

**Ecology of elk parturition across winter feeding opportunities in the brucellosis
endemic area of Wyoming**

by

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TABLE OF CONTENTS

ACKNOWLEDGMENTS	iv
ABSTRACT	vii
CHAPTER 1. GENERAL INTRODUCTION	1
Introduction	1
Study Area	3
Thesis Organization	5
Literature Cited	6
CHAPTER 2. EFFECTIVENESS OF VAGINAL IMPLANT TRANSMITTERS FOR LOCATING ELK PARTURITION SITES	9
Abstract	9
Introduction	9
Study Area	11
Methods	12
Results	15
Discussion	19
Management Implications	21
Acknowledgments	22
Literature Cited	23
CHAPTER 3. ELK PARTURITION SITE SELECTION AND EFFECTS OF WINTER FEEDING AT LOCAL AND LANDSCAPE SCALES IN WESTERN WYOMING	25
Abstract	25
Introduction	25
Materials and Methods	28
Results	37
Discussion	44
Acknowledgments	51
Literature Cited	51
CHAPTER 4. RELATIONSHIPS OF WINTER FEEDING AND NATIVE HABITAT IMPROVEMENTS TO SPATIAL PATTERNS OF PARTURITION SITES WITH IMPLICATIONS FOR BRUCELLOSIS TRANSMISSION RISK	59
Abstract	59
Introduction	60
Methods	63
Results	70
Discussion	76
Management Implications	81

Acknowledgments	82
Literature Cited	82
CHAPTER 5. GENERAL CONCLUSIONS	89
Conclusions	89
Literature Cited	93
APPENDIX. CLASSIFICATION OF CALVING RANGES BASED ON GLOBAL MACROHABITAT MODEL	95

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ABSTRACT

This study was initiated to examine parturition related behavior both from an ecological perspective and to investigate implications for brucellosis transmission risk among elk and between elk and cattle. These aspects were investigated for elk fed during the winter, elk using improved winter feedlines, and free-ranging elk. Brucellosis is a disease causing abortion in elk (*Cervus elaphus nelsoni*), bison (*Bos bison*), and cattle (*Bos* spp.). The most common transmission route is through oral contact with aborted fetuses or parturition tissues/fluids and transmission risk is dependent on contact rates. Vaginal implant transmitters were deployed on winter free-ranging elk and elk using feedgrounds to define parturition and abortion sites. Habitat variables were collected and modeled for parturition sites at the microhabitat and macrohabitat spatial scale on the basis of biotic, abiotic, and anthropogenic factors. We collected data on a total of 169 parturition sites, representing the largest ever study of elk calving behavior. Elk were selective with respect to parturition habitat at both macrohabitat and microhabitat scales but we did not find evidence for differences in selection behavior among feeding types. Parturition site selection appears to be driven by cover rather than by forage at both scales. Use of feedgrounds and length of feeding season were associated with decreased distance from winter range and increased clustering of parturition locations. This study will facilitate evaluation and development of best management practices regarding feedground management, elk, habitat manipulation, and risk of brucellosis transmission.

CHAPTER 1: GENERAL INTRODUCTION

Calving ecology of elk (*Cervus elaphus nelsoni*) in western Wyoming is important from both an ecological and a management perspective. While this aspect of ungulate ecology was one of the earliest studied (Johnson 1951, Troyer 1960, Dalke et al. 1965, Stevens 1966, Harper et al. 1967), the advent of new technology and analysis methods allows us new insights into this basic, but important aspect of elk life history. Elk are an economically important species in Wyoming, accounting for \$7.7 million (Smith 2001) in license fee revenue for the state, as well as creating revenue for associated industries. Elk experience higher predation risk and nutritional stress during calving. The effects of drought, loss of winter range, and a shifting predator community may impact population and habitat use dynamics both relative to calving and in general. Increasing the body of knowledge on calving ecology and the factors driving parturition habitat selection is important from a theoretical and a management perspective.

An aspect of elk management practice unique in scale, at least, to western Wyoming is the supplemental winter feeding of elk. Elk were relatively infrequent in the first records from the region during the 1800s and winter-summer migrations routes were thought to stretch 100-200 miles (Anderson 1958). The last reported incidence of this migration was 1913. New agricultural land use quickly altered migration patterns and also reduced available winter range. A 1941 report by the U.S. Fish and Wildlife Service indicated that there was available winter range for about half of the Jackson Hole population (Anderson 1958). Elk were first fed during the winter on the National Elk Refuge in 1911 and then feedgrounds established by the state of Wyoming. Winter feeding was initiated to reduce deaths associated with malnutrition and haystack depredations on private land that increased

as a result of loss of winter range associated with agricultural development. Feedgrounds have come with their own set of political and ecological complications. As far back as 1935, the potential effects of disease and domestication associated with feedgrounds were recognized (Sheldon et al. 1935).

Feedgrounds have been implicated in maintaining brucellosis within the elk of western Wyoming (Thorne et al. 1991, Smith 2001, Kreeger 2002). Brucellosis, which causes reproductive failure in ungulates, is endemic in the elk and bison of western Wyoming and can be transferred to cattle through oral contact with infective tissues and fluids associated with abortion or parturition events. A nationwide brucellosis eradication program was initiated in the 1950's and has been nearly successful in eradicating the disease in cattle (Ragan 2002). Elk and bison represent one of the few remaining threats to brucellosis eradication in the United States. Elk have been implicated in cattle outbreaks in western states since 2002 (Smith 2001, Kreeger 2002, Wyoming Brucellosis Coordination Team 2005). There are two transmission periods; 1) from February through April, when the majority of abortions occur, and 2) from May through June, during the parturition season. This study addresses parturition-specific behavior and potential implications for brucellosis transmission risk.

We used vaginal implant transmitter (VIT) technology to mark parturition locations. This technology is relatively new and has been used primarily to locate neonatal ungulates for survival studies (Bowman and Jacobsen 1998, Vore and Schmidt 2001, Cartensen et al. 2003, Seward et al. 2005, Bishop et al. 2007). Prior to this study only one study (Reardon 2005) has addressed the specific parturition location. VITs allow for exact location of the parturition site, which represents a significant methodological improvement over search-

based locations used in previous studies. Because early studies used locations based on sightability of cows and calves, these locations were most likely neonatal rather than parturition locations and may have been biased toward locations in more open habitats.

We conducted this study to investigate calving behavior of elk, the effects of winter feeding on calving behavior, and how winter feeding and parturition behavior may interact to affect brucellosis transmission risk. Our objectives in this study were 1) to evaluate the efficacy of VIT technology in marking parturition locations; 2) to determine parturition habitat selection at two scales and examine how winter feeding opportunity affected parturition behavior; and 3) to determine the effects of winter feeding opportunity on the spatial arrangement of parturition locations. This final objective speaks to indirect effects of feeding that may contribute to brucellosis transmission risk.

STUDY AREA

The Greater Yellowstone Ecosystem (GYE) covers areas of Wyoming, Montana, and Idaho totaling approximately 16,000 km². It is a unique system in that it is one of the largest ecologically intact systems in North America. This ecosystem includes a full complement of large-bodied herbivores such as white tailed (*Odocoileus virginianus*) and mule deer (*O. hemionus*), elk, moose (*Alces alces*), and bighorn sheep, and carnivores such as wolves (*Canis lupus*), mountain lions (*Felis concolor*), grizzly bears (*Ursus arctos*), black bears (*Ursus americanus*), wolverines (*Gulo gulo*), and coyotes (*C. latrans*). Our study area was encompassed by the western Wyoming portion of the GYE from the northern extreme in southern Yellowstone National Park south to the Green River valley.

