,152
46	Cow	100	3,096	3,789	4,212	684	909	1,035
48	Cow	76	3,429	4,491	4,806	747	1,116	1,332
49	Cow	97	5,526	6,921	7,497	1,188	1,665	1,953
50	Cow	114	4,446	5,418	5,931	774	1,089	1,368
51	Cow	81	3,393	4,356	4,752	765	1,071	1,251
52	Cow	49	6,948	10,773	12,564	1,053	1,989	2,691
53	Cow	97	4,806	6,012	6,642	1,044	1,395	1,638
54	Cow	112	5,976	7,902	8,424	1,080	1,449	1,737
55	Cow	79	2,529	3,564	4,104	315	477	747
56	Cow	108	7,965	9,927	10,683	1,746	2,277	2,601
57	Cow	93	3,519	4,887	5,940	729	1,053	1,278
58	Cow	681	2,435	2,813	2,797	298	368	414
59	Cow	809	2,989	3,209	3,297	663	746	798
61	Cow	733	4,649	5,654	5,879	427	484	554
64	Cow	97	2,781	3,735	4,059	459	621	792
66	Cow	51	1,755	3,222	3,906	315	495	711

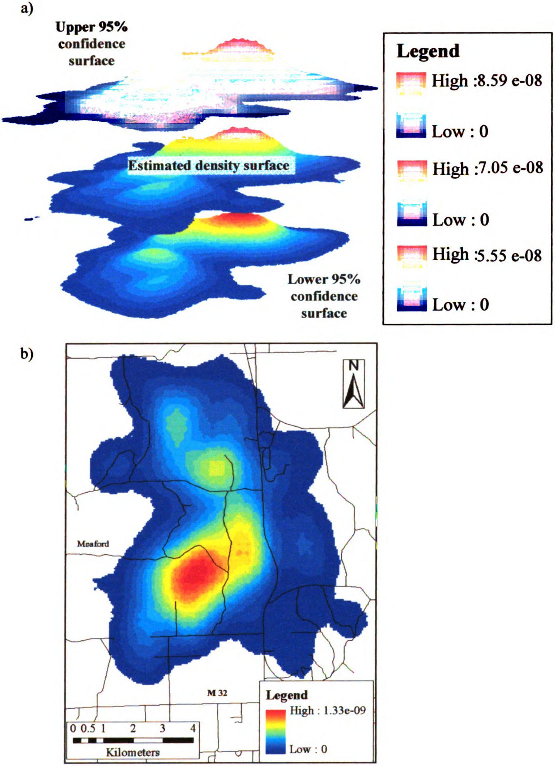


Figure 23. Kernel density estimate surface and associated 95% confidence surfaces (a), and intensity map of kernel density estimates (b) of elk #12's home range in Michigan, 2003–2005.

Table 16. Estimates of mean annual home range size (ha) at the 95% probability contour, associated 95% confidence limits (LCL, UCL), number of elk (*n*) for radiocollared elk in Michigan, 2003–2005.

	Bull			**Cow**		
	2003	**2004**	**2005**	**2003**	**2004**	**2005**
Mean	12,780	7,722	7,401	7,342	6,323	5,459
SE	378	163	179	178	133	134
n	18	18	16	18	18	14
UCL	13,520	8,041	7,751	7,691	6,583	5,722
LCL	12,040	7,404	7,050	6,993	6,063	5,196

Table 17. Estimates of mean annual home range size (ha) at the 50% probability contour, associated 95% confidence limits (LCL, UCL), number of elk (n) for radiocollared elk in Michigan, 2003–2005.

	Bull			Cow		
	2003	**2004**	**2005**	**2003**	**2004**	**2005**
Mean	2,578	1,557	1,544	1,436	1,365	1,218
SE	200	53	57	48	45	40
n	18	18	16	18	18	14
UCL	2,971	1,661	1,655	1,531	1,454	1,296
LCL	2,185	1,454	1,432	1,341	1,277	1,140

Table 18. Matrix of Mann-Whitney test statistics and associated P–values for sex and year comparisons of mean annual home range size (ha) at the 95% probability contour, for radiocollared elk in Michigan, 2003–2005.

		Bull			**Cow**		
		2003	**2004**	**2005**	**2003**	**2004**	**2005**
Bull	2003		261 ($\leq$0.001)	228 ($\leq$0.001)	273 (0.002)	284 ($\leq$0.001)	240 ($\leq$0.001)
	2004			161 (0.287)	178 (0.314)	225 (0.024)	190 (0.007)
	2005				144 (0.5068)	204 (0.019)	163 (0.017)
Cow	2003					248 (0.003)	197 (0.003)
	2004						133 (0.404)
	2005						

Table 19. Matrix of Mann-Whitney test statistics and associated *P*–values for sex and year comparisons of mean annual home range size (ha) at the 50% probability contour, for radiocollared elk in Michigan, 2003–2005.

		Bull			**Cow**		
		2003	**2004**	**2005**	**2003**	**2004**	**2005**
Bull	2003		253 (0.002)	212 (0.009)	266 (≤0.001)	278 (≤0.001)	221 (≤0.001)
	2004			139 (0.5743)	177.5 (0.318)	221 (0.063)	169.5 (0.051)
	2005				172 (0.1737)	204.5 (0.019)	153 (0.046)
Cow	2003					201 (0.1131)	156 (0.1312)
	2004						125 (0.5152)
	2005						

Table 20. Estimates of bull annual home range size (ha) at the 95% probability contour, associated confidence limit (LCL, UCL), and number of locations used to generate kernel density estimates (n), for radiocollared elk in Michigan, 2003–2005.

		2003				2004				2005			
ID	Sex	n	LCL	Area	UCL	n	LCL	Area	UCL	n	LCL	Area	UCL
3	Bull	110	7,415	10,347	11,549	130	5,403	6,522	7,001	112	4,056	5,263	5,916
6	Bull	109	8,837	12,240	12,921	131	7,993	9,806	10,603	116	4,931	6,206	6,809
10	Bull	111	5,198	7,192	7,912	118	3,245	4,273	4,683	NA	NA	NA	NA
13	Bull	88	13,841	20,031	21,720	136	12,209	14,654	15,460	110	10,425	12,986	14,253
14	Bull	111	5,335	7,296	8,073	132	4,719	6,364	6,690	109	4,574	6,333	6,788
15	Bull	111	6,540	8,809	9,912	130	3,380	4,069	4,315	114	3,626	4,398	4,680
16	Bull	108	20,694	26,128	31,051	133	5,537	7,278	7,674	107	5,688	8,153	8,925
20	Bull	109	4,724	6,252	6,858	141	3,155	3,800	4,012	175	3,810	4,924	5,006
22	Bull	112	4,667	6,897	7,431	120	6,656	8,503	8,923	NA	NA	NA	NA
23	Bull	102	15,426	19,873	21,261	138	3,515	5,193	5,488	118	11,393	14,162	15,255
25	Bull	110	8,912	11,298	12,163	141	6,478	7,786	8,148	213	3,440	4,644	4,729
29	Bull	110	6,933	9,876	10,368	127	6,439	8,241	8,985	108	4,374	5,449	5,827
30	Bull	112	8,964	11,963	12,968	131	9,184	11,722	12,370	111	5,006	6,105	6,488
33	Bull	111	12,240	16,061	17,296	121	6,257	8,752	9,606	104	5,773	7,842	8,521
34	Bull	105	8,441	11,336	12,036	138	5,105	6,638	7,164	120	4,600	5,996	6,540
35	Bull	107	9,003	11,632	12,235	140	7,648	9,327	9,785	114	8,987	11,046	11,536
36	Bull	108	7,055	9,601	10,132	129	4,854	6,553	6,920	110	2,054	2,606	2,870
38	Bull	110	17,656	23,209	24,936	131	7,343	9,523	10,176	108	9,456	12,297	12,735

Table 21. Estimates of cow annual home range size (ha) at the 95% probability contour, associated confidence limit (LCL, UCL), and number of locations used to generate kernel density estimates (n), for radiocollared elk in Michigan, 2003–2005.

		2003				2004				2005			
ID	Sex	n	LCL	Area	UCL	n	LCL	Area	UCL	n	LCL	Area	UCL
1	Cow	122	5,514	7,363	7,814	127	3,546	4,222	4,553	116	4,255	5,338	5,755
2	Cow	131	6,314	8,019	8,386	126	2,600	3,548	3,696	NA	NA	NA	NA
4	Cow	128	7,252	9,650	10,373	127	4,007	4,952	5,281	113	2,455	3,486	3,856
5	Cow	131	4,854	6,418	6,949	127	3,654	4,672	5,006	117	3,452	4,292	4,991
7	Cow	132	7,545	9,396	10,135	132	4,431	5,641	5,962	NA	NA	NA	NA
8	Cow	127	4,538	6,112	6,871	131	2,924	3,696	4,118	120	2,608	3,188	3,644
9	Cow	94	9,415	12,471	13,968	137	12,214	15,361	16,079	NA	NA	NA	NA
11	Cow	137	4,341	5,196	5,667	137	3,688	4,387	4,690	122	5,032	6,775	7,055
12	Cow	130	4,279	5,387	5,752	140	3,766	4,665	4,900	124	4,382	5,149	5,732
17	Cow	100	6,120	8,596	9,301	138	9,402	11,582	12,297	123	6,255	8,324	8,982
19	Cow	98	5,638	7,835	8,568	134	10,205	12,916	13,494	NA	NA	NA	NA
21	Cow	124	7,053	9,485	9,951	137	4,419	5,385	5,576	121	5,864	7,234	7,848
24	Cow	129	4,564	5,807	6,268	129	3,680	4,416	4,758	114	3,149	4,263	4,538
26	Cow	125	4,579	6,268	6,731	133	4,473	5,840	6,260	117	2,655	3,463	3,722
27	Cow	122	5,903	7,361	7,964	127	6,786	8,169	8,666	115	7,563	8,726	9,249
28	Cow	125	4,349	5,941	6,278	126	3,701	4,711	5,188	114	4,499	5,623	6,213
31	Cow	131	3,553	4,960	5,410	128	3,512	4,483	4,740	119	4,248	5,423	5,840
39	Cow	129	4,245	5,890	6,288	126	3,981	5,167	5,457	121	3,955	5,146	5,493

Table 22. Estimates of bull annual home range size (ha) at the 50% probability contour, associated confidence limit (LCL, UCL), and number of locations used to generate kernel density estimates (*n*), for radiocollared elk in Michigan, 2003–2005.

		2003				2004				2005			
ID	**Sex**	***n***	**LCL**	**Area**	**UCL**	***n***	**LCL**	**Area**	**UCL**	***n***	**LCL**	**Area**	**UCL**
3	Bull	110	1,746	2,341	2,717	130	1,165	1,487	1,738	112	865	1,119	1,334
6	Bull	109	1,417	2,054	2,549	131	1,621	2,189	2,593	116	958	1,292	1,526
10	Bull	111	914	1,176	1,458	118	479	673	857	NA	NA	NA	NA
13	Bull	88	2,235	3,559	4,507	136	2,510	3,569	4,066	110	2,401	3,144	3,585
14	Bull	111	969	1,347	1,647	132	927	1,197	1,378	109	787	1,085	1,362
15	Bull	111	1,199	1,541	1,930	130	821	1,041	1,202	114	803	1,153	1,287
16	Bull	108	4,126	5,978	7,156	133	1,052	1,383	1,650	107	1,165	1,590	1,834
20	Bull	109	1,096	1,404	1,645	141	764	979	1,075	175	875	1,155	1,254
22	Bull	112	927	1,199	1,412	120	1,305	1,774	2,059	NA	NA	NA	NA
23	Bull	102	2,486	3,662	4,439	138	650	821	974	118	2,018	2,919	3,489
25	Bull	110	2,080	2,751	3,105	141	1,300	1,652	1,911	213	1,181	1,637	1,992
29	Bull	110	1,261	1,730	2,082	127	1,002	1,344	1,691	108	914	1,225	1,409
30	Bull	112	2,145	2,849	3,225	131	1,720	2,274	2,644	111	1,075	1,500	1,761
33	Bull	111	2,523	3,509	4,180	121	922	1,380	1,733	104	873	1,308	1,709
34	Bull	105	1,582	2,217	2,642	138	1,010	1,365	1,595	120	1,002	1,342	1,582
35	Bull	107	2,041	2,740	3,157	140	1,585	2,044	2,357	114	2,059	2,681	3,015
36	Bull	108	1,652	2,137	2,419	129	865	1,129	1,336	110	497	671	767
38	Bull	110	2,841	4,217	5,224	131	1,228	1,733	2,142	108	2,328	3,090	3,300

Table 23. Estimates of cow annual home range size (ha) at the 50% probability contour, associated confidence limit (LCL, UCL), and number of locations used to generate kernel density estimates (n), for radiocollared elk in Michigan, 2003–2005.

		2003				2004				2005			
ID	**Sex**	***n***	**LCL**	**Area**	**UCL**	***n***	**LCL**	**Area**	**UCL**	***n***	**LCL**	**Area**	**UCL**
1	Cow	122	1235	1580	1813	127	961	1184	1298	116	1171	1487	1614
2	Cow	131	1202	1564	1834	126	422	546	679	NA	NA	NA	NA
4	Cow	128	1717	2181	2492	127	873	1090	1290	113	523	671	805
5	Cow	131	684	963	1274	127	730	935	1111	117	702	886	1052
7	Cow	132	1461	1893	2240	132	694	912	1142	NA	NA	NA	NA
8	Cow	127	795	1064	1347	131	575	723	883	120	409	500	684
9	Cow	94	1953	2712	3209	137	2515	3263	3789	NA	NA	NA	NA
11	Cow	137	992	1311	1513	137	963	1225	1323	122	982	1300	1523
12	Cow	130	948	1228	1412	140	769	1002	1173	124	1052	1316	1507
17	Cow	100	1238	1722	2121	138	1665	2297	2792	123	1292	1722	2007
19	Cow	98	1031	1466	1790	134	2093	2862	3276	NA	NA	NA	NA
21	Cow	124	1171	1629	1958	137	1013	1316	1466	121	1222	1637	1922
24	Cow	129	995	1287	1528	129	883	1134	1287	114	692	940	1070
26	Cow	125	798	1062	1355	133	663	906	1168	117	541	686	793
27	Cow	122	1142	1487	1777	127	1507	1979	2295	115	1844	2347	2608
28	Cow	125	572	800	1046	126	808	1049	1194	114	1041	1326	1510
31	Cow	131	658	855	1015	128	780	1005	1145	119	914	1178	1386
39	Cow	129	800	1052	1235	126	917	1147	1300	121	844	1059	1230

across all radiocollared elk. Areas of high use included the following regions in no particular order: Osmun/Clark Bridge region, Camp 30 Hills, Blue Lakes region, Tin Shanty Road region, Black River and Canada Creek Ranches, Buttles Road region, Meaford Hills, Bone Yard/Hubert Road region, and the Chipper Pile Road region (i.e, region north of Voyer Lake Road between M-33 and Steven Springs Road). These areas of high probability density are depicted in the kernel density surface and associated standard error surface displayed in Figures 24 and 25.

The amount of area used in 2003 by 36 radiocollared elk was 58,864 ha based on the 95% contour of the averaged kernel density surface. In 2004 the area of range used was 54,112 ha for the same elk, and 30 elk used 48,335 ha in 2005. It also should be noted that care must be taken in comparing surfaces from 2005 with other years, as 6 elk (i.e., 1 from Black River Ranch, 2 from Bone Yard, 1 from Elk Hill Trail Camp, 1 from Camp 30 Hills, and 1 from Canada Creek) were removed due to mortalities. Annual, averaged kernel density surfaces and associated standard error surfaces are displayed in Figures 26–31. The areas previously described with high elk use for the kernel density surface averaged across all years and radiomarked elk, are also the regions that were used heavily by elk for each year of the study. Differences across years in these surfaces include the following: in 2003 and 2004, the Brush Creek Truck Trail/Grass Lake region was used; however, this did not occur in 2005 with the marked elk remaining in the Bone Yard area. In 2004, elk used the region north and northeast of the Morrow/Hubert Road intersection, an area with elk crop damage complaints. This area was not used during other years of the study. The Elk Hill Trail Camp region was used in 2003 and 2004, but not during 2005. However, this was likely due to loss of radiocollared elk in this region.

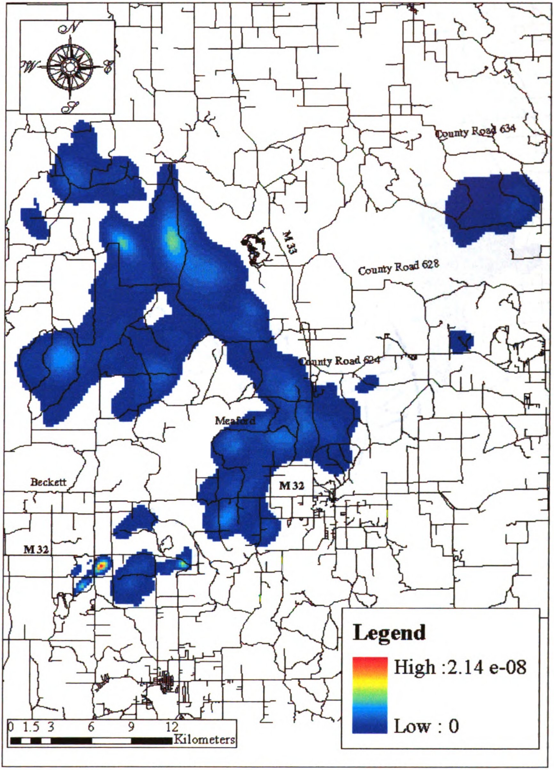


Figure 24. Averaged kernel density estimates of space use for 58 elk in Michigan, 2003–2005.

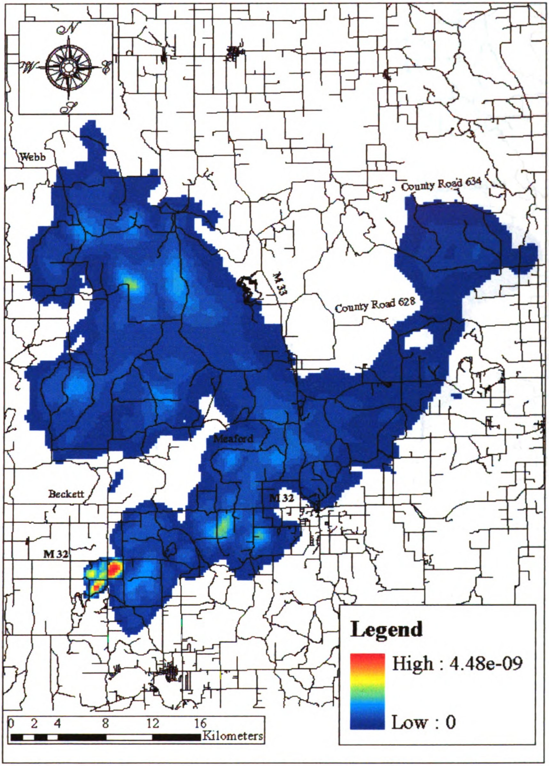


Figure 25. Estimates of standard error associated with averaged kernel density estimates of space use for 58 elk in Michigan, 2003–2005.

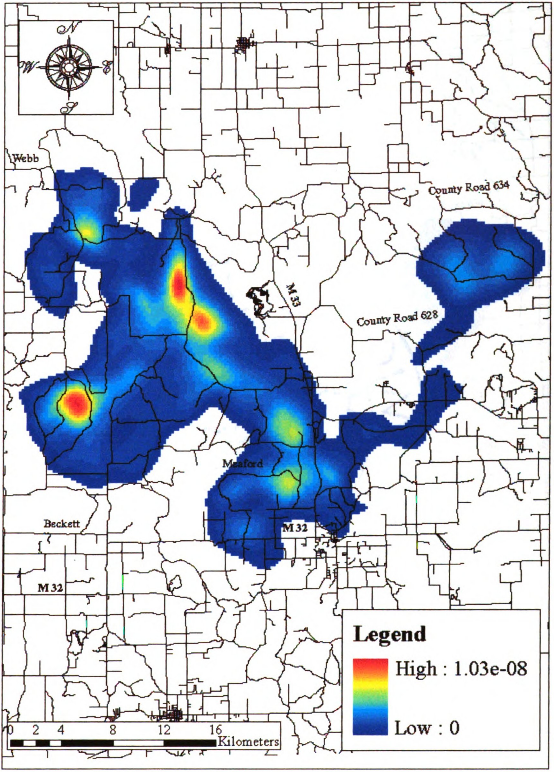


Figure 26. Averaged kernel density estimates of annual space use for 36 elk in Michigan, 2003.

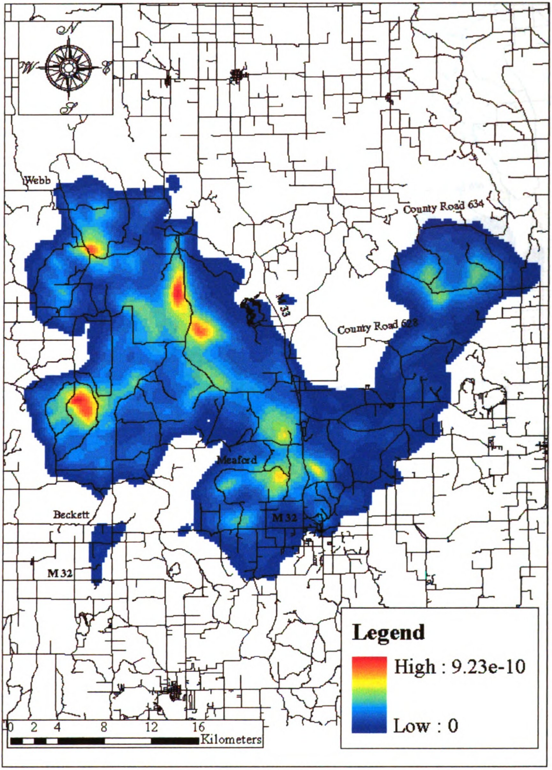


Figure 27. Estimates of standard error associated with averaged kernel density estimates of space use for 36 elk in Michigan, 2003.

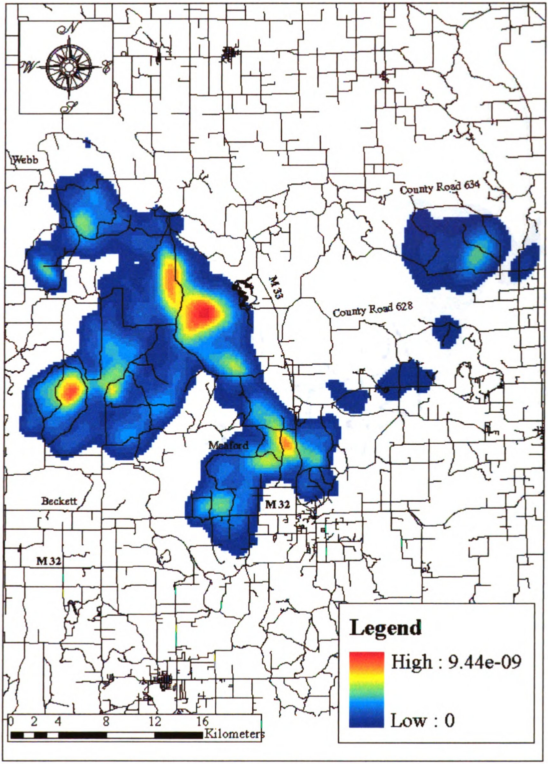


Figure 28. Averaged kernel density estimates of annual space use for 36 elk in Michigan, 2004.

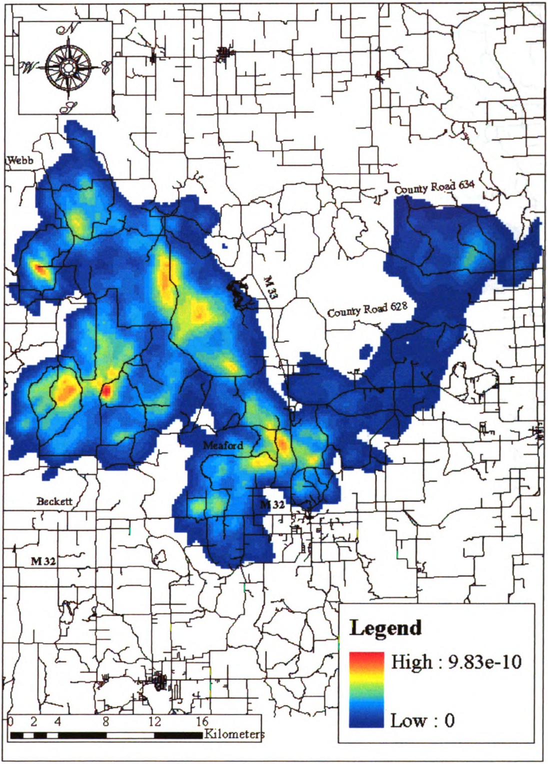


Figure 29. Estimates of standard error associated with averaged kernel density estimates of space use for 36 elk in Michigan, 2004.

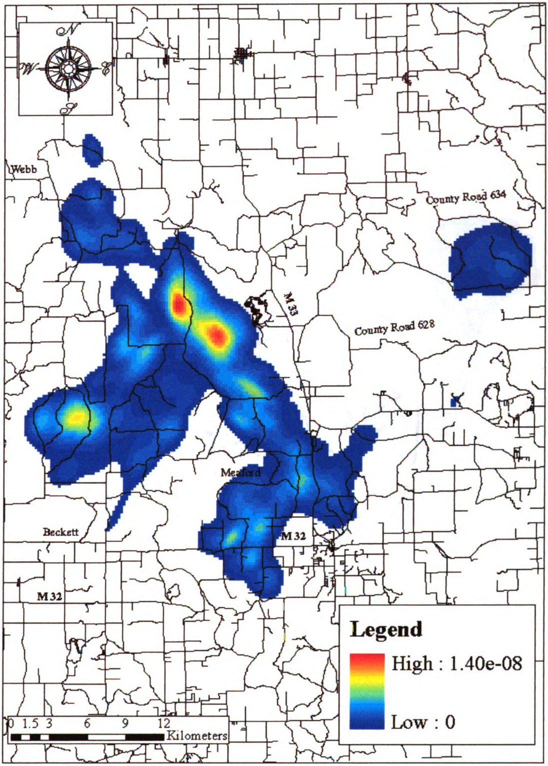


Figure 30. Averaged kernel density estimates of annual space use for 30 elk in Michigan, 2005.

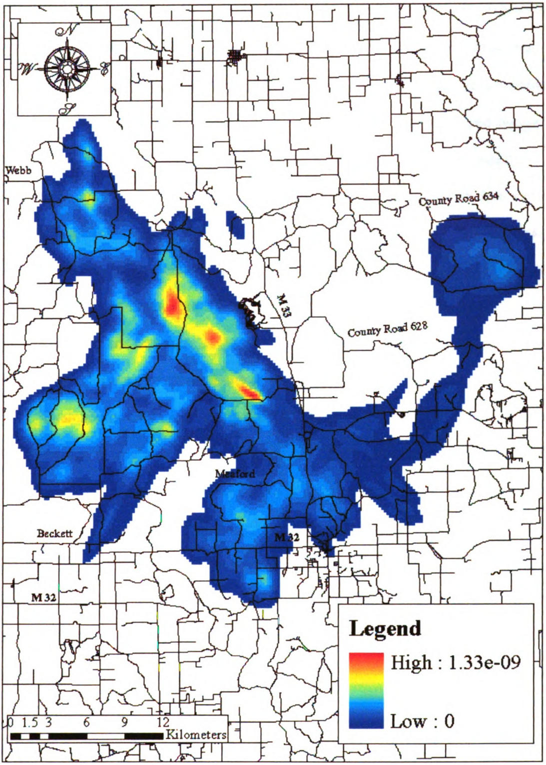


Figure 31. Estimates of standard error associated with averaged kernel density estimates of annual space use for 30 elk in Michigan, 2005.

Other noticeable differences are associated with varying intensities of use of regions used across years, which can be assessed by visual inspection of the surfaces in Figures 26–31.

Joint space use between elk groups.–Based on summer locations of radiomarked elk, 10 summering areas were defined. These are displayed in Figure 32, and are named as follows: Black River, Bone Yard, Camp 30 Hills, Canada Creek, M-32 South, Meaford, Osmun, Tin Shanty, Vienna and Voyer Lake. Interchange of elk from various summering areas occurred across the range (Figure 32), with all summering areas having an influx of elk from different summering areas. The only summering area to have no elk depart from the summering area for other regions was the Vienna area. However, animals utilizing this area were only collared for 1 season, which may have not allowed adequate time for them to exhibit movement into other summering areas.

Examination of the joint density surface, for 7 radiocollared elk from the Black River summering area and 7 elk from the Camp 30 Hills area, shows the areas of joint space use occurs on the southern and eastern portions of Black River Ranch, along Blue Lakes and Black River roads and in the Tin Shanty Road area (Figure 33). Joint space use, for elk from the Black River summering area and 9 elk from the Canada Creek, occurs mainly on the western portion of Canada Creek Ranch, the eastern portion of Black River Ranch, and the southwest reaches of Black River Ranch (Figure 34). For elk from the Black River Ranch area and the 5 elk from Osmun Road area, joint space use occurs throughout Black River Ranch and the region north of Clark Bridge Road to just west of its intersection with Osmun Road (Figure 35). The western portion of Black River Ranch and the region between Tin Shanty and Saw Dust Pile Roads are the areas of joint space use for elk from Black River area and the 5 elk from Tin Shanty summering

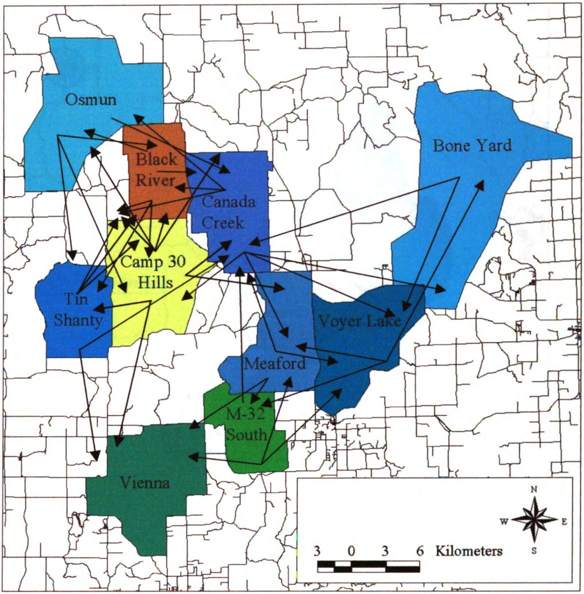


Figure 32. Summering areas and general interchange patterns between areas for radiocollared elk in Michigan, 2003–2005 (arrows represent movement of at least 1 radiocollared elk).

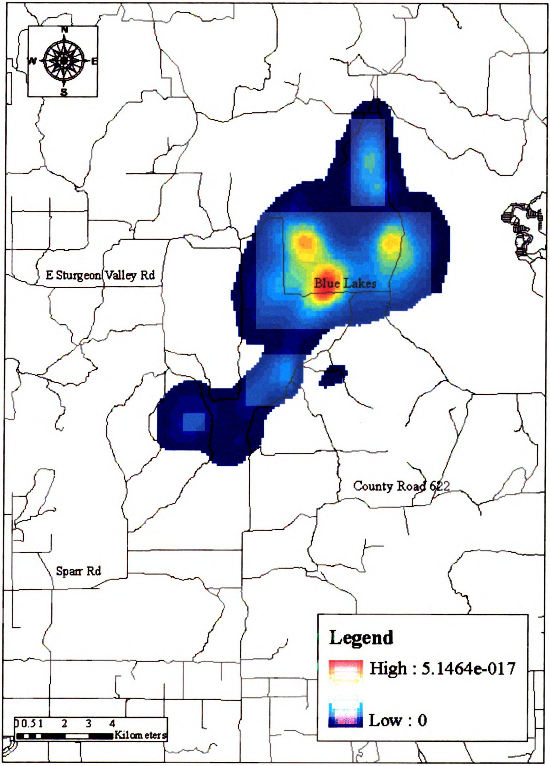


Figure 33. Joint density kernel surface depicting areas of joint space use between 7 radiocollared elk from the Black River summering area and 7 elk from the Camp 30 Hills summering area in Michigan, 2003–2005.

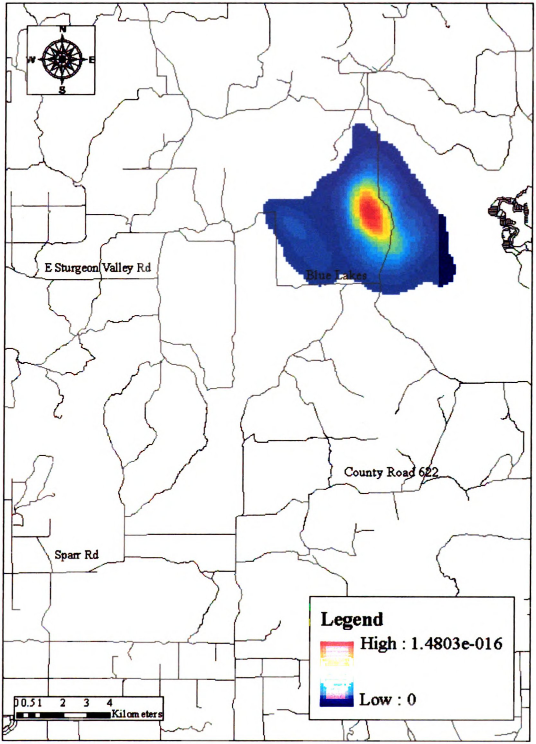


Figure 34. Joint density kernel surface depicting areas of joint space use between 7 radiocollared elk from the Black River summering area and 9 elk from the Canada Creek summering area in Michigan, 2003–2005.

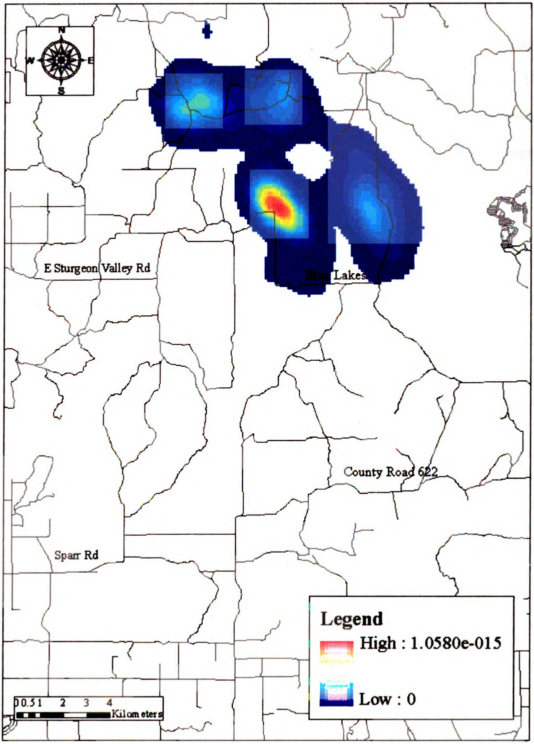


Figure 35. Joint density kernel surface depicting areas of joint space use between 7 radiocollared elk from the Black River summering area and 5 elk from the Osmun summering area in Michigan, 2003–2005.

area (Figure 36). Joint space use mainly occurred on the southwest corner of Canada Creek Ranch and the southern portion of Black River Ranch between the radiomarked elk from the Camp 30 Hills summering area and the Canada Creek area (Figure 37). The majority of the joint space use between the Camp 30 Hills elk and the Osmun Road elk occurred in the Blue Lakes region and southern portion of Black River Ranch (Figure 38). For theCamp 30 Hills elk and the Tin Shanty Road elk joint space use was primarily between Tin Shanty and Saw Dust Pile roads and south of Blue Lakes (Figure 39). Joint space was limited and occurred only at 2 areas along Rouse road, and in the region between Decheau Lake road and M-33 for elk from the Canada Creek summering area and the 6 elk from the Meaford area (Figure 40). The western portion of Black River Ranch and the western portion of Canada Creek Ranch were the sites of joint space use for elk from the Canada Creek area and elk from the Osmun summering area (Figure 41). For Canada Creek elk and the 4 elk from the Voyer Lake area, joint space use was isolated to the region near the intersection of M-33 and Voyer Lake road (Figure 42). Meaford road elk and the 6 elk from the M-32 South summering area, jointly used space throughout the Meaford hills area and the Elk Ridge Golf course region (Figure 43). Elk from the Meaford area and elk from the Voyer Lake area, had joint space use mainly in the region between Decheau Lake road and M-33, and in southern portion of the Elk Ridge Golf Course (Figure 44). M-32 South elk and the 4 elk from Vienna jointly used space north of M-32 in the Camp 8 road region (Figure 45). Elk from Voyer Lake summering area jointly used space in the Hubert road and Brush Creek Truck Trail regions with 5 elk from the Bone Yard area (Figure 46). Lastly, Voyer Lake elk and M-32 South elk had joint space use in the region between Decheau Lake and M-33, Elk

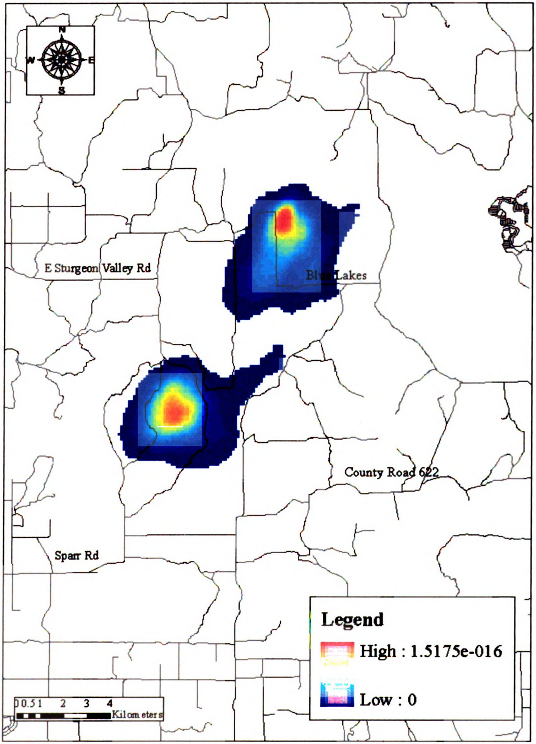


Figure 36. Joint density kernel surface depicting areas of joint space use between 7 radiocollared elk from the Black River summering area and 5 elk from the Tin Shanty summering area in Michigan, 2003–2005.

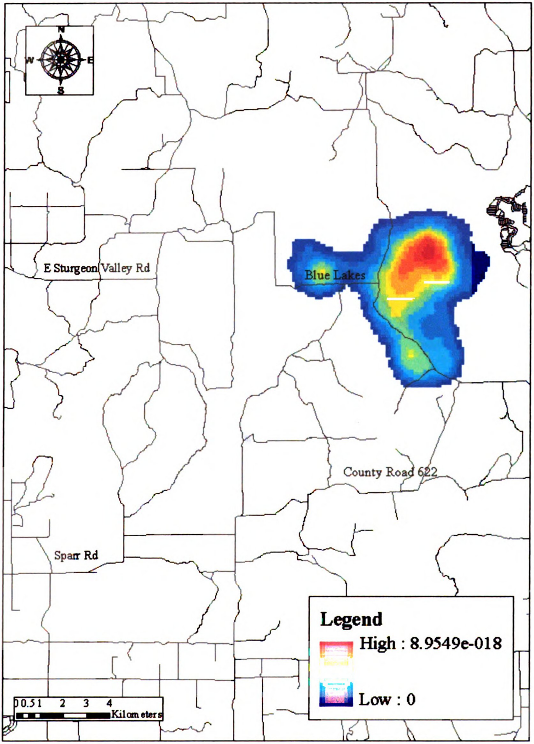


Figure 37. Joint density kernel surface depicting areas of joint space use between 7 radiocollared elk from the Camp 30 Hills summering area and 9 elk from the Canada Creek summering area in Michigan, 2003–2005.

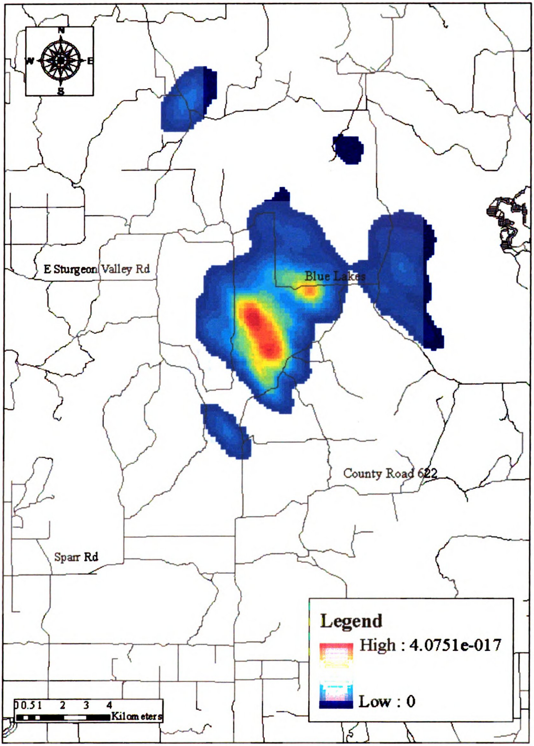


Figure 38. Joint density kernel surface depicting areas of joint space use between 7 radiocollared elk from the Camp 30 Hills summering area and 5 elk from the Osmun summering area in Michigan, 2003–2005.

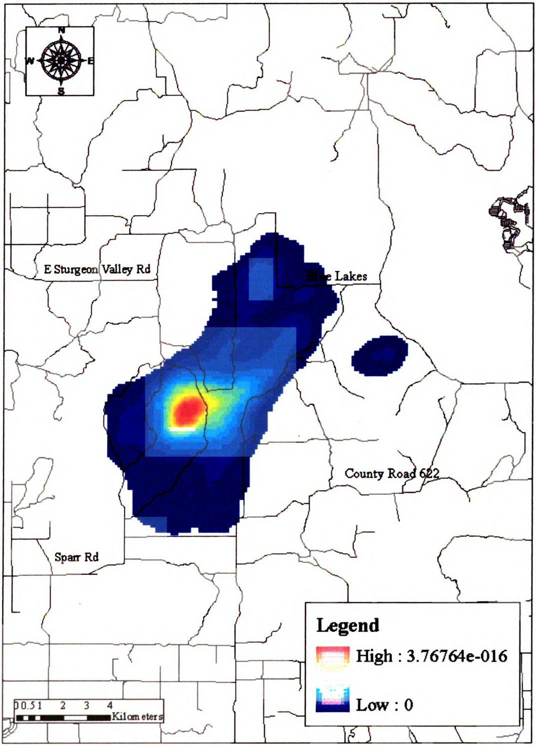


Figure 39. Joint density kernel surface depicting areas of joint space use between 7 radiocollared elk from the Camp 30 Hills summering area and 5 elk from the Tin Shanty summering area in Michigan, 2003–2005.

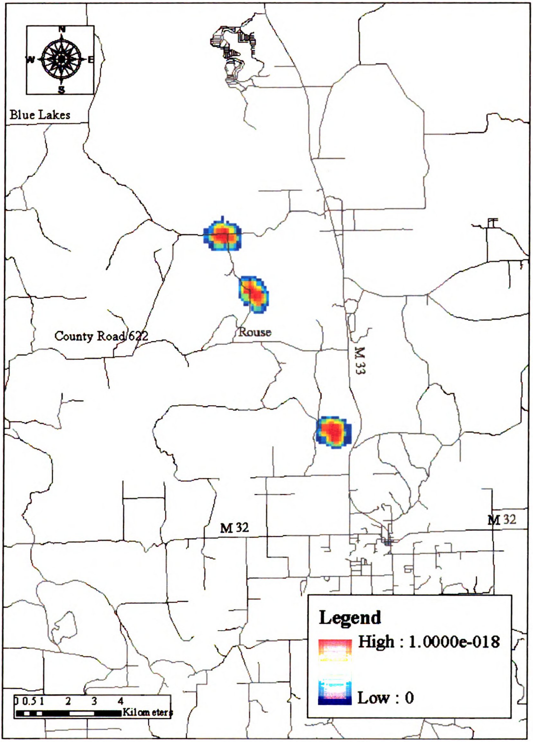


Figure 40. Joint density kernel surface depicting areas of joint space use between 9 radiocollared elk from the Canada Creek summering area and 6 elk from the Meaford summering area in Michigan, 2003–2005.

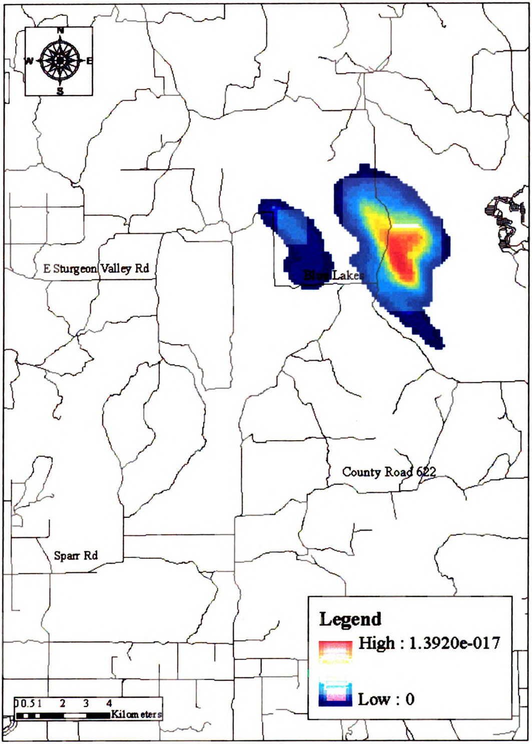


Figure 41. Joint density kernel surface depicting areas of joint space use between 9 radiocollared elk from the Canada Creek summering area and 5 elk from the Osmun summering area in Michigan, 2003–2005.

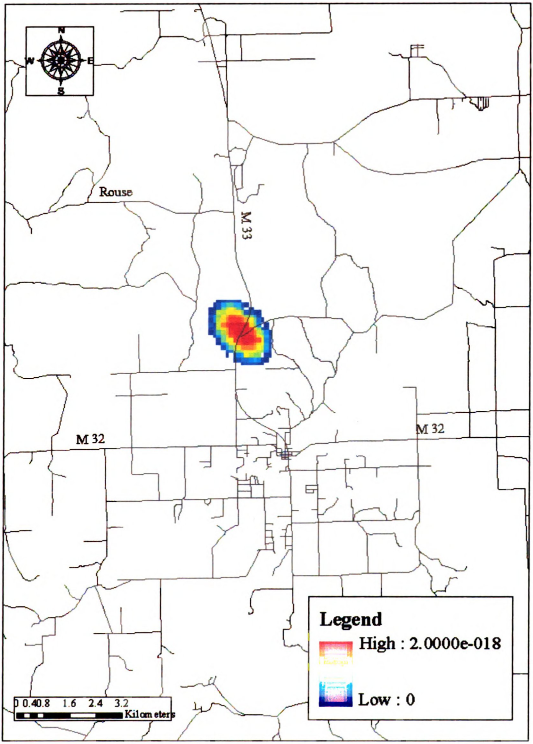


Figure 42. Joint density kernel surface depicting areas of joint space use between 9 radiocollared elk from the Canada Creek summering area and 4 elk from the Voyer Lake summering area in Michigan, 2003–2005.

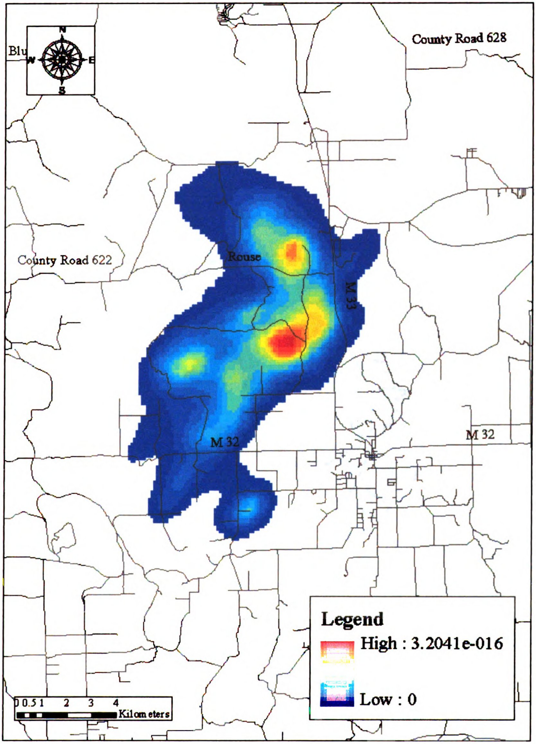


Figure 43. Joint density kernel surface depicting areas of joint space use between 6 radiocollared elk from the Meaford summering area and 6 elk from the M-32 South summering area in Michigan, 2003–2005.

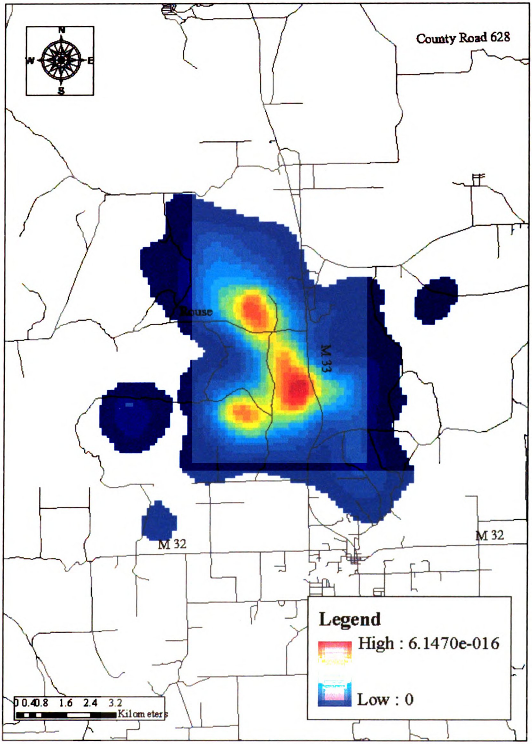


Figure 44. Joint density kernel surface depicting areas of joint space use between 6 radiocollared elk from the Meaford summering area and 4 elk from the Voyer Lake summering area in Michigan, 2003–2005.

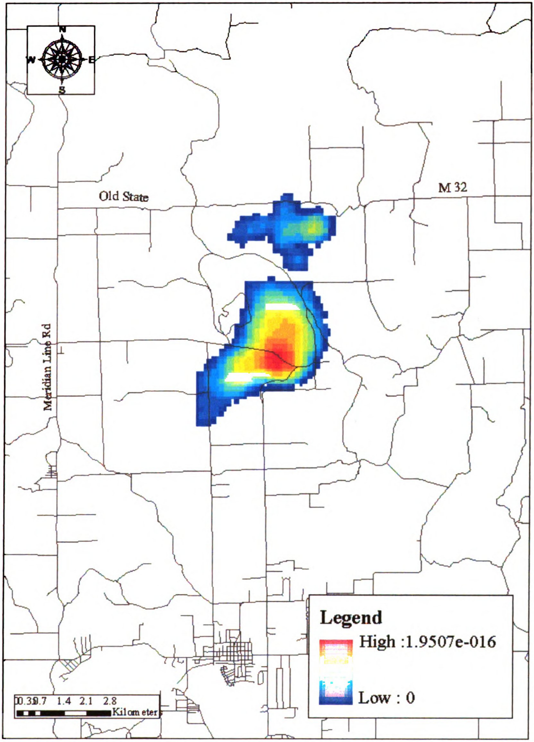


Figure 45. Joint density kernel surface depicting areas of joint space use between 6 radiocollared elk from the M-32 South summering area and 4 elk from the Vienna summering area in Michigan, 2003–2005.

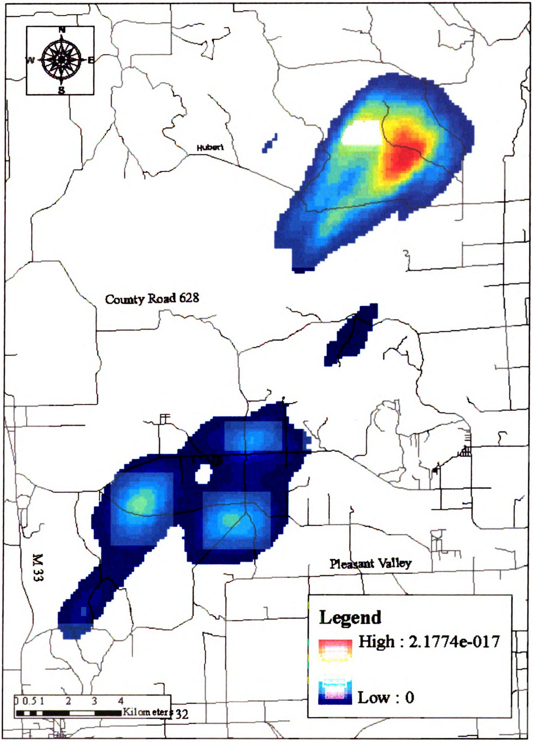


Figure 46. Joint density kernel surface depicting areas of joint space use between 4 radiocollared elk from the Voyer Lake summering area and 5 elk from the Bone Yard summering area in Michigan, 2003–2005.

Ridge Golf Course and the region northwest of the intersection of M-32 and Thornton road (Figure 47).

Elk captured during the winter months dispersed from the few capture sites across the range. Elk from several different summering areas were often captured at the same locations during the major capture operations in 2003 and 2005 (Figure 48). The 2003 capture sites in the Blue Lakes region and the ridges east of M-33 and north of Voyer Lake Road had the greatest intermingling of elk from various summering areas. The capture site on Canada Creek Ranch where a large number of individuals were radiocollared showed limited dispersal to other regions. Dispersal of elk from 2005 capture sites was limited with most animals utilizing summer range near capture sites. A notable exception was 1 cow from the Bone Yard that moved to the Canada Creek summering area.

Elk use of club lands in the core elk range.–Radiocollared elk used both Black River Ranch and Canada Creek Ranch throughout the study. In addition, animals summering on these ranches jointly used space with elk from 7 of the 10 summering areas (Figure 32). Locations of joint space were previously described. Radiomarked bulls, which used Canada Creek Ranch (i.e., no radiomarked bulls used Black River Ranch) during the summer, distributed themselves throughout the elk range during the rut for all years of the study (Figure 49–51).

Elk use of Black River Ranch averaged across years was typically heaviest on the eastern portion of the ranch and the region just east of the Vanderbilt gate (Figure 52). Changes in intensity of use of various regions within the range are evident, and can be qualitatively assessed by examining Figures 53–55. Most noticeably is a shift of space

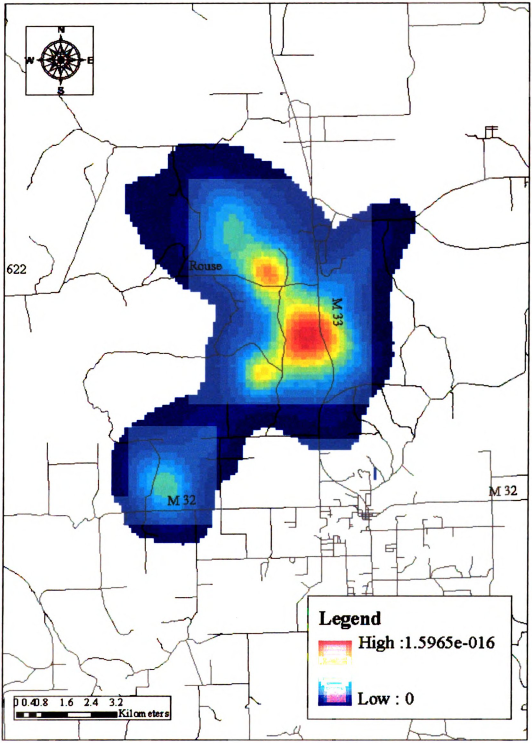


Figure 47. Joint density kernel surface depicting areas of joint space use between 4 radiocollared elk from the Voyer Lake summering area and 6 elk from the M-32 South summering area in Michigan, 2003–2005.

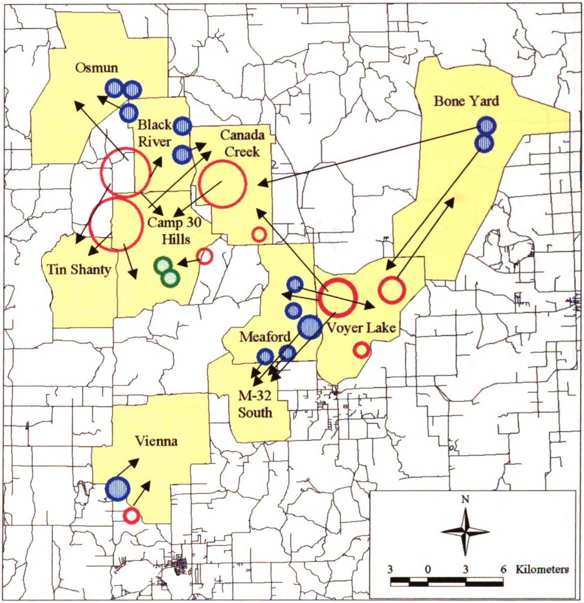


Figure 48. General movements of at least 1 radiomarked elk away from winter capture sites (unfilled circles represent 2003 capture sites, cross-hatched circles represent 2004 capture sites, and line-filled circles represent 2005 capture sites, and size of circles represent the relative number of elk captured) in Michigan, 2003–2005.

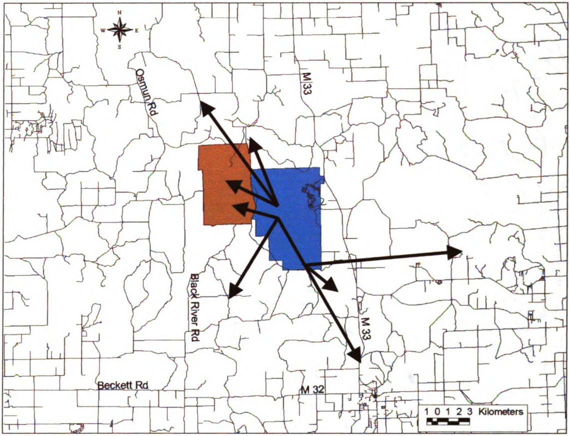


Figure 49. General movements of radiomarked bulls from Canada Creek Ranch during the rut (August–November) in Michigan, 2003.

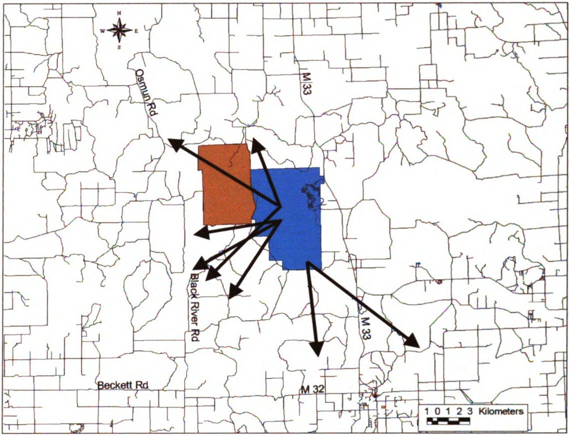


Figure 50. General movements of radiomarked bulls from Canada Creek Ranch during the rut (August–November) in Michigan, 2004.

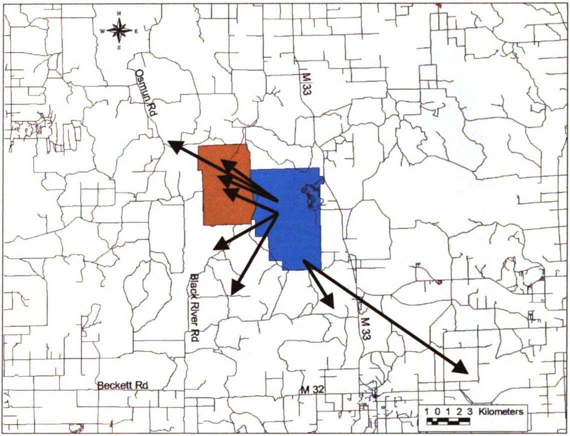


Figure 51. General movements of radiomarked bulls from Canada Creek Ranch during the rut (August–November) in Michigan, 2005.

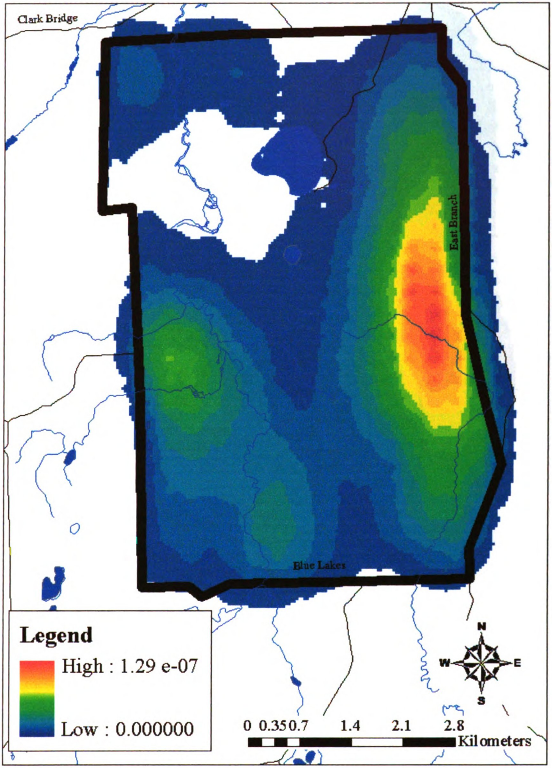


Figure 52. Kernel density map of radiomarked elk use of Black River Ranch based on 1,443 locations in Michigan, 2003–2005.

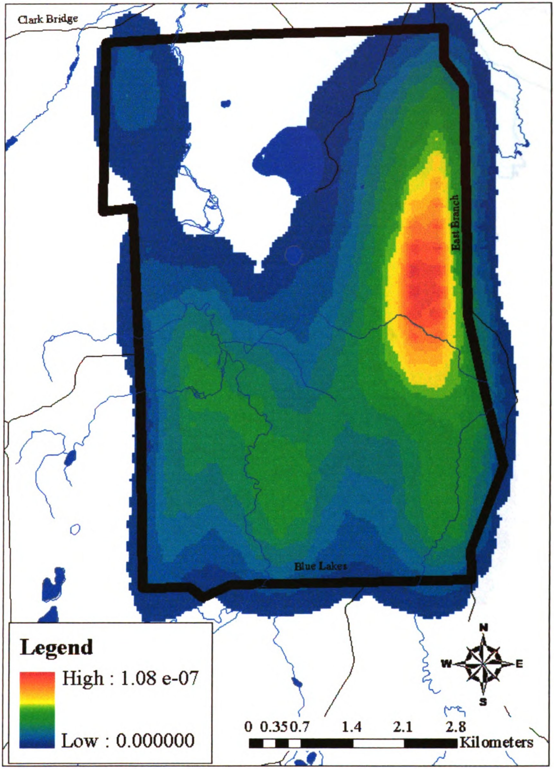


Figure 53. Kernel density map of radiomarked elk use of Black River Ranch based on 503 locations in Michigan, 2003.

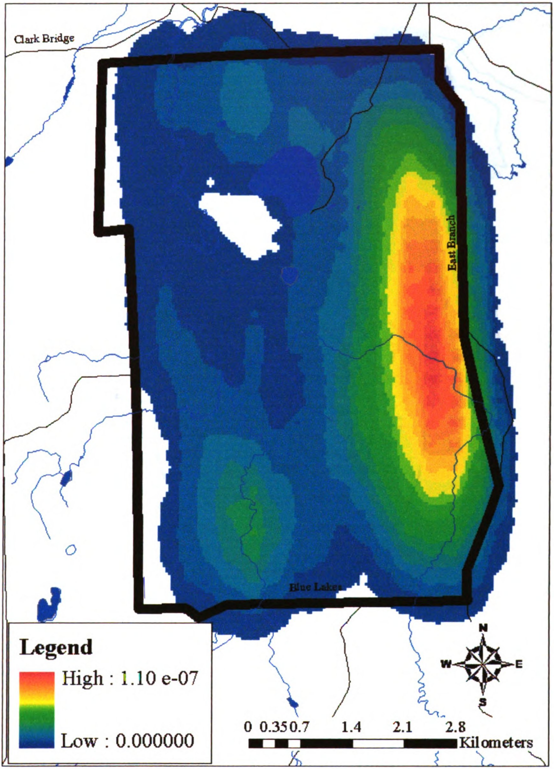


Figure 54. Kernel density map of radiomarked elk use of Black River Ranch based on 381 locations in Michigan, 2004.

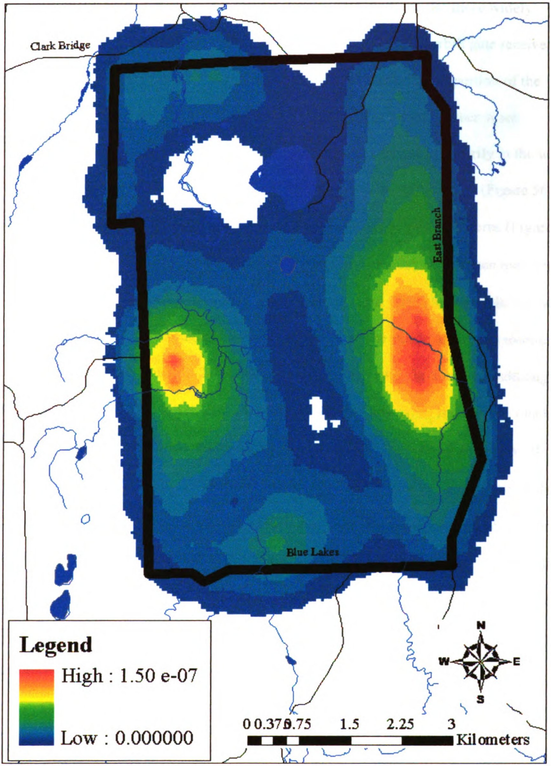


Figure 55. Kernel density map of radiomarked elk use of Black River Ranch based on 559 locations in Michigan, 2005.

use towards the eastern portion of the range during 2004, with the use more widely distributed in 2003 and 2005. Also in 2005, the area near the Vanderbilt gate received more intense use than in other years. Lastly, in 2003 the south central portion of the ranch (i.e., The Burn and Bucket Hill regions) was used more than in other years.

Elk use of Canada Creek Ranch averaged across years was focused primarily in the west central portion, as well as the northwest and southeast corners of the ranch (Figure 56). Examination of elk use across years shows shifting distribution of use patterns (Figures 57–59). In 2003, elk activity was focused in the region along the West Fence road near food plot 5, and in the southwest corner near the Homestead Gate. In 2004, elk use was more widely distributed throughout the central portion of the ranch, and in the southeast corner near the South Gate. In 2005, elk use was similar to the previous year, although it was concentrated in a narrower band running southeast to northwest through the ranch.

Elk use of Black River Ranch within a year was greatest during the spring months of March and April, and again in the fall during September–November for all years of the study (Figure 60) based on the number of locations of radiomarked elk occurring within the boundaries of the ranch. Elk use by sex followed the same trends across years with radiomarked bulls using Black River Ranch for the most part only during these peak times. Radiomarked cows used the ranch more heavily during these peak times, but used the ranch throughout the year (Figures 61–63).

Canada Creek was used by radiomarked elk throughout the year with peaks in March, the summer months of June–August, and in the winter months of November and December (Figure 64). Bulls used the ranch throughout the year, but showed decrease use during September–November for all years of the study. They also displayed some

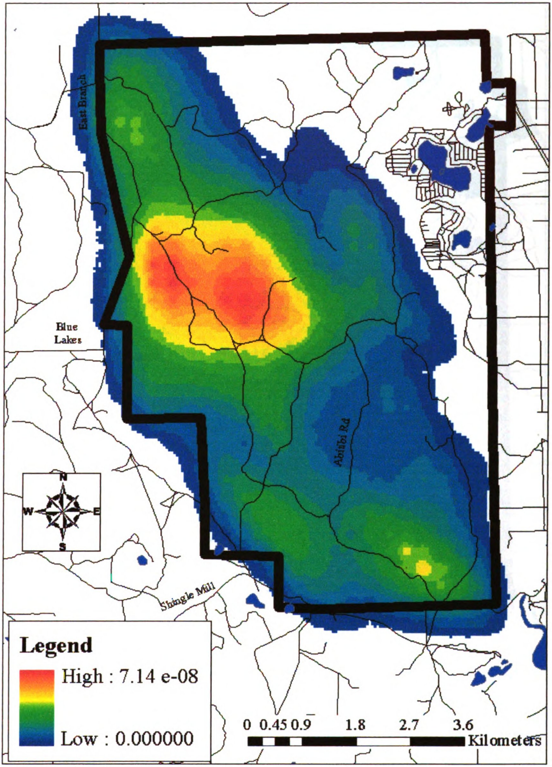


Figure 56. Kernel density map of radiomarked elk use of Canada Creek Ranch based on 1,957 locations in Michigan, 2003–2005.

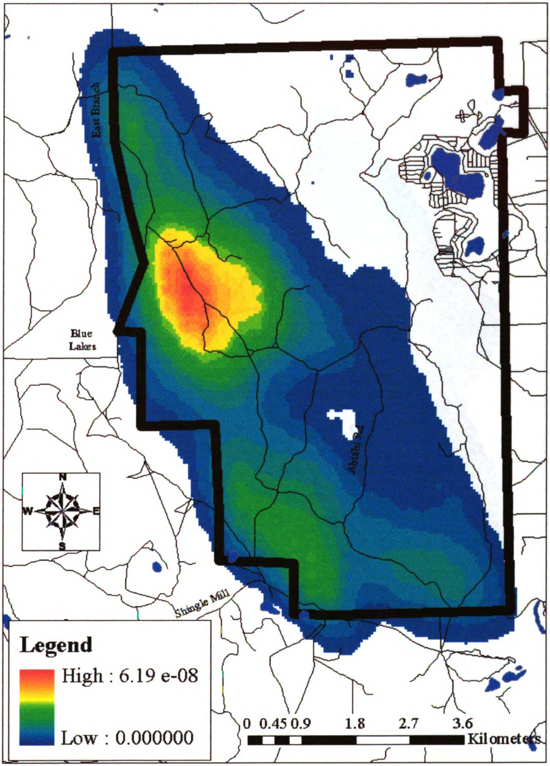


Figure 57. Kernel density map of radiomarked elk use of Canada Creek Ranch based on 477 locations in Michigan, 2003.

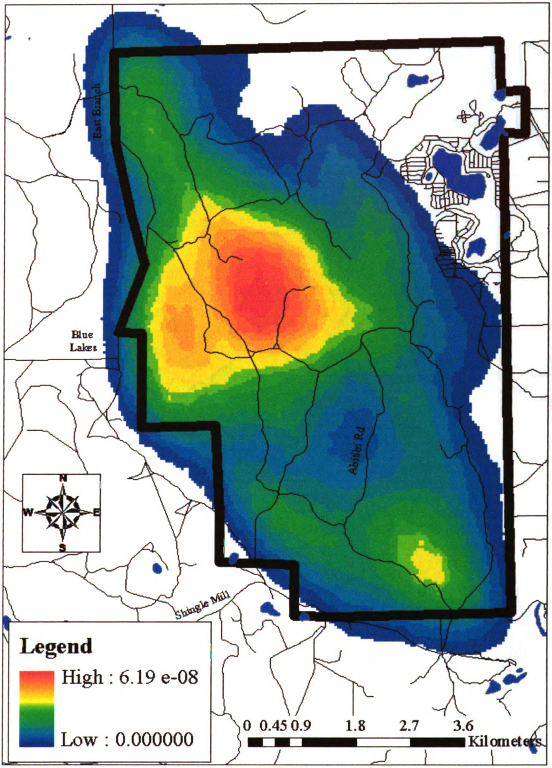


Figure 58. Kernel density map of radiomarked elk use of Canada Creek Ranch based on 805 locations in Michigan, 2004.

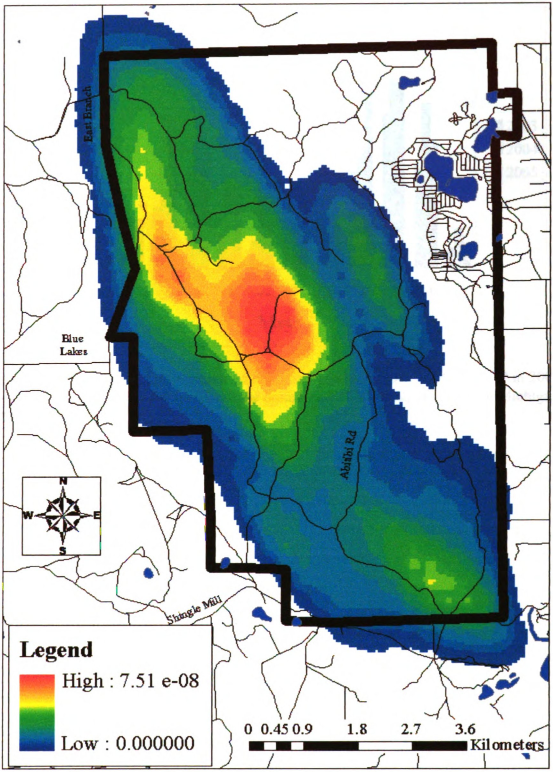


Figure 59. Kernel density map of radiomarked elk use of Canada Creek Ranch based on 675 locations in Michigan, 2005.

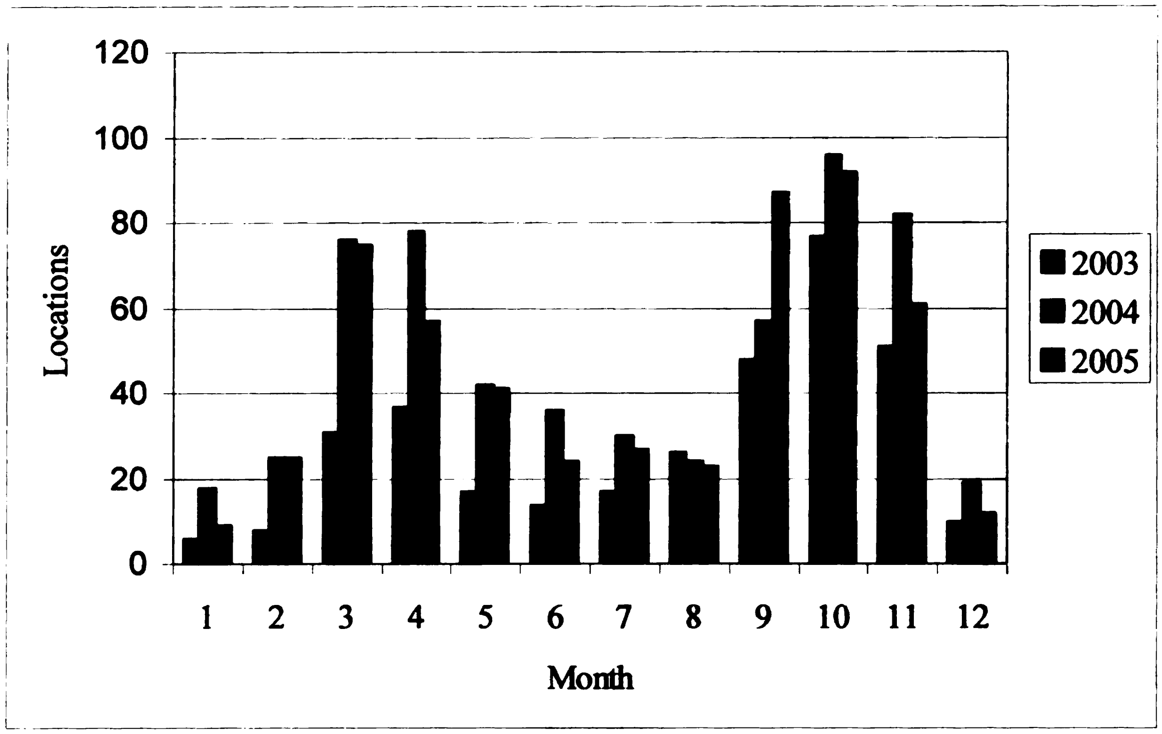


Figure 60. The number of locations of radiomarked elk (n = 40 in 2003, n = 39 in 2004, and n = 39 in 2005) occurring within the boundaries of Black River Ranch in Michigan, 2003–2005.

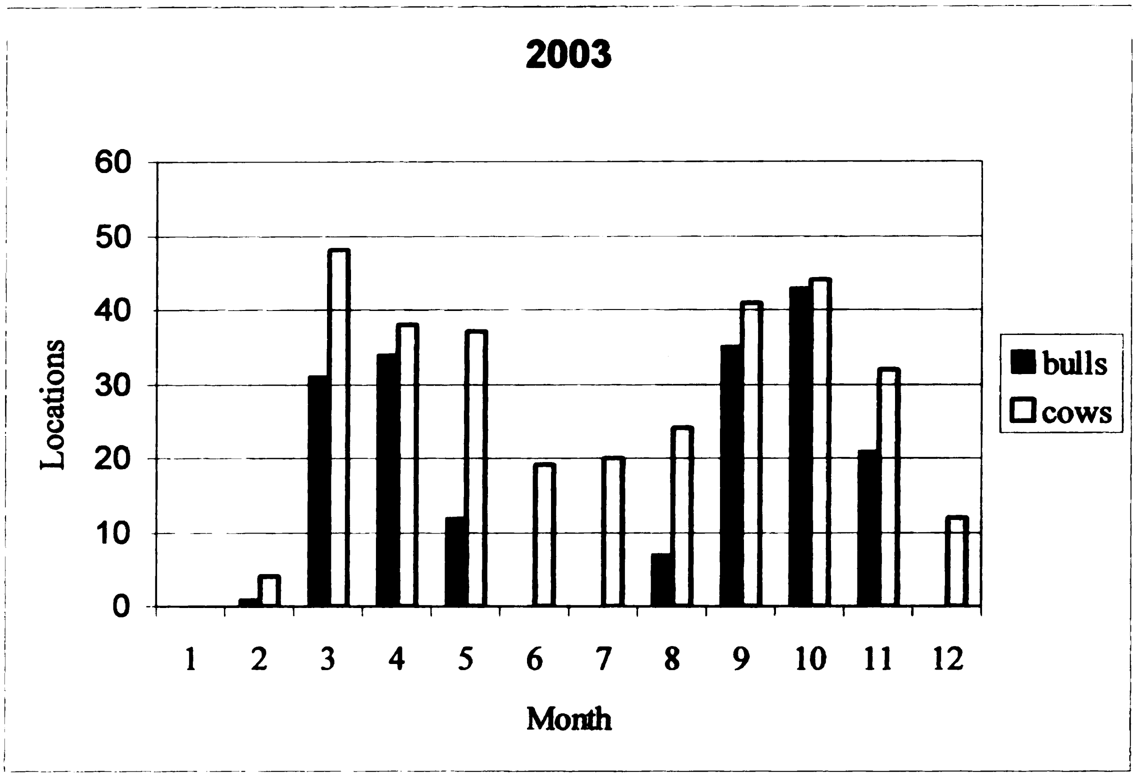


Figure 61. The number of locations of radiomarked elk (n = 20 bulls and n = 20 cows in 2003) by sex occurring within the boundaries of Black River Ranch in Michigan, 2003.

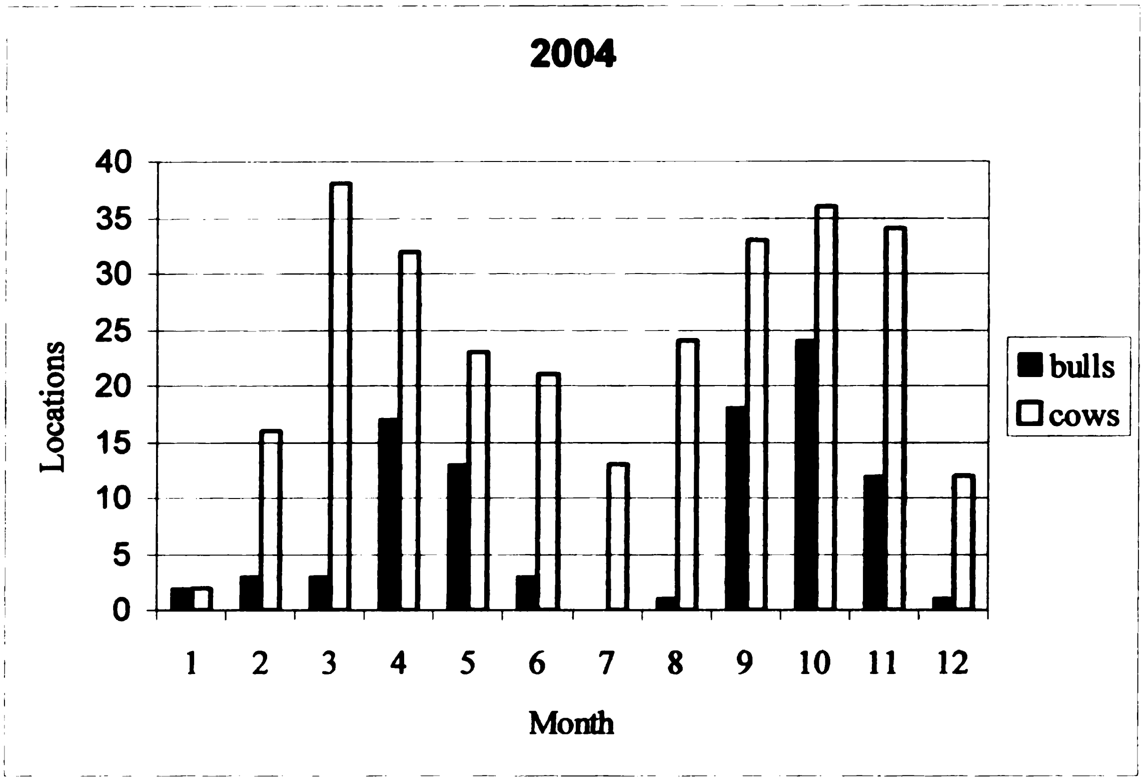


Figure 62. The number of locations of radiomarked elk (n = 18 bulls and n = 20 cows in 2004) by sex occurring within the boundaries of Black River Ranch in Michigan, 2004.

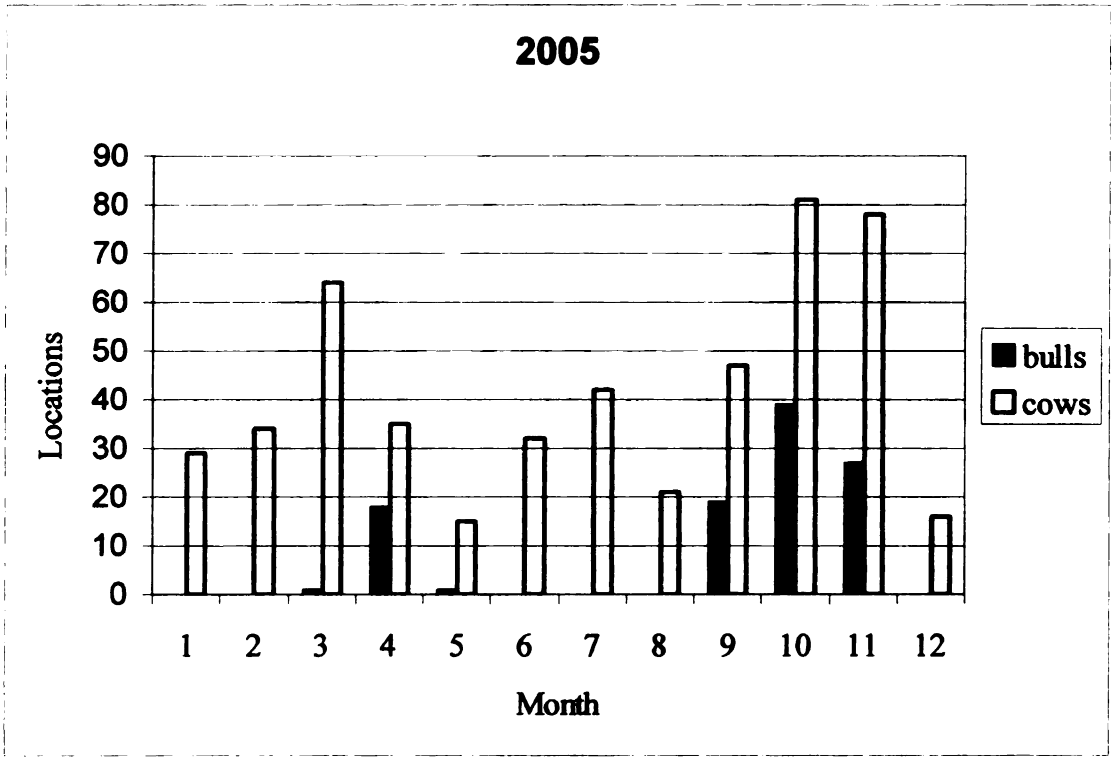


Figure 63. The number of locations of radiomarked elk (n = 16 bulls and n = 23 cows in 2005) by sex occurring within the boundaries of Black River Ranch in Michigan, 2005.

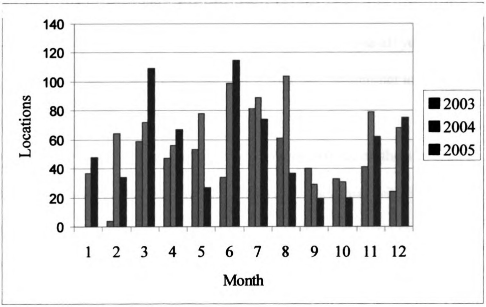


Figure 64. The number of locations of radiomarked elk ($n = 40$ in 2003, $n = 39$ in 2004, and $n = 39$ in 2005) occurring within the boundaries of Canada Creek Ranch in Michigan, 2003–2005.

reduction in use during the April and May, but the amount of reduction was variable across years. Cows showed limited use of the ranch across all years, although use increased during the study with highest use during the summer and winter months (Figures 65–67).

Probability of use of various cover types.–Based on the averaged kernel density estimates radiocollared elk used the following cover types with decreasing probability: openings, aspen, oaks, northern hardwoods, conifers, lowland forest, mixed conifer/deciduous, other, mixed upland deciduous, agriculture, managed openings and water (Table 24). The average CV across all probabilities was 13%. Comparison of the amount of overlap in confidence intervals shows that many of the probabilities are not statistically different from each other.

Managed openings were used at higher probability than expected. The expected probability of use was 0.811%, and estimated probability of use was 1.26% (SE = 0.0014).

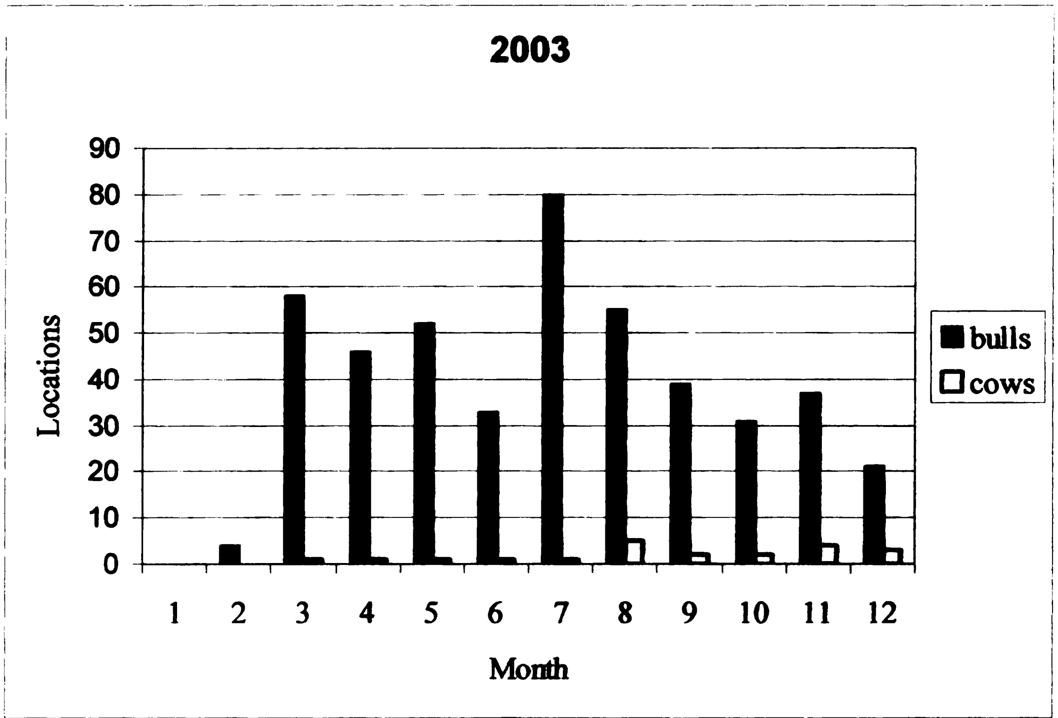


Figure 65. The number of locations of radiomarked elk (n = 20 bulls and n = 20 cows in 2003) by sex occurring within the boundaries of Canada Creek Ranch in Michigan, 2003.

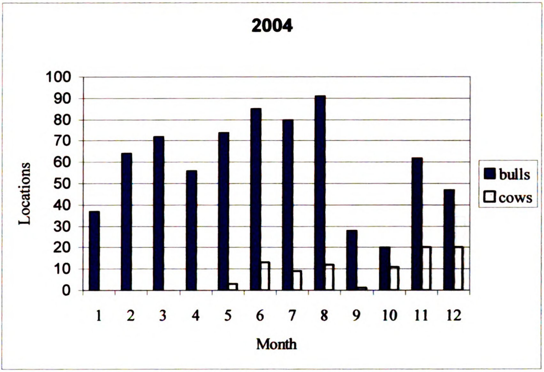


Figure 66. The number of locations of radiomarked elk ($n = 18$ bulls and $n = 20$ cows in 2004) by sex occurring within the boundaries of Canada Creek Ranch in Michigan, 2004.

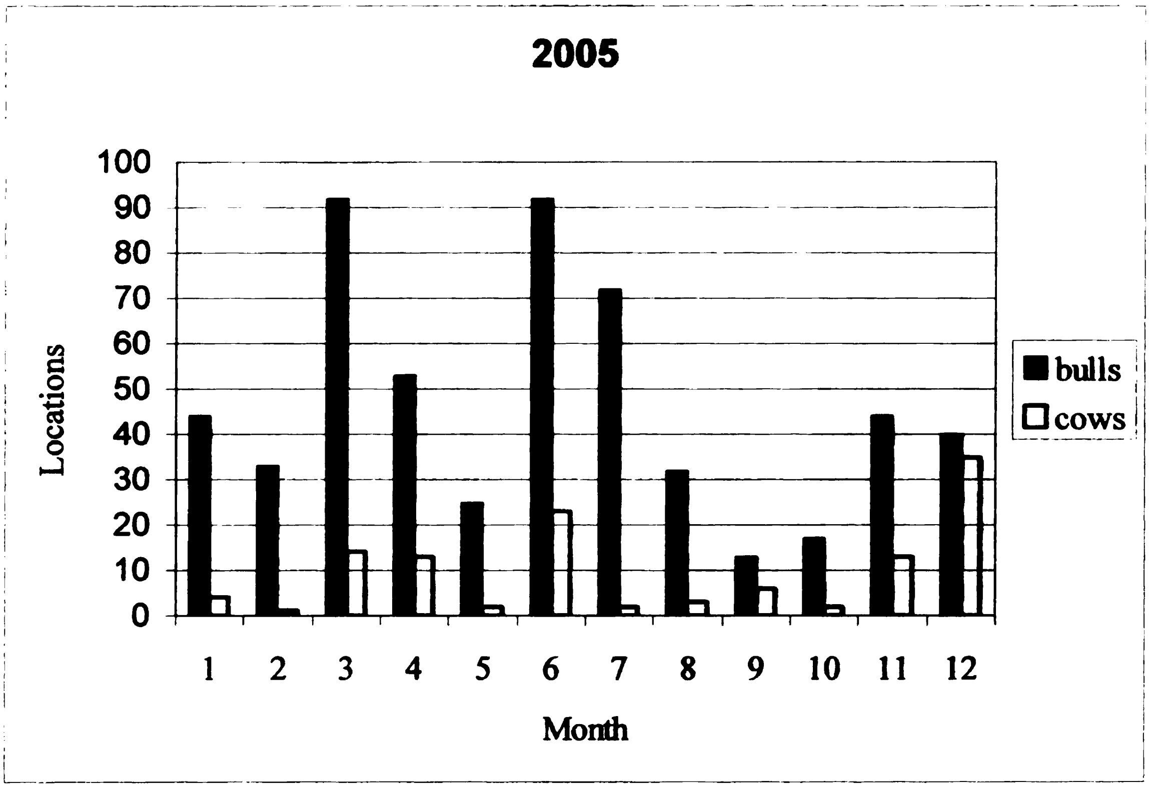


Figure 67. The number of locations of radiomarked elk (n = 16 bulls and n = 23 cows in 2005) by sex occurring within the boundaries of Canada Creek Ranch in Michigan, 2005.

Table 24. Probability of elk use of various cover types and associated standard errors (SE), coefficients of variation (CV), and standard normal 95% confidence limits (LCL, UCL) in Michigan, 2003–2005.

Cover type	**Probability**	**SE**	**CV**	**LCL**	**UCL**
Agriculture	0.0152	0.0023	0.1526	0.0107	0.0198
Aspen	0.1558	0.0168	0.1075	0.1230	0.1887
Conifers	0.1178	0.0143	0.1213	0.0898	0.1459
Lowland forest	0.0977	0.0126	0.1288	0.0731	0.1224
Managed openings	0.0126	0.0014	0.1102	0.0099	0.0153
Mixed conifer/deciduous	0.0859	0.0100	0.1164	0.0663	0.1055
Mixed upland deciduous	0.0224	0.0034	0.1519	0.0157	0.0291
Northern hardwood	0.1154	0.0139	0.1201	0.0882	0.1425
Oaks	0.1348	0.0155	0.1151	0.1044	0.1651
Openings	0.1870	0.0205	0.1099	0.1467	0.2272
Other	0.0583	0.0077	0.1321	0.0432	0.0735
Water	0.0094	0.0014	0.1444	0.0068	0.0121

Discussion

The sampling regime employed during this study allowed for the acquisition of a large amount of location data from the sample of radiocollared elk. The bimodal distribution of collection times of triangulated locations is a reflection of the 2-shifts used during the study. Although this distribution is far from uniform, it does demonstrate that there was a large amount of locations collected in both diurnal and nocturnal periods, and as a result there is likely negligible bias in our home range or probability estimates as a result oftime-specific movements or selection of resources (Beyer and Haufler 1994). Triangulated locations were relatively imprecise compared to GPS fixes, and standard deviation of bearings was larger than the 6° reported and used for other studies in this region (Ruhl 1984, Beyer 1987). This discrepancy could be due to differences in types of cover and topography at which transmitters were placed, distance from transmitters, or ability of observers.

The GPS collars provided highly precise location information and fixes times were nearly uniformly distributed throughout the day. Thus they may be more appropriate for habitat selection studies, or for studies where detailed use information is required. The major drawback with these collars is reliability and design flaws. Collars on 2 bulls stopped functioning in March 2005, less than 2 months after deployment. The malfunction in both cases was due to an exposed antenna wire, which was severed by the elk during normal activities. The antenna wire was exposed during deployment, as the collars were being adjusted to fit the bulls' necks, and sit with both the antenna and receiver vertically oriented on the animal. This design flaw limited the usefulness of these collars, and the manufacturers are currently looking for solutions to this problem.

Thus all these factors should be weighted into the decision of whether to use GPS or traditional VHF collars.

Estimates of mean home range sizes reported here agree closely with Beyer (1987), who estimated a mean non-rut, home range size for bulls of 9,363 ha and mean non-rut, home range size of 6,444 ha for cows. However, Bender (1992) reported home range sizes of 2,600 ha for bulls and 2,970 ha for cows. The difference may be attributed to the smaller sample size of elk (i.e., 28), number of locations used, the high quality habitat in the core of the elk range from which he sampled elk, and the fact that he only monitored calves and yearlings. Ruhl (1984) reported only seasonal home ranges, however, if his estimates of fall and spring home range sizes, the times of greatest movement in Michigan, are summed then his estimates are similar to those reported herein. All 3 of these studies, however, employ the use of 100% minimum convex polygon (MCP) home range estimation techniques (Mohr 1947), which for a given sample size will tend to yield larger home range estimates than those produced by fixed kernel methods, as used in this study. This is due to the fact that MCP methods assume a uniform density function, and it includes all boundary points in the delineation of home ranges. Thus, it is likely elk home range sizes noted in this study are larger than those reported previously.

Researchers in other eastern states have reported a variety of home range sizes for elk, all of which are less than those reported herein. Peterson et al. (2006) reported a mean home range size of 4,156 ha for 54 radiocollared bulls in Arkansas using kernel methods. In Pennsylvania, bull home range sizes were reported as 5,309 ha and cow home ranges as 1,748 ha (Pennsylvania Game Commission 2007). In Wisconsin, mean home range of 22 cows was estimates as 2,134 ha for summer and 2,841 ha for winter based on kernel methods (Anderson et al. 2005). Although no annual home range size was provided for direct comparison, given the non-migratory nature of the Wisconsin elk herd it is likely the annual home range size would not exceed the sum of summer and winter home range sizes. Estimates of annual home range sizes of elk in western states tend to be much larger than in eastern states. These estimates do not provide a good comparison of this study's estimates as elk in western states are often at higher population densities, migratory, and inhabit vastly different topographic terrains and cover types relative to eastern states. For example, Van Dyke et al. (1998) reported a range of mean annual home range sizes for different elk herds in south-central Montana and northwestern Wyoming. These sizes ranged from 8,360 ha to 37,660 ha based on 95% MCP methods. Thus, compared to other elk herds in eastern states, where home range sizes were available, Michigan elk have the largest estimated mean annual home range. These large home ranges may be an artifact of over 20 years of hunting pressure, since it has been shown that flight distances and daily movements have increased in Michigan since the hunting was resumed in 1984 (Beyer 1987, Bender 1992). Also differences may be attributed to differences in elk range conditions between the various states, or overall differences in elk densities between states (Anderson et al. 2005).

Mean bull annual home range sizes were larger than associated mean cow home range size across all years of this study at the both the 95% and 50% contours. Beyer (1987) and Ruhl (1984) made similar findings during their investigations of the Michigan elk herd. These findings are not surprising as bull home ranges are expected to be larger given the differences in foraging strategies and anti-predator defenses between the sexes, as well as rutting behavior (Geist 2002). However, Bender (1992) examining calves and yearlings in Michigan found no difference in home range size between the sexes. This finding is likely due to the fact that both male and female calves and yearlings remain with their maternal group through much of the year in Michigan (Moran 1973, Bender 1992), and thus would be expected to have similar home range sizes as a result.

Home range sizes decreased throughout the study period for the 95% and 50% contours. Both bull and cow home range sizes were considerably larger during 2003 than in other years of the study. This difference may be attributed to the below average temperatures experienced during this year, or differences in mast production, forest management practices and snow depths. Also age of collared animals may have been a factor, particularly for the bulls, since we collared primarily subdominant animals, which tend to move greater distances then older bulls (Bender 1992).

Elk use of the range was highly variable with many peaks and valleys in the kernel surfaces. Although many high and low use areas remained such throughout the study, examination of annual averaged kernel density surfaces across times shows variability in intensity of use of these areas. Some of these changes are undoubtedly due to habitat and forest management practices as well as natural food production throughout the range. For example, in 2003 several managed openings northeast of the Osmun/Clark Bridge road intersection were replanted with clover and buckwheat, and that area received intense use by radiocollared elk that year. The amount of use lessened in subsequent years presumably as forage quality lessened, and as forest cutting activities occurred in adjacent areas distributing the intensity of use more widely throughout the region.

Interchange between groups of elk from various portions of the range is likely common in Michigan based on the joint space use analyses and dispersal from capture sites. Regions in the central or core elk range as expected had the most joint space use with other regions. Not surprisingly, the periphery areas such as the Bone Yard and Vienna summering areas seemed to be characterized by considerably fewer movements of elk into and out of these areas. Also this interchange between groups appears to be highest during winter based on a qualitative assessment of location data, and examination of the dispersal patterns of radiocollared elk from their capture sites. This is supported by findings of Moran (1973) and Bender (1992) who noted intermingling of elk from various portions of the range particularly during the winter when elk groups are the largest. Intermingling of elk groups is variable from year to year as the different dispersal patterns from capture sites across years demonstrate (i.e., large amount of dispersal in 2003 and limited in 2005). In 2003, the sites with the largest concentrations of elk from across the range were in fresh timber cuts or along oak ridges (i.e., there was an exceptional acorn crop in fall 2002). During capture operations in February 2005, the winter was mild with warm temperatures and little snow accumulation relative to the weather conditions during the 2003 capture. Therefore, it is likely that local concentrations of elk from across the region are undoubtedly largely affected by weather conditions and forage availability.

In addition to understanding interchange between elk groups, the delineation of joint space use areas provides elk managers with knowledge of areas that are used in common by elk from across the range, which can be targeted for habitat or population management practices. Also knowledge of the regions that concentrate elk can be useful for focused disease surveillance or control efforts. Thus understanding, interchange, joint space use and knowledge of where and how they occur are important considerations in elk management in Michigan with implications for population, habitat and disease management issues.

Private club lands in the central portion of the elk range provide a vital role for elk in Michigan both currently as well as historically. Black River and Canada Creek ranches were used by a large number of radiocollared elk throughout the study. This use does vary by season and sex. Interestingly, most radiocollared elk use of Black River Ranch, outside the early spring and fall periods, was by cows, whereas the opposite was true for Canada Creek Ranch with mainly only radiocollared bulls using it during those time periods. Sexual segregation in elk for a majority of the year is well documented (Moran 1973, Bender 1992, Geist 2002). The cause of this sexual segregation is often habitat related. It is postulated that cows tend to select areas of better security cover for calf rearing purposes compared to bulls, which select areas with more nutritious forage to recover from the previous and prepare for forthcoming winter and rutting activities (Geist 2002). Thus, the segregation of sexes in the case of these clubs may be related to the various habitat conditions and management practices each club employs, or a function of differences in the amount of disturbance due to human use.

In the early spring during green-up many of the radiocollared elk normally associated with Canada Creek moved to Black River Ranch. However, by late spring and early summer the elk returned to Canada Creek. This short-term movement was presumably due to food availability, which would indicate an earlier green-up or more nutritious food source in early spring on Black River Ranch.

The decrease in elk use of Canada Creek during the fall is due to bulls, which spend most of the year on the ranch, distributing themselves across the range for the rutting purposes. This suggests that Canada Creek likely supports a large number of bulls that are important for breeding purposes for a wide area of the range, and it is critical to consider this fact when determining harvest objectives for this region. Elk on Black River Ranch demonstrate the opposite trend in the fall as bull use increases, which is undoubtedly due to the larger number of cows inhabiting this ranch.

Intensity of elk use on both clubs was uneven with a few areas of high concentration. Interestingly, changes in intensity of use as measured by the kernel surfaces, particularly, on Canada Creek can be attributed to forest management activities. Canada Creek has conducted a number of timber harvest operations in various portions of the club over the duration of this study. These newly cut and regenerating areas attracted elk to these regions, and these distribution shifts are evident in the kernel surfaces. An example of this phenomenon is the region south of the Bald Mountain Ravine, east of the Homestead road. In 2003 and 2004, this area received only minor elk use, but in the winter of 2004–2005 the timber in this area was harvested. The subsequent year this area reached a much greater intensity of use, as the elk responded to the additional forage available resulting from the harvest. This increased use of recently timbered areas, and associated regeneration problems has been a source of controversy in recent years.

These issues are not new as historically, the region where Black River and Canada Creek ranches occur, has had large concentrations of both deer and elk, and similar issues have constantly arose over the years (Moran 1973). Currently, to address these issues the MDNR has worked to reduce the population of elk on the club and adjacent areas, restructured harvest unit boundaries to facilitate this reduction, and improved habitat in the region outside the club in an effort to attract and hold elk that inhabited the club (D. Smith, Michigan Department of Natural Resources, personal communication). However, these actions alone will likely be insufficient to reduce regeneration problems if forestry practices and management polices within the boundaries of the club are not altered. Thus, the weight of responsibility for reducing browse problems ultimately lies with forest managers of the club. Managers need to set forth realistic objectives at both the stand and club levels that account for the natural potential of the site (e.g., a hardwood stand should not be managed for oak regeneration) as well as the other biological influences acting on the club such as the high elk and deer densities. Also forest managers need to accept the fact that by conducting habitat work (i.e., planting food plots, etc.) to provide habitat for deer, the club is attracting larger number of deer and elk than would naturally occur in the region. This can lead to browsing problems from both species when these concentrations of animals browse for food during the winter months. Therefore, forest management objectives need to incorporate the club's other objectives such as maintaining large deer and elk herds for viewing and hunting purposes if they are to set achievable timber management objectives. Secondly, a continual evaluation of the success or failure of these objectives should be conducted to determine the most effective timber management strategies for the range of conditions present on the club lands. Evaluations should include but not be limited to the following: the effects of the size and distribution of timber cuts on regeneration success, effects of the removal of security cover in and around fresh cuts (i.e., removal of conifers and other hiding cover in and adjacent to cuts), the long-term production and recovery of stands that receive browsing pressure (e.g., is the production of heavily browsed stand in 10 years comparable to those without major browsing pressure), and the effects of various harvest strategies for both deer and elk. These actions and continued cooperation between public and private stakeholders, I believe, will ultimately lead to a reduction or resolution of these elk/human conflicts.

The findings, regarding the probability of use of the various cover types of interest, are similar to the patterns of use reported by other Michigan researchers (Moran 1973, Ruhl 1984, Beyer 1987). Most importantly, these findings reinforce the importance of openings for elk, and validate the management efforts of both public and private entities working to improve opening conditions, as elk are using managed openings throughout the range at a higher probability than unmanaged openings.

The use of the averaging of kernels of individual animals is a new concept to the analysis of animal home range and space use. It provides a powerful tool to make population level inference based on a sample of radiocollared animals, provided its assumptions are met. Failure to meet these assumptions would result in bias in the averaged kernel density surface and in associated variance estimates. For this study, I believe the assumptions were reasonably met. Given the dispersal of collared elk from capture sites to regions across the range and qualitative examination of the averaged and individual kernel density surfaces, it appears that most areas with elk use in my study area are represented in the movements of the collared elk, and thus in the averaged kernel surface. The assumption of independence of collared elk was likely met based on the fact that only adult elk were collared, and the lack of any long-term or lasting associations between collared animals. Lastly, the assumption of the individual kernel density estimates adequately describing each elk's home range I do not believe was extensively violated given the large number of locations used to estimate the individual kernel densities for most animals. However, for animals with fewer locations due to mortalities or being collared late in the study, kernel density estimates may not have fully described their home range, which would have introduced bias into the averaged kernel surface. But, the minimum number of locations used in estimating the individual kernel density across all collared elk was 51, which is above the minimum number recommended for home range estimation (Otis and White 1999, Seaman et al. 1999 and Garton et al. 2001).

This averaging technique provides a means of overcoming differences in the number of locations associated with individuals, which can often be substantial. Also, no information is lost with this technique; unlike other analysis procedures such as resampling that discards data to generate equal sample sizes of locations. One of the utilities of this technique demonstrated here is the ability to calculate the probability that a population of interest is using a particular region or cover type, utilizing the information contained in the probability density function. These probabilities can be used by elk managers to quantify elk range use patterns, measure the effects of habitat and forest management practices, or even determine the effects of recreational activities in various regions. Additionally, the estimation of variances associated with the averaged kernel density estimates is critical for determining the precision associated with probability estimates generated using the average kernel density estimates, and the variance surfaces can be examined to determine the precision of kernel density estimates throughout the averaged kernel surface. However, more study is needed to determine the performance of this estimator in the context of ecological studies, and examine means of estimating parameters of covariance functions associated with calculated probabilities as opposed to assigning them *ad hoc* values. But, this technique holds promise for providing a means to answer a wide array of management and research questions.

I provided a simple means of incorporating the error associated with estimating animals' locations into the estimated variances for the kernel density estimates. Incorporation of this error is important to avoid negatively biased variance estimates, resulting from the false assumption that locations input into the kernel functions have no associated measurement error. Also the use of the DPI bandwidth selector provides another option to the commonly used LSCV selector, and given its asymptotic properties and simulation results it appears to be the superior of the 2 selectors (Wand and Jones 1995).

Lastly, the use of a joint density function to examine joint space use, as described, provides several benefits over other metrics of joint space use such as the volume of intersection index (Seidel 1992). Joint density functions provide measures of the intensity of use between 2 individuals or groups of interest, and this intensity can be easily represented graphically. Most importantly, integration of the joint density function allows for estimation of probabilities of interest, and facilitates examination of joint space use on a probabilistic basis. Once again more research is needed to determine the properties and performance of these estimators, but they are appealing and may be an important component of the study of animal interactions.

Management Implications

The information provided on the movements, range use, and interchange on public and private lands is important for wildlife and forest managers. This knowledge is critical for determining the most effective locations for habitat improvement projects, and the delineation of areas where habitat manipulations are having or not resulting in the desired effects with regards to elk use. These data also can help in conservation planning for elk by identifying areas with high probability of elk use that can be the focus of protection efforts, or if these areas are in the hands of private land owners they can be targeted for easements or acquisition. From a forest management perspective, my findings can be useful for setting realistic timber production objectives by isolating regions with high elk use. These areas likely will not be as productive as areas where elk do not occur or densities are lower, and this needs to be factored into timber planning if achievable objectives are desired. From a public relations perspective, information regarding elk use of agricultural areas and surrounding lands is useful for dealing with agricultural complaints. Also the general range use information can be an asset when attempting to provide private citizens with elk viewing or hunting opportunities. Lastly, elk population management strategies can be derived in part based on the results of this study. Knowledge of how elk from various locations throughout the range interact, how they distribute themselves, and the variability of this distribution is useful for establishing elk hunt units and setting harvest objectives that recognize the spatial structure of Michigan's elk herd and allow for a more focused targeting of problem animals.

The increase in the understanding and knowledge of Michigan's elk herd generated by this study provides a critical element to the management of elk, and will aid managers as they strive to make sound management decisions that benefit Michigan's elk resource.

Conclusion

The goal of this project was to gain valuable information regarding current elk movement patterns and distribution particularly on the eastern portion of the Michigan elk range. This goal was realized by achieving the objectives set forth. The wealth of information gained, the new ideas and analysis techniques set forth, and the overall increase in understanding of elk in Michigan, I believe are all valuable constructs resulting from this research effort. I hope these products will enhance elk management in Michigan for the enjoyment of current and future generations.

CHAPTER 5: ELK AND BOVINE TUBERCULOSIS IN MICHIGAN

Introduction

Michigan has the dubious distinction of being home to the first documented epidemic occurrence of bovine tuberculosis (TB; *Mycobaterium bovis*) in free-ranging cervids in North America (Schmitt et al. 1997). Discovery of TB, in free-ranging white-tailed deer (*Odocoileus virginanus*) in the northeastern corner of the lower peninsula of Michigan, was precipitated by the submission to the Michigan Department of Natural Resources [MDNR] of a hunter-killed 4.5-yr-old male deer in 1994 that had suspicious thoracic lesions, which were tentatively diagnosed as TB. Laboratory analysis later confirmed this diagnosis with the isolation of *M. bovis* from the lung tissue of this animal (Schmitt et al. 1997). In 1995, a survey of hunter-harvested deer from the region was initiated to determine if TB existed in free-ranging white-tailed deer. The survey resulted in the estimation of an apparent TB prevalence of 4.8% in the study area (O'Brien et al. 2002). In subsequent years, local and statewide surveys for the disease, documented the highest prevalence in the area known as DMU 452 (~1561 km^2) with decreasing prevalence moving away from this core area (Hickling 2002, O'Brien et al. 2002). It was believed that the biological and social characteristics particular to this region of Michigan allowed for the perpetuation of the disease in the deer herd. These factors included large-scale supplemental feeding programs, high deer densities, land ownership patterns (i.e., a large proportion of the area is owned by private hunt clubs), extensive deer baiting for hunting purposes, and a local economy based largely on recreational activities with hunting being foremost (Hickling 2002, O'Brien et al. 2002, Miller et al. 2003, Rudolph et al. 2006). The MDNR instituted several management polices aimed at controlling the spread and ultimately eradicating the disease from the state based largely on addressing these factors. In 1998 they instituted a ban on baiting and supplemental feeding of ungulates in the 5-counties containing and surrounding the core area. They also instituted liberal antlerless deer harvests throughout the region in an attempt to lower deer densities, continued extensive disease surveillance of hunter-harvested deer to estimate apparent prevalence and track any potential spread of the disease, and lastly they instituted an educational campaign to inform the general public about the health and biological issues associated with this epidemic (Hickling 2002, Rudolph 2006). The results of these efforts appear to be positive as deer densities have decreased significantly (Rudolph et al. 2006), the disease does not appear to be spreading (Hickling 2002), and apparent prevalence has decreased significantly (O'Brien et al. 2002).

Although, white-tailed deer are the primary reservoir host for *M. bovis*, other spill-over hosts have been documented in Michigan including: black bear (*Ursus americanus*), bobcat (*Felis rufus*) coyote (*Canis latrans*), red fox (*Vulpes vulpes*), and raccoons (*Procyon lotor*) (Bruning-Fann et al. 2001). Additionally, 4 elk (*Cervus elaphus*), 2 bulls and 2 cows, have tested TB positive in Michigan the last case being in 2003.

Elk are known to be susceptible to *M. bovis*, and in the Riding Mountain National Park region of Manitoba, Canada the species functions as the primary reservoir host with an apparent prevalence of 1% in the population (Lees 2004). Both deer and elk in Michigan have been shown to utilize openings in the spring, summer and fall (Ruhl 1984, Beyer 1987, Sitar 1996, Garner 2001), and demonstrate similar affinities for wooded vegetation types especially upland deciduous stands and regenerating stands throughout the year (Moran 1973, Ruhl 1984, Beyer 1987, Sitar 1996). Other studies across the United States have shown potential overlap in habitat use between elk and various species of deer. Collins and Urness (1983) noted similar use of vegetation types in Utah, USA between tame mule deer (*Odocoileus hemionus*) and elk especially in late summer, although intensity of use of the various habitat types varied between species. Hanley (1984) studying black-tailed deer (*Odocoileus hemionus columbianus*) and elk in Washington, USA noted different dietary habits and habitat preference between the species along a moisture gradient. However, as graminoids senesced and became less nutritionally valuable, a greater overlap in habitat preference was documented. Johnson et al. (2000) noted that mule deer and elk in Oregon selected resources similarly, however, mule deer exhibited an avoidance of elk.

Thus previous research demonstrates the potential for transmission to occur between white-tailed deer and elk in Michigan resulting from home range overlap and concurrent habitat utilization, but elk-deer interactions are generally believed to be limited (Miller 2002). However, historical human activities in Michigan that mutually concentrated deer and elk, such as baiting and particularly supplemental feeding, provided an ample avenue for inter-species transmission either through aerosol transmission during direct contact, or from ingestion of feed material contaminated by feces, saliva or nasal secretions of infected animals (Miller et al. 2003, Lees 2004). *M. bovis* can also persist in cool, moist and dark environments for months, and infected animals can potentially shed a substantial amount of infectious material throughout their home range (Francis 1971, Lees 2004). Thus, elk in Michigan are at risk of contracting and possibly becoming a second reservoir host for TB either by direct or indirect contact with infected deer and their infected environments. In addition, elk social structure and breeding activities (i.e., harem holding behaviors) puts the species at a high risk of intraspecies transmission should the disease become established in the elk herd at any significant prevalence.

In December 2003, an elk hunter legally harvested a 2.5-yr-old cow radiocollared in February 2003 (elk #32). This cow was confirmed to be TB positive. This provided a rare opportunity to examine the movement patterns of a TB positive elk for a 10-month period. Also the amount and location of joint space use of this elk with other radiocollared elk could provide important information regarding the risk to other elk that may have come contact with this individual post-infection.

Thus, to gain an understanding of the potential risks associated with TB to the elk herd in Michigan, the following objectives were addressed:

1. Identify areas of the elk range where elk are at high risk for being exposed to *M. bovis* based on apparent prevalence of TB in deer and elk use of the region.
2. Calculate the probability of elk using these high-risk areas, and compare these areas to the location of known TB positive elk. High-risk areas are defined as areas in which there is a greater risk of elk being exposed to *M. bovis* as a result of relatively higher prevalence levels in deer and correspondingly higher probability of elk use.
3. Determine the range use of elk #32, a radiocollared cow that was TB positive, and estimate location and amount of the joint space use of this cow with other radiocollared elk in the region.

4. Introduce new analytical techniques using fixed kernel analyses to address previous objectives, and thereby demonstrated their usefulness in epidemiological investigations.

Study area

The study site selected for this project is the current elk range located primarily in Cheboygan, Montmorency, Otsego and Presque Isle counties in the northern portion of the Lower Peninsula of Michigan (Figure 3: Chapter 1). The historic range (i.e., prior to 1990's) was estimated at approximately 1550 km^2, including the Pigeon River State Forest near Vanderbilt, Michigan (Bender 1992). The current elk range is estimated at approximately 3,450 km^2 (D. E. Beyer, Michigan Department of Natural Resources, unpublished report). We focused our study on the eastern region of the elk range near Atlanta in Montmorency County.

Topography of the area slopes northerly and consists of flat-topped ridges interspersed with headwater swamps and outwash plains created through glacial actions (Moran 1973).

Mean annual temperature is 6.3 °C with January having the lowest mean monthly temperature (-7.7 °C) and the highest (19.7 °C) occurring in July (NOAA 2006). Mean annual rainfall is 67.3 cm, and mean annual snowfall is 189 cm (NOAA 2006) with precipitation being generally well distributed throughout the year.

Due to wide array of soil fertilities, aspects and moisture levels, vegetation types are diverse and well interspersed. In addition, human activities such as logging, agriculture and forest management practices further complicate the pattern of vegetation types throughout the area. Dominant cover types include upland and lowland deciduous and coniferous forests interspersed with typically human-induced openings. Moran (1973) provides a detailed description of the vegetation of the region.

Methods

TB Prevalence in Deer

Data acquisition.–O'Brien et al. (2002) documented the procedures used to determine TB infection in free-ranging deer in detail. Since 1995, the number of TB positive, free-ranging deer has been determined by personnel at the MDNR Wildlife Disease Laboratory, East Lansing, Michigan, mainly through surveillance of hunter-harvested deer heads and carcasses voluntarily submitted to the MDNR. Other deer collected by various means (e.g., vehicle collisions, crop damage permits) were also included in the survey, although these animals represent only a limited percentage of the total deer surveyed. Information generally collected for each submitted specimen included: date of harvest/collection, sex, age (via tooth eruption/wear patterns) and harvest location by township, range and section.

Examination of specimens for *M. bovis* began with gross examination of the submandibular, parotid and retropharyngeal cranial lymph nodes. If nodes exhibited gross enlargement with abscessation or granuloma formation, the specimen was designated as TB suspect, and specimens were then sent for histopathology, acid-fast staining, and mycobacterial culture for final determination of *M. bovis* infection. The sensitivity and specificity of these examination procedures were estimated as 75% and 100%, and apparent prevalence was linearly related to true prevalence (Fitzgerald et al. 2000, O'Brien et al.2004)

Analysis. –All information was entered into the Bovine Tuberculosis Surveillance Database (Michigan Department of Natural Resources 2006). From this database, I extracted TB prevalence data from 1999–2005 for Cheboygan, Montmorency, Otsego and Presque Isle counties (i.e., the counties containing the elk range). These years represented the time since the MDNR ban on supplemental baiting and feeding of ungulates, and also a period of relatively stable deer harvest and management strategies for this region (Rudolph et al. 2006). The resolution of the data was at the section level (2.59 km^2) based on the General Land Office Survey. I calculated apparent prevalence by dividing the sum of the number of TB positive deer by the total number sampled for each section. Apparent prevalence was calculated for 2 time periods, 1999–2005, and for 2003–2005 (i.e., the time period from which elk data was collected). For each time period, using the Spatial Analyst extension in ARCGIS version 9.0 (ESRI, Redlands, California, USA), I used ordinary kriging to develop a prediction surface of apparent TB prevalence. Parameters for the spherical variogram model were calculated automatically using weighted-least squares to fit the model (Cressie 1985). I chose to use ordinary kriging since it requires fewer assumptions, as the mean is not assumed to be known. Also, since the mean surface is estimated this technique does not drift to the global mean away from sample points as in simple kriging, but only moves to the local mean.

Elk Range Use

Location estimation. –Elk range use was estimated based on the location data collected from 2003–2005 on 58 radiocollared adult elk (20 bulls, 38 cows). Forty of these elk were collared in 2003, 2 were collared in 2004 and the remainder were collared in 2005. Location data were collected primarily using triangulation techniques via the loudest point method (Springer 1979, White and Garrott 1990) with locations being estimated using Lenth's estimator in Locate III (Nams 2006). I also obtained location information from visually sighting collared animals either by homing in on collared animals or incidental sightings. Locations in these instances were determined by using a hand-held GPS unit (Garmin, Olathe, Kansas, USA). Lastly, 5 animals in 2005 were collared with radiocollars equipped with GPS units (Advanced Telemetry Systems, Isanti, Minnesota, USA) which automatically recorded the GPS location of these animals every 7hrs.

Range use estimation.–Based on this location data and using Gaussian fixed kernel methods (Wand and Jones 1995), for each individual elk I developed probability density estimates for each point on a common grid that described the probability of each elk's use of the elk range at that point. Grid points were spaced at 160.9344 m intervals, and the grid encompassed all elk locations with an additional 1,609.344 m border. The bandwidth for each kernel was determined using a direct plug-in automatic bandwidth selector (Wand and Jones 1995). I used a bootstrap procedure to develop variance estimates for each grid point at which the kernel density function was evaluated (Efron and Tibshirani 1993). To allow for population level inference, I averaged the individual kernel density functions across all radiocollared animals. Variance estimates for this averaged kernel density function were determined for each grid point by summing the individual variances for each elk under the assumption that each individual was independent. These kernel averaging analyses require the following assumptions to allow population level inference: 1) Individuals collared represent a random sample of the population and, therefore, their range use reflects that of the population. 2) Collared elk are independent. 3) Individual kernel density estimates provide unbiased density estimates and adequately describe range use. A detailed description of the methodologies used in the above analyses is presented in Chapter 4.

Identifying High Risk Areas

Locations where elk have a high risk of being exposed to *M. bovis* were determined by multiplying the averaged kernel density surface for the radiocollared elk with the kriged surfaces of apparent TB prevalence for the 2 time periods of interest using Spatial Analyst in ARCGIS. Then I determined the regions with peaks in the joint use surface, and delineated these locations with high elk use and relatively high TB prevalence as high-risk areas. The locations of harvest/collection of elk known to be TB positive were plotted against the high-risk areas in ARCGIS as a qualitative assessment of the delineation of high-risk areas.

As the prevalence data were problematic since sample size varies markedly from section to section ranging from 1 to 66 animals sampled, I did not calculate joint probability estimates between elk use and apparent TB prevalence. However, I did examine the probability elk used the high-risk areas. These probabilities were calculated by intersecting the grid of points at which the averaged kernel density was calculated with the grid of cells associated with the high risk areas using Hawth's Analysis Tools (Beyer 2006) in ARCGIS. This provided in indicator variable of the grid points associated with the high-risk areas. These grid points were taken into R Version 2.4.1 (2006), and the probability of using the high-risk areas was calculated by summing the density estimates at each of the grid points that were contained within the high-risk areas multiplied by the grid cell area (i.e., 25,900 m^2). Variance estimates for these probabilities were estimated as follows:

$$\hat{\text{var}}(\hat{p}) = (25{,}900)^2 \times \left[\sum_{i=1}^{n} \hat{\text{var}}(\hat{f}(x_i, y_i)) + \sum_{i}^{n} \sum_{i \neq j}^{n} \hat{\text{cov}}(\hat{f}(x_i, y_i), \hat{f}(x_j, y_j)) \right],$$

where n = the number of grid points contained in the high risk areas, the $\hat{\text{var}}(\hat{f}(x_i, y_i))$ = bootstrap variance estimate for the averaged kernel density estimate at the i^{th} grid point, and $\hat{\text{cov}}(\hat{f}(x_i, y_i), \hat{f}(x_j, y_j))$ is estimated by multiplying the bootstrap standard errors for the i^{th} and j^{th} grid point by their correlation as determined by a Matern correlation function. A Matern correlation function, with a smoothing parameter of 0.5 and a range parameter equal to the average bandwidth matrix of all radiocollared elk, was used in variance calculations to account for the spatial autocorrelation between grid points associated with the probabilities of interest.

Examination of Range Use of a TB Positive Elk

Location data collection and home range estimation followed the same techniques previously described. Movement patterns of the TB positive cow were plotted in ArcView 3.2 (ESRI, Redlands, California, USA) using Animal Movements Extension (Hooge and Eichenlaub 1997). The 95% and 50% probability contour home range areas were calculated for this animal using R. The 95% percent upper and lower confidence limits for home range area were calculated using bootstrapping and the quantile method (Efron and Tibshirani 1993).

Averaged kernel density estimates for 15 elk (#9, #11, #12, #13, #17, #19, #20, #21, #23, #25, #33, #34, #35, #36 and #37) from the region for 2003 were multiplied by the kernel density estimates for elk #32 at the common grid points previously described. This created a joint density estimate at each grid point from which the probability of elk #32 jointly using the elk range with another elk in the area was calculated. It is important to note that the density estimates at each grid point estimate the probability density of an "average" elk from the eastern region using exactly same location (i.e., grid cell) as elk #32. I graphically displayed this joint density surface using ARCGIS. Variance estimates at the grid points were approximated using the delta method:

$$\hat{\text{var}}(\hat{f}_i(\boldsymbol{x}) * \hat{f}_j(\boldsymbol{x})) \approx \hat{f}_i(\boldsymbol{x})^2 \hat{\sigma}_i^2 + \hat{f}_j(\boldsymbol{x})^2 \hat{\sigma}_j^2,$$

where $\hat{f}_i(\boldsymbol{x})$ is the density estimate of the i^{th} kernel at a common grid point, $\boldsymbol{x}$, and $\hat{\sigma}_i^2$ is the estimated bootstrap variance of the density estimate at the common grid point from the i^{th} kernel. This process assumes that individuals or groups for which joint space use was examined were independent.

One of the areas that held a large number of elk from across the eastern portion of the study area, including elk #32, during the winter of 2003 was the Elk Ridge Golf Course. I determined the probability, of elk #32 and another elk from the region, using the golf course jointly conditioned on the probability that joint space use occurred, based on the above joint density surface. I conditioned on the occurrence of joint space use, to effectively reweight the joint density surface, so probabilities are readily interpretable (i.e., the unconditional joint density surface yields extremely low probabilities). This conditioning results in the following biological interpretation: for a particular location of interest, the estimated conditional probability was the probability there was joint space use at this location given there was a simultaneous use of some location. Thus the conditional probability was calculated as follows:

$$\Pr(use \mid X = 1) = \frac{\Pr(use)}{\Pr(X = 1)},$$

where $\Pr(use \mid X = 1)$ is the conditional probability of jointly using the golf course, $\Pr(use)$ is the unconditional probability, and $\Pr(X = 1)$ is the probability of joint space use (i.e., the overall probability of jointly using the elk range, calculated by finding the volume under the joint density surface). The variance of the unconditional probability was approximated using the delta method as follows:

$$\hat{\mathrm{var}}(\Pr(use \mid X = 1) \approx \boldsymbol{\delta}' \begin{bmatrix} \hat{\mathrm{var}}(\Pr(use)) & \hat{\mathrm{cov}}(\Pr(use), \Pr(X = 1)) \\ \hat{\mathrm{cov}}(\Pr(use), \Pr(X = 1)) & \hat{\mathrm{var}}(\Pr(X = 1)) \end{bmatrix} \boldsymbol{\delta},$$

where $\boldsymbol{\delta} = \begin{bmatrix} \dfrac{-\Pr(use)}{(\Pr(X = 1))^2} & \dfrac{1}{\Pr(X = 1)} \end{bmatrix}'$, $\hat{\mathrm{var}}(\Pr(use))$ is estimated as follows:

$$\hat{\mathrm{var}}(\Pr(use)) = (25{,}900)^4 \times \left[\sum_{i=1}^{n} \hat{\mathrm{var}}(\hat{f}(x_i, y_i)) + \sum_{i}^{n} \sum_{i \neq j}^{n} \hat{\mathrm{cov}}(\hat{f}(x_i, y_i), \hat{f}(x_j, y_j)) \right],$$

with n = the number of grid points contained in the golf course, the $\hat{\mathrm{var}}(\hat{f}_i(x_i, y_i))$ = approximate variance estimate for the joint density estimate at the i^{th} grid point, and the $\hat{\mathrm{cov}}(\hat{f}_i(x_i, y_i), \hat{f}_j(x_j, y_j))$ estimated by multiplying the approximate standard errors for the i^{th} and j^{th} grid points by their correlation as determined by a Matern correlation function with the same smoothing and range parameters described previously, the $\hat{\mathrm{var}}(\Pr(X = 1))$ is estimated in the same manner, however, n = all grid points, and lastly $\hat{\mathrm{cov}}(\Pr(use), \Pr(X = 1)) = \sum_{i=1}^{n} \sum_{i \neq j}^{m} \hat{\sigma}_i \hat{\sigma}_j \hat{corr}_{ij}$, where $\hat{\sigma}_i$ = is the bootstrap estimate of the standard error at the i^{th} grid point, $\hat{corr}_{ij}$ = is the correlation coefficient between the i^{th} and j^{th} grid points as determined by the Matern correlation function parameterized as before, and n = the number of grid points contained in the golf course and m = the total number of grid points.

Results

TB prevalence in the 4 counties averaged across the years of 1999–2005 ranged from 0–0.3333 with a mean of 0.0018 (SD = 0.0169) with 2,360 deer surveyed. For the interval of 2003–2005, TB prevalence ranged from 0–1 with a mean of 0.0019 (SD = 0.0299) for 1,735 animals examined.

Elk range use was described previously (Chapter 4). Areas with a high probability of elk use and corresponding relatively high TB prevalence for 1999–2005 were the regions around the Hardwood Lake/Osmun Road intersection, Canada Creek Ranch, the region along County Road 622 east of Camp 30 Hills, the region around Steven Springs Road, the Hubert Road region, and the area around Tomahawk Lake (Figures 68 and 69). Examining just the years of 2003–2005, identified 3 main locales of high-risk: the region around Steven Springs Road, the Hubert Road region, and the area around Tomahawk Lake (Figures 70 and 71).

Locations of known positive cases of TB elk are plotted along with high-risk areas (Figures 69 and 71). All positive cases were east of M-33, and visual examination reveals that these 4 cases are all located in or adjacent to identified high-risk areas.

The probability of using the high-risk areas based on the 1999–2005 TB prevalence data was 22.27% (SE = 2.04%). The probability of using the high-risk areas based on the 2003–2005 data was estimated as 8.96% (SE = 0.899%).

The movements of elk #32 were concentrated between Voyer Lake Road and County Road 634 with forays east to south of Grass Lake (Figure 72). Early locations

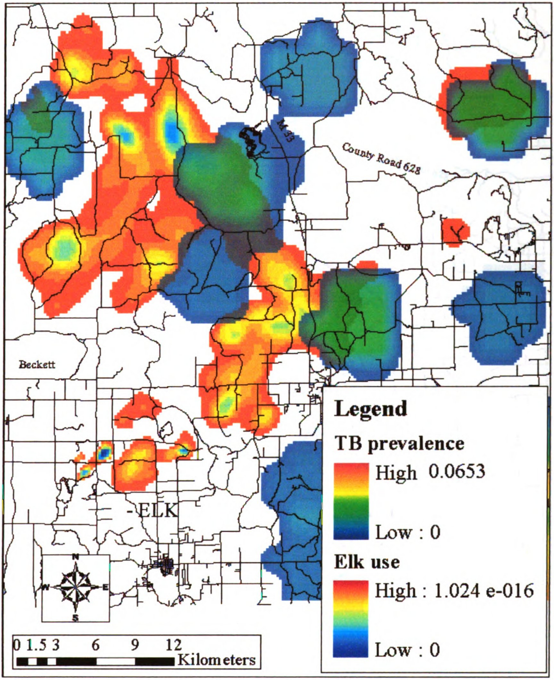


Figure 68. Averaged kernel density surface of elk use for 58 radiocollared elk overlaid with the kriging prediction surface of apparent TB prevalence of white-tailed deer in Michigan, 1999–2005.

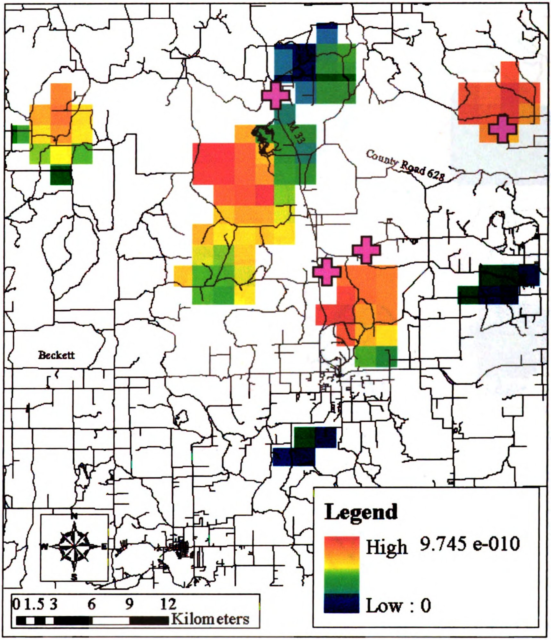


Figure 69. Areas of high-risk of TB transmission based on elk usage and apparent TB prevalence rates in white-tailed deer in Michigan, 1999–2005, and locations of harvest/collection of known TB positive elk (crosses).

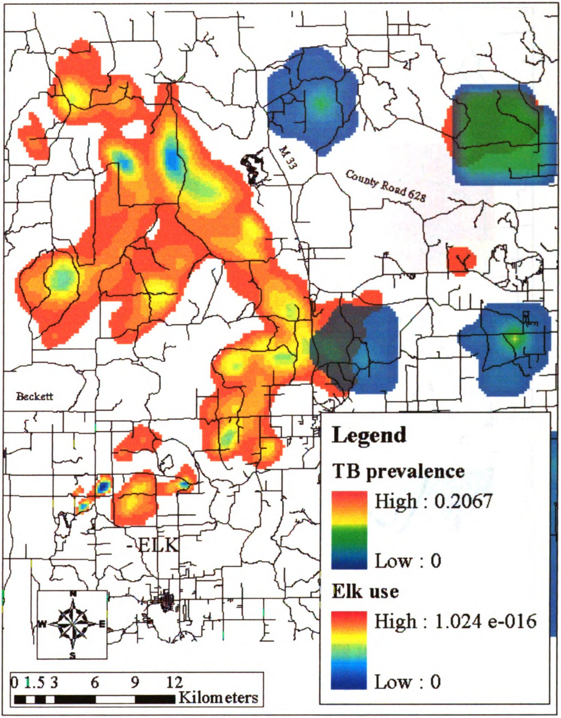


Figure 70. Averaged kernel density surface of elk use for 58 radiocollared elk overlaid with the kriging prediction surface of apparent TB prevalence of white-tailed deer in Michigan, 2003–2005.

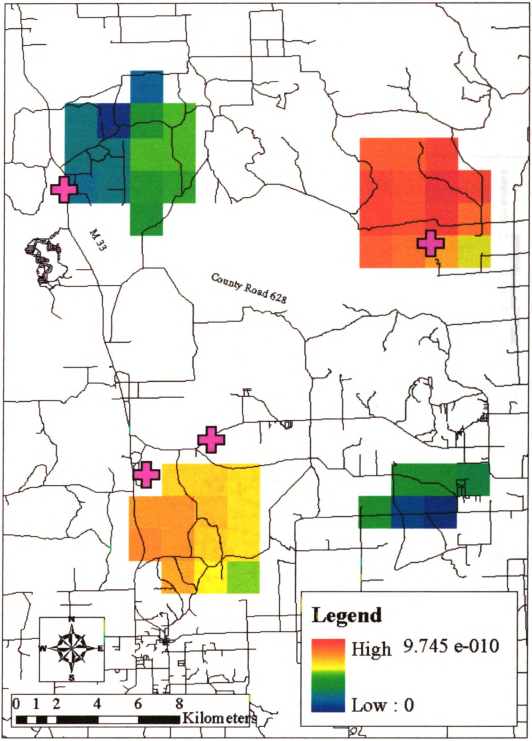


Figure 71. Areas of high-risk of TB transmission based on elk usage and apparent TB prevalence rates in white-tailed deer in Michigan, 2003–2005, and locations of harvest/collection of known TB positive elk (crosses).

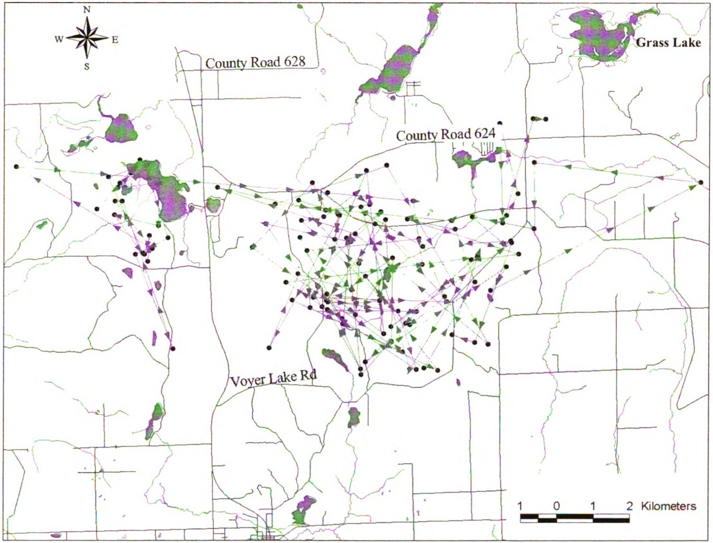


Figure 72. Locations and movement patterns of a radiocollared TB-positive adult cow elk in Michigan, 2003.

were centered on the Elk Ridge Golf Course before she moved east across M-33 for the remainder of the study. Based on 121 locations, the home range of elk #32 at the 95% contour encompassed 8,856 ha with 95% lower and upper confidence limits of 6,975 ha and 9,630 ha, respectively. Elk #32 had a larger home range than the mean cow home range of 7,342 ha (SE = 178) for all radiocollared cows for 2003, although the difference was not statistically significant based on overlap of 95% confidence intervals. Her home range size at the 50% contour encompassed 2,340 ha with 95% lower and upper confidence limits of 1,791 ha and 2,565 ha, respectively. This size was significantly different from the mean cow 50% contour home range area of 1,436 ha (SE = 48) based on overlap of 95% confidence intervals. This elk had 3 main locations with high probability of use: the Elk Ridge Golf Course, the area near the Brush Creek Truck Trail/County Road 624 intersection and the area north of Sportsmans Dam (Figure 73).

The average kernel density surface for elk from the eastern portion of the study area portrays 3 main high use areas: Elk Ridge Golf Course, the region west of the Decheau Lake/Meaford Road intersection, and the Hubert Road region in Presque Isle County (Figure 74). The standard error surface demonstrates the precision of the average kernel density surface with precision changing considerably across the surface (Figure 75).

The joint density surface between elk #32 and the other elk utilizing the eastern portion of the study area isolates the Elk Ridge Golf Course, as the site with the highest probability of joint space use (Figure 76). A secondary site is located southeast of the Brush Creek Truck Trail/County Road 624 intersection.

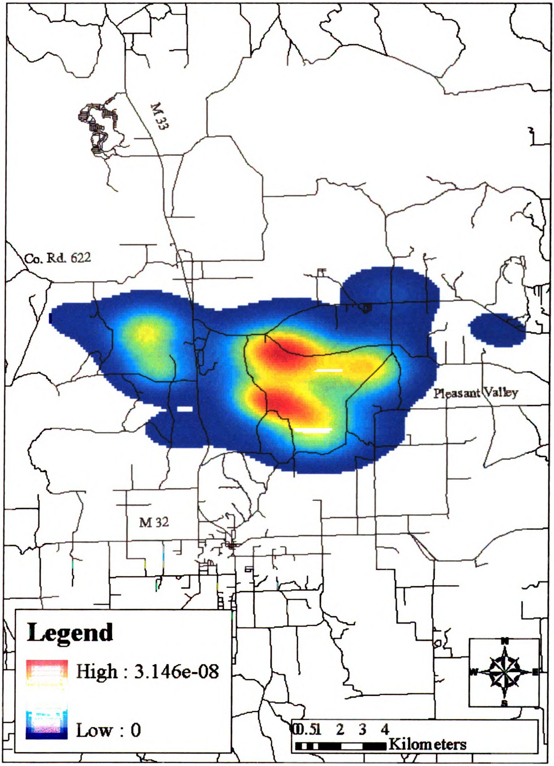


Figure 73. Kernel density surface estimating the home range of a radiocollared, TB-positive cow elk (elk #32) based on 121 locations in Michigan, 2003.

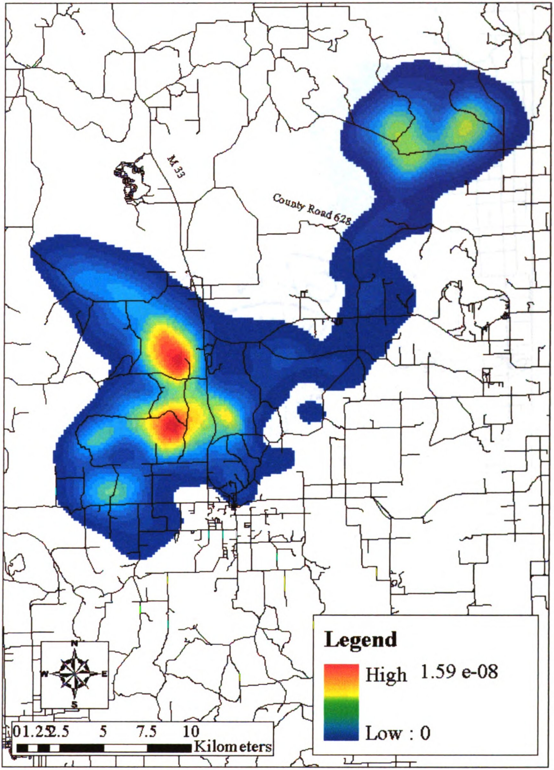


Figure 74. Average kernel density surface estimating probability of use of 15 radiocollared elk utilizing the eastern portion of the study area in Michigan, 2003.

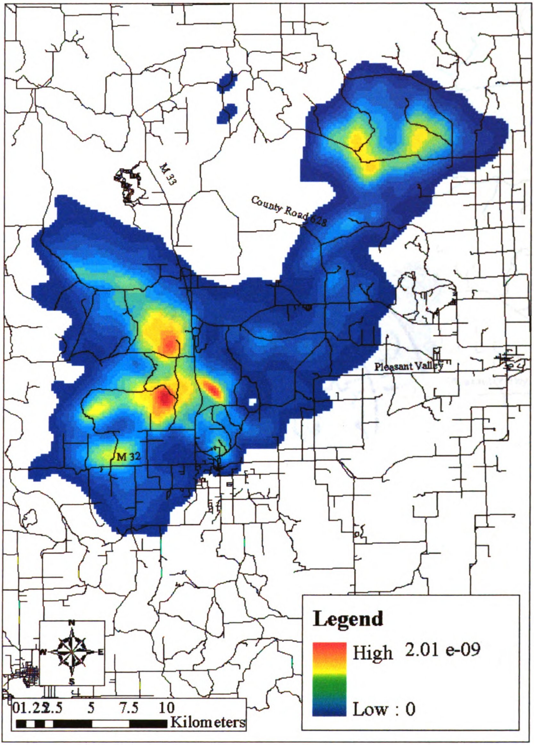


Figure 75. The standard error surface for the average kernel density surface estimating probability of use of 15 radiocollared elk utilizing the eastern portion of the study area in Michigan, 2003.

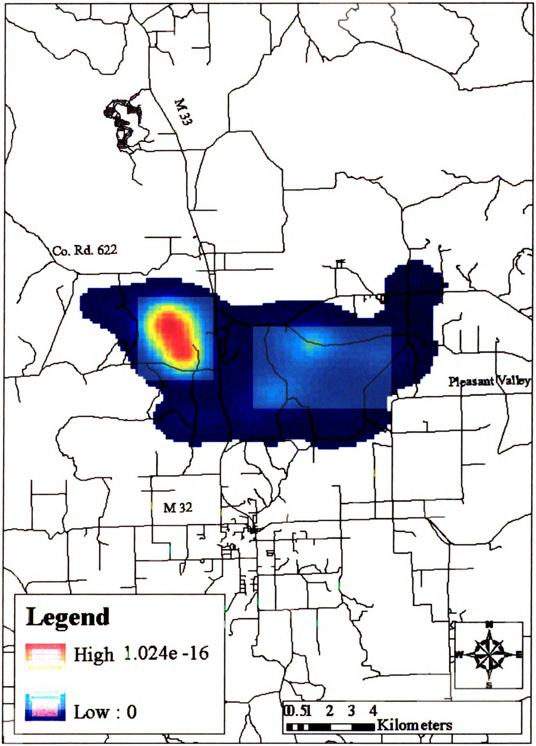


Figure 76. Joint kernel density surface estimating the joint space use of a radiocollared, TB-positive cow elk (elk #32), and the 15 other radiocollared elk utilizing this portion of the elk range in Michigan, 2003.

The overall probability of joint space use was estimated as 3.01 e-07% (SE = 2.62 e-12%). The conditional probability of jointly using the Elk Ridge Golf Course, the site of highest probability of joint space use, was 44.59% (SE = 5.17%).

Discussion

All the analyses, based on characterizing TB prevalence, assume that the sample of heads/carcasses submitted by hunters, upon which prevalence estimates are based represent, a random sample with regards to infected and non-infected deer from the region. If diseased deer are harvested at a higher probability, and/or submitted at a higher probability then resulting prevalence estimates will be biased high. Conversely, if there is a conscious effort to avoid submitting deer for testing, for example, to avoid regulative changes (e.g., ban on baiting) then prevalence estimates may be biased low. However, bias should only arise in the latter case if hunters were able to only avoid submitting infected deer. Given the fact that many of the TB positive deer do not exhibit readily distinguishable, clinical signs of infection, particularly to the untrained eye, this is highly unlikely. These potential sources of bias to my knowledge have not been investigated, and I assumed for this study they were negligible.

Apparent TB prevalence in deer throughout the elk range is generally low compared to prevalence further to the east in the core TB area (O'Brien et al. 2002). However, there exist pockets of higher prevalence where elk are at risk of being exposed and contracting the disease. My analyses were useful at identifying the locations where estimated TB prevalence was relatively high, and the probability of elk use was correspondingly high. The high-risk areas identified in 2003–2005 were also identified as high-risk for the entire time period of 1999–2005, indicating that these areas have been historically and continue to be high-risk locations. Interestingly, a comparison of the known harvest/collection locations of TB positive elk with the high-risk areas demonstrates that all 4 positive elk are located in or adjacent to the high-risk areas for 2003–2005. Although, this was only a small sample size, this close correspondence suggests that this analytical technique is useful for delineating high-risk areas for elk exposure to *M. bovis*. Also notable from these analyses is the reduction in the number of high-risk areas and corresponding reduction in probability of elk using high-risk areas when examining only the latter years. This would seem to indicate the management and disease control efforts are having the desired effects. Future research efforts should concentrate on targeting the 2003–2005 high-risk areas to determine the causative factors contributing to their high elk use, as well as, their consistently higher TB prevalence relative to other locations in the region.

The radiocollared, TB-positive cow had a slightly larger than average home range size at the 95% contour; however, at the 50% contour it was significantly greater than other cows in the study. This larger core home range area (i.e., the region containing 50% of her locations) could be attributed to her age, more human disturbance in the region (i.e., this area is open to and receives extensive off-road vehicle traffic), or other habitat conditions within her core area. Also I noted that she did not bear a calf in 2003, which may have allowed her to roam more widely than other calf-rearing cows during the spring and summer.

The standard error surface for the average kernel density surface for the eastern elk demonstrates the precision of the density surface and how it changes with location. It is also a critical component for estimating the variability of any probabilities generated with the density surface.

Joint space use analyses of elk from the eastern portion of the study area demonstrated that the overall probability of joint space use of elk #32 and an elk from the eastern portion of the study area was low. However, it should be noted that this probability is the probability of elk #32 jointly using space with an "average" elk. Thus, the probability of joint space use of elk #32 with all elk from the eastern portion of the study would be calculated as this estimated probability of joint space use for an average elk multiplied by the size of the elk population that use the same region as elk #32. Although population size at this scale is unknown, the estimated probability of joint space use is still a useful tool for estimating the location of and the probability of joint space use with all elk from the area, since it only differs by a constant. Thus, the probability of joint space use with an average elk is a useful metric for assessing the amount and location of possible elk interactions that could facilitate disease transmission between elk #32 and another elk.

If I assumed that joint space use did occur, it was evident that Elk Ridge Golf Course was the most likely site where the interaction occurred. This assumption seems reasonable given the social structure of elk, particularly, the maternal grouping of cows and harem gathering behaviors of the bulls. Also it is not surprising that the golf course has such a high probability of joint space use for 2003. In 2003 there was a large acorn crop, which concentrated elk during much of the winter in the areas dominated by oak ridges. Elk Ridge is one of those regions. Also from personal observation deer were also heavily concentrated throughout the oak ridges providing more opportunity for interspecies transmission of TB. Future work on disease risk should examine the effects of large mast crops on subsequent prevalence rates, as these range-wide events concentrate both elk and deer in space and time.

One of the limitations of these joint space use analyses is that time, is not incorporated into the kernel estimates. Thus, the probability of joint space use should ultimately be the probability of using the same location at the same time. Examination of joint space using 3-dimensions is an area of future research opportunity.

Management Implications

These findings are useful for both disease and wildlife managers attempting to control and eradicate TB from Michigan's deer herd, as well as, minimize the potential for interspecies transmission from deer to elk. The high-risk areas identified, particularly, in 2003–2005 were mostly on public land. This provides an opportunity to effectively manage these areas through habitat or population management of both deer and elk. Also the examination of the home range and joint space use of a TB positive elk relative to other elk in the region demonstrates the large area potentially exposed to input of infectious material by this elk, and the potential risk of infection to other elk through direct or indirect contact with this infected elk. Thus, these findings clearly portray the potential threat of TB becoming established in the elk herd.

Lastly, the analytical techniques described provide a template for identifying high-risk areas for other species and infectious diseases, and demonstrate a metric for examining potential transmission risk by analyzing joint space use. The power of these techniques is their ability to combine disease or prevalence information with knowledge of the biology of wildlife species. These tools can also be used to target areas for sampling to determine spread or emergence of infectious diseases or for control efforts, as well as assessing the risk to various geographic segments of a population based on how they utilize common resources/space.

Conclusion

Wildlife disease issues are becoming increasingly more prevalent in recent years with often substantial biological and economical costs. The threat of zoonotics and other human health issues in conjunction with decreasing habitat resulting in increased human/wildlife interactions assures that these issues will remain in the forefront both locally as well as nationally. I hope that the techniques and findings described herein will provide useful information and ideas that will help combat the spread and control of current and emerging wildlife diseases.

APPENDICES

APPENDIX A

SIGHTABILITY MODEL DATA SHEETS

MDNR FIXED-WING ELK SURVEY DATA FORM

Sheet ____ of ____

DATE: ________________ PLOT #: ________________ PILOT: ____________________ STRATA: HIGH MED LOW

OBSERVERS: ____

WEATHER: CLOUDS _____% PRECIPITATION _____ TEMPERATURE _____°C WIND ____knots WIND DIRECTION _____

TURBULANCE: None Light Chop Moderate Chop Heavy Chop

LIGHT

Type: Bright ☐ Flat ☐

Intensity: High ☐ Medium ☐ Low ☐

SNOW AGE & COVER

Fresh ☐ Moderate ☐ Old ☐

Complete ☐ Some Low Veg. Showing ☐ Some Bare Ground ☐

SEARCH TIME

Finish: ____________

Start: ____________

Group	Survey or Telemetry	**Bulls**	**Cows**	**Calves**	Unknown Sex/Age	Total Elk	Group contains marked elk (id #)	Behavior[1]	Canopy Cover Density[2]/Est[3]	GPS[4] Latitude	GPS[4] Longitude
1											
2											
3											
4											
5											
6											

1. Behavior-Bedded (B), Standing (S) or Running (R) (Classify as Bedded only if all animals were bedded etc.)
2. Canopy Cover – 0-33%, 34-66% or 67-100% (See Crown Closure Dot Diagram) – 10 meter radius around the first elk that is spotted
3. Est.—Estimate canopy cover to the nearest 5%
4. GPS location taken at the location of the initial sighting of first elk sighted.

Comments:

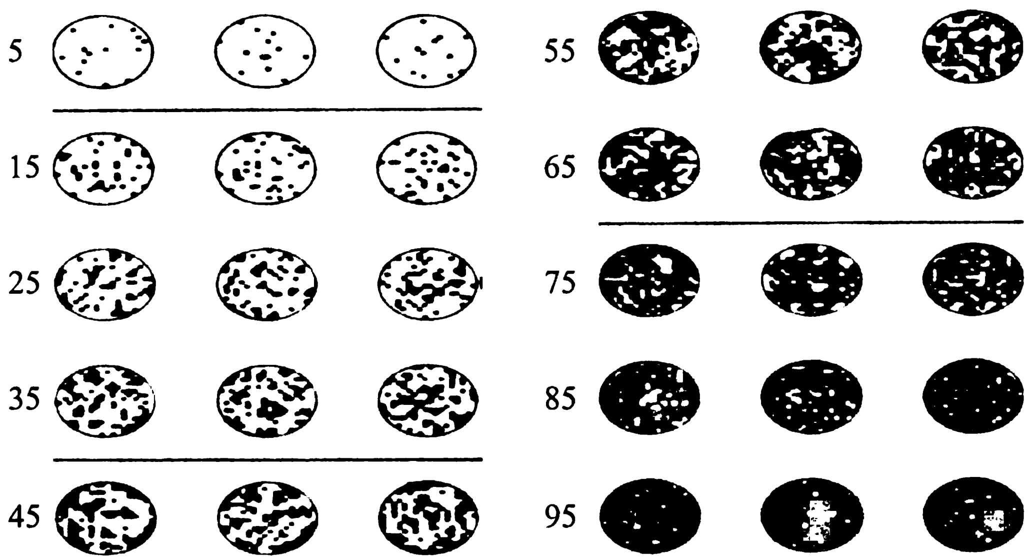
Snow Age:

1. *Fresh* – Generally less than or equal to 1 week since snowfall or greater than 3 inches. Old tracks are covered.
2. *Moderate* – Generally greater than 1 and less than or equal to 2 weeks since fresh snow conditions. Newly fallen snow of less than 3 inches often is inadequate to renew the snow surface so that it appears smooth and disturbance-free; therefore, shallow new snow may be classed as moderate-aged based on appearance.
3. *Old* – Generally greater than 2 weeks since fresh snow conditions. However, newly fallen snow subjected to melting conditions can rapidly appear like old snow, i.e., depressions around trees and shrubs, irregular surface, and enlarge animal tracks. Therefore, new snow may be classed as old after only 2 or 3 days.

Snow Cover:

1. *Complete* – Low vegetation covered. Generally 6 to 12 inches of snow are required.
2. *Some low vegetation showing* – Tops of some grasses, forbs, or very low shrubs protruding through snow. Snow cover has brownish cast.
3. *Distracting amounts of bare ground or herbaceous vegetation showing* – Distinct brown patches exist that reduce observer efficiency.

Crown Density Scale



APPENDIX B

SURVEY DATA SHEETS AND PROTOCOL

PROTOCOL FOR ELK SURVEY

Daniel Walsh, Henry Campa III, Scott Winterstein

January 2005

Flight time and weather conditions. Surveys for sightability model development will be conducted in late January through early February, since elk group size tends to be largest during this time of year (Moran 1973, Beyer 1987) increasing the probability of observing elk groups (Samuel et al. 1987). Also snow conditions generally provide a good background against which elk can be easily observed from the air. All flights will be conducted between 0900-1600 hrs to take advantage of good light conditions and minimize the effects of shadows.

Flights will ideally be made under clear skies with calm winds, temperatures at or above –12 C° after a fresh snowfall (Otten 1989). However, due to the time constraints and the amount of data needed for adequate estimation of the sightability function, flights will be conducted whenever conditions have been deemed safe by the pilots. For safety reasons, the pilots will make the final determination of whether a flight will occur. Thus, it is possible flights will be conducted under less than ideal conditions.

Surveys will be conducted in two 3 hr shifts with a 1hr break between shifts to allow for aircraft refueling and for recuperation of observers.

Personnel and equipment. The survey procedure will require 1-2 fixed-wing aircraft with wheel covers removed. The planes will contain a pilot and 2 experienced observers. Observers will be seated at the rear of the plane. Each plane will be equipped with a radio for inter-plane communications, a book containing all the quadrat and flight line locations, and Global Positioning System (GPS) equipment for locating flight lines and recording location of observed elk groups and radio-marked individuals.

Quadrat design. The study area is divided into quadrats/cells with length (N/S) 9.66 km (6 mi) and width (E/W) 3.22 km (2 mi). The study area will be defined by MSU and DNR personnel. Each quadrat was given a unique identification. Parallel, 0.40 km (0.25 mi) wide, flight lines running north to south were created within each quadrat, and the starting point and ending point of each line was recorded. Enough flight lines have been delineated to assure 100% coverage of the quadrat.

Survey plane procedures. The survey plane(s) will fly to the designated cell and begin to fly the designated flight lines within the cell starting in the southwest corner of the quadrat. I will provide location of the starting points and ending points of these flight lines for each quadrat in the sampling area to the observation plane pilot. Pilots will fly at an air speed of approximately 129 km/hr at a height of 152 m above the ground. The 2 experienced observers will visually scan out each side of the plane to a distance of 0.20 km for elk groups, which will be delineated by markers on the wing struts. Once a group is located, observers will communicate to the pilot they located a group. The pilot will leave the designated flight line and reduce altitude while circling the group, and record the GPS location. One observer will count all elk in the group. A group will be defined as all elk visible in an area. However, if distinct groups are clearly noticeable by the observer over the area (i.e. there is a clear separation between groups of animals), or if elk are distributed in areas of different conifer cover classes then these will be treated as separate groups. He/she will also record the number of bulls, the number of cows and the number of calves, as well as the percent conifer cover and behavior of the animals. The percent conifer cover will be classified into 3 classes: 1) 0–33% conifer cover, 2) 34–66% conifer cover and 3) 67–100% conifer cover at a 10 m radius around the first elk initially sighted. Behavior will be classified as bedded, standing or moving. A standardized data sheet will be provided to aid in data collection. Once the first observer has completed his/her data collection, the pilot will circle the plane in the opposite direction, and the second observer will repeat the process. Observers will not communicate their findings until both have completed their data collection (i.e., observers will remain independent). The pilot will also count the number of the elk in the group and provide his independent estimate of group size to the observers whom will record the pilot's count on the datasheet (*The pilot will only be involved in counting elk group size not in detecting elk groups while flying flight lines!!*). Once the group has been counted the pilot will return to the flight line and continue to survey the quadrat. Once the survey of the quadrat is complete, the pilot will fly to nearest quadrat and begin the process again. Observers will record any problems or unusual circumstances they encounter during the flight on the provided data sheet.

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MDNR FIXED-WING ELK SURVEY DATA FORM

Sheet ____ of _____

DATE: ________________ PLOT #: ________________ PILOT: ____________________ STRATA: HIGH MED LOW

OBSERVERS: ____

WEATHER: CLOUDS _____% PRECIPITATION _____ TEMPERATURE _____°C WIND _____knots WIND DIRECTION _____

TURBULANCE: None Light Chop Moderate Chop Heavy Chop

LIGHT

Type ☐ Bright ☐ Flat

Intensity ☐ High ☐ Medium ☐ Low

SNOW AGE & COVER

Fresh ☐ Moderate ☐ Old ☐

Complete ☐ Some Low Veg. Showing ☐ Some Bare Ground ☐

SEARCH TIME

Start: ____________

Finish: ____________

Group	**Bulls**	**Cows**	**Calves**	Unknown Sex/Age	Total Elk	Pilot Count	Behavior[1]	Canopy Cover Density[2]/Est[3]	GPS[4] Latitude	GPS[4] Longitude
1										
2										
3										
4										
5										
6										

1. Behavior-Bedded (B), Standing (S) or Bedded/Standing (B/S) (Classify based on first animal seen, or B/S if multiple animals were seen simultaneously)
2. Canopy Cover – 0-33% = Class 1, or 34-100% = Class 2 (See Crown Closure Dot Diagram) – 10 meter radius around the first elk that is spotted
3. Est.—Estimate canopy cover to the nearest 5%
4. GPS location taken at the location of the initial sighting of first elk sighted.

Comments:

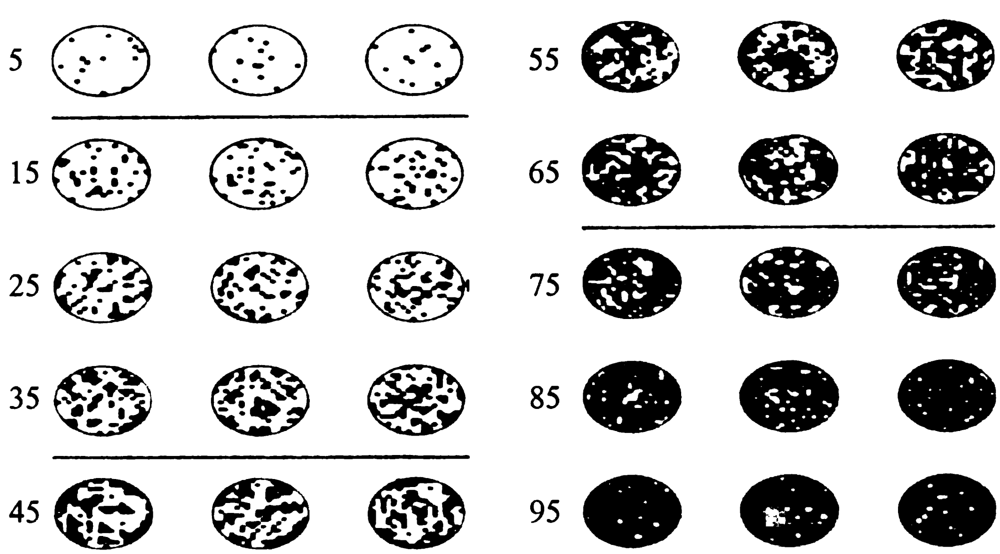
Snow Age:

1. *Fresh* – Generally less than or equal to 1 week since snowfall or greater than 3 inches. Old tracks are covered.
2. *Moderate* – Generally greater than 1 and less than or equal to 2 weeks since fresh snow conditions. Newly fallen snow of less than 3 inches often is inadequate to renew the snow surface so that it appears smooth and disturbance-free; therefore, shallow new snow may be classed as moderate-aged based on appearance.
3. *Old* – Generally greater than 2 weeks since fresh snow conditions. However, newly fallen snow subjected to melting conditions can rapidly appear like old snow, i.e., depressions around trees and shrubs, irregular surface, and enlarge animal tracks. Therefore, new snow may be classed as old after only 2 or 3 days.

Snow Cover:

4. *Complete* – Low vegetation covered. Generally 6 to 12 inches of snow are required.
5. *Some low vegetation showing* – Tops of some grasses, forbs, or very low shrubs protruding through snow. Snow cover has brownish cast.
6. *Distracting amounts of bare ground or herbaceous vegetation showing* – Distinct brown patches exist that reduce observer efficiency.

CROWN DENSITY SCALE



APPENDIX C

EXPECTATION ANALYSIS

Let $\hat{m}_{i(k)}$ = the estimate of group size for the i[th] group in the k[th] land unit, and let $\hat{\Theta}_{i(k)}$ = the probability of detecting that group which is estimated from some sightability model whose parameters were derived independently of the estimation of $\hat{m}_{i(k)}$ and includes $\hat{m}_{i(k)}$ as a predictor variable. Then by the conditional expectation formula (Ross 2003) the following is true:

$$\begin{aligned} \mathrm{E}[\hat{m}_{i(k)}\hat{\Theta}_{i(k)}] &= \mathrm{E}[\mathrm{E}[\hat{m}_{i(k)}\hat{\Theta}_{i(k)} \mid \hat{m}_{i(k)}]] \\ &= \mathrm{E}[\hat{m}_{i(k)}\mathrm{E}[\hat{\Theta}_{i(k)} \mid \hat{m}_{i(k)}]] \end{aligned}.$$

Since the parameters for the sightability model used to estimate $\hat{\Theta}_{i(k)}$ are derived independently from the estimation of $\hat{m}_{i(k)}$ thus

$$\mathrm{E}[\hat{\Theta}_{i(k)} \mid \hat{m}_{i(k)}] = \Theta,$$

and therefore,

$$\mathrm{E}[\hat{m}_{i(k)}\hat{\Theta}_{i(k)}] = \mathrm{E}[\mathrm{E}[\hat{m}_{i(k)}\hat{\Theta}_{i(k)} \mid \hat{m}_{i(k)}]] = \Theta_{i(k)}\mathrm{E}[\hat{m}_{i(k)}].$$

Although the estimator of $\hat{m}_{i(k)}$ in equation (4) is asymptotically unbiased (DasGupta and Rubin 2005), with only 3 independent counts on group size the estimator shows some bias. The amount of bias was assessed by generating 3 random counts from a binomial distribution with N ranging from 1–50 and p ranging from 0.70–0.99. These values were chosen based on field observations of elk group size and values of p from the literature (Cogan and Diefenbach 1998). N was then estimated using equation (4). For each combination of N and p, 1,000 estimates were generated and the average bias was calculated. Figure 1 shows the simulation results. Based on these results the bias of the estimator of $\hat{m}_{i(k)}$ even with only 3 counts is relatively small with the mean percent bias

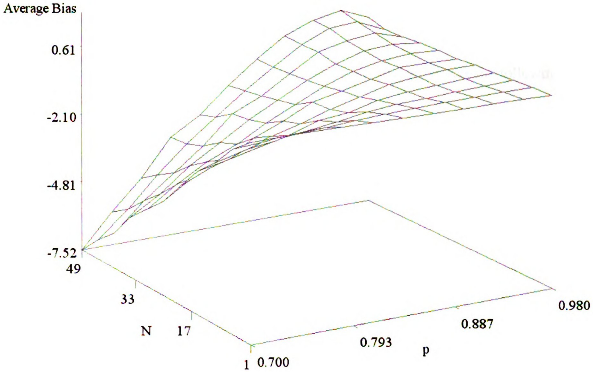


Figure C. 1. The average bias of the method-of-moments estimator of group size (DasGupta and Rubin 2005) given 3 independent counts with 1,000 repetitions at each combination of N and p.

of -0.047 (SD = 0.049). The largest bias occurs at the lowest p and highest N values and reaches a maximum of -7.52 at $p = 0.70$ and $N = 50$.

Based on these simulation results, it is reasonable to approximate the following:

$$\mathrm{E}[\hat{m}_{i(k)}] \approx m_{i(k)},$$

and therefore the following statement can be inferred:

$$\Theta_{i(k)}\mathrm{E}[\hat{m}_{i(k)}] \approx \Theta_{i(k)} m_{i(k)}.$$

APPENDIX D

COVARIANCE ANALYSIS

The last term in the lemma can be estimated as follows:

$$\mathrm{var}_{B|R,D}(T) = \mathrm{var}\left(\sum_{k}^{l}\sum_{i}^{n_k}\frac{\hat{m}_{i(k)}\hat{\Theta}_{i(k)}}{p_k}\right) =$$

$$\sum_{k}^{l}\sum_{i}^{n_k}\mathrm{var}\left(\frac{\hat{m}_{i(k)}\hat{\Theta}_{i(k)}}{p_k}\right) + \sum_{i(k)\neq i'(k')}\mathrm{cov}\left(\frac{\hat{m}_{i(k)}\hat{\Theta}_{i(k)}}{p_k}, \frac{\hat{m}_{i(k)}\hat{\Theta}_{i(k)}}{p_k}\right).$$

The variance can be approximated using the delta method as previously described. The

$$\mathrm{cov}\left(\hat{m}_{i(k)}\hat{\Theta}_{i(k)}, \hat{m}_{i'(k')}\hat{\Theta}_{i'(k')}\right) = \mathrm{E}[\mathrm{cov}\left(\hat{m}_{i(k)}\hat{\Theta}_{i(k)}, \hat{m}_{i'(k')}\hat{\Theta}_{i'(k')} \mid \hat{m}_{i(k)}, \hat{m}_{i'(k')}\right)]$$
$$+ \mathrm{cov}\left(\mathrm{E}[\hat{m}_{i(k)}\hat{\Theta}_{i(k)} \mid \hat{m}_{i(k)}], \mathrm{E}[\hat{m}_{i'(k')}\hat{\Theta}_{i'(k')} \mid \hat{m}_{i'(k')}]\right)$$

However, based on the independence of $\hat{m}_{i(k)}$ and $\hat{m}_{i'(k')}$, and the independence of the parameters of the sightability model used to estimate $\hat{\Theta}_{i(k)}$ and $\hat{m}_{i(k)}$ the following is true:

$$\begin{aligned}
&\mathrm{cov}\left(\mathrm{E}[\hat{m}_{i(k)}\hat{\Theta}_{i(k)} \mid \hat{m}_{i(k)}], \mathrm{E}[\hat{m}_{i'(k')}\hat{\Theta}_{i'(k')} \mid \hat{m}_{i'(k')}]\right) \\
&= \mathrm{cov}\left(\hat{m}_{i(k)}\mathrm{E}[\hat{\Theta}_{i(k)} \mid \hat{m}_{i(k)}], \hat{m}_{i'(k')}\mathrm{E}[\hat{\Theta}_{i'(k')} \mid \hat{m}_{i'(k')}]\right) \\
&= \mathrm{cov}\left(\hat{m}_{i(k)}\Theta_{i(k)}, \hat{m}_{i'(k')}\Theta_{i'(k')}]\right) \\
&= \Theta_{i(k)}\Theta_{i'(k')}\,\mathrm{cov}\left(\hat{m}_{i(k)}, \hat{m}_{i'(k')}\right) \\
&= 0.
\end{aligned}$$

Thus,

$$\begin{aligned}
&\mathrm{cov}\left(\hat{m}_{i(k)}\hat{\Theta}_{i(k)}, \hat{m}_{i'(k')}\hat{\Theta}_{i'(k')}\right) \\
&= \mathrm{E}[\mathrm{cov}\left(\hat{m}_{i(k)}\hat{\Theta}_{i(k)}, \hat{m}_{i'(k')}\hat{\Theta}_{i'(k')} \mid \hat{m}_{i(k)}, \hat{m}_{i'(k')}\right)] \\
&= \mathrm{E}[\hat{m}_{i(k)}\hat{m}_{i'(k')}\mathrm{cov}\left(\hat{\Theta}_{i(k)}, \hat{\Theta}_{i'(k')} \mid \hat{m}_{i(k)}, \hat{m}_{i'(k')}\right)],
\end{aligned}$$

and $\mathrm{E}_D[\mathrm{E}_{R|D}[\mathrm{var}_{B|R,D}(T)]]$ is estimated as follows:

$$\boldsymbol{\delta}'\Sigma\boldsymbol{\delta} + \sum_{i(k)\neq i'(k')}\mathrm{E}_{m_{i(k)}m_{i'(k')}}\left[\frac{1}{p_k p_{k'}}\hat{m}_{i(k)}\hat{m}_{i'(k')}\,\mathrm{cov}\left(\hat{\Theta}_{i(k)}, \hat{\Theta}_{i'(k')}\right)\right].$$

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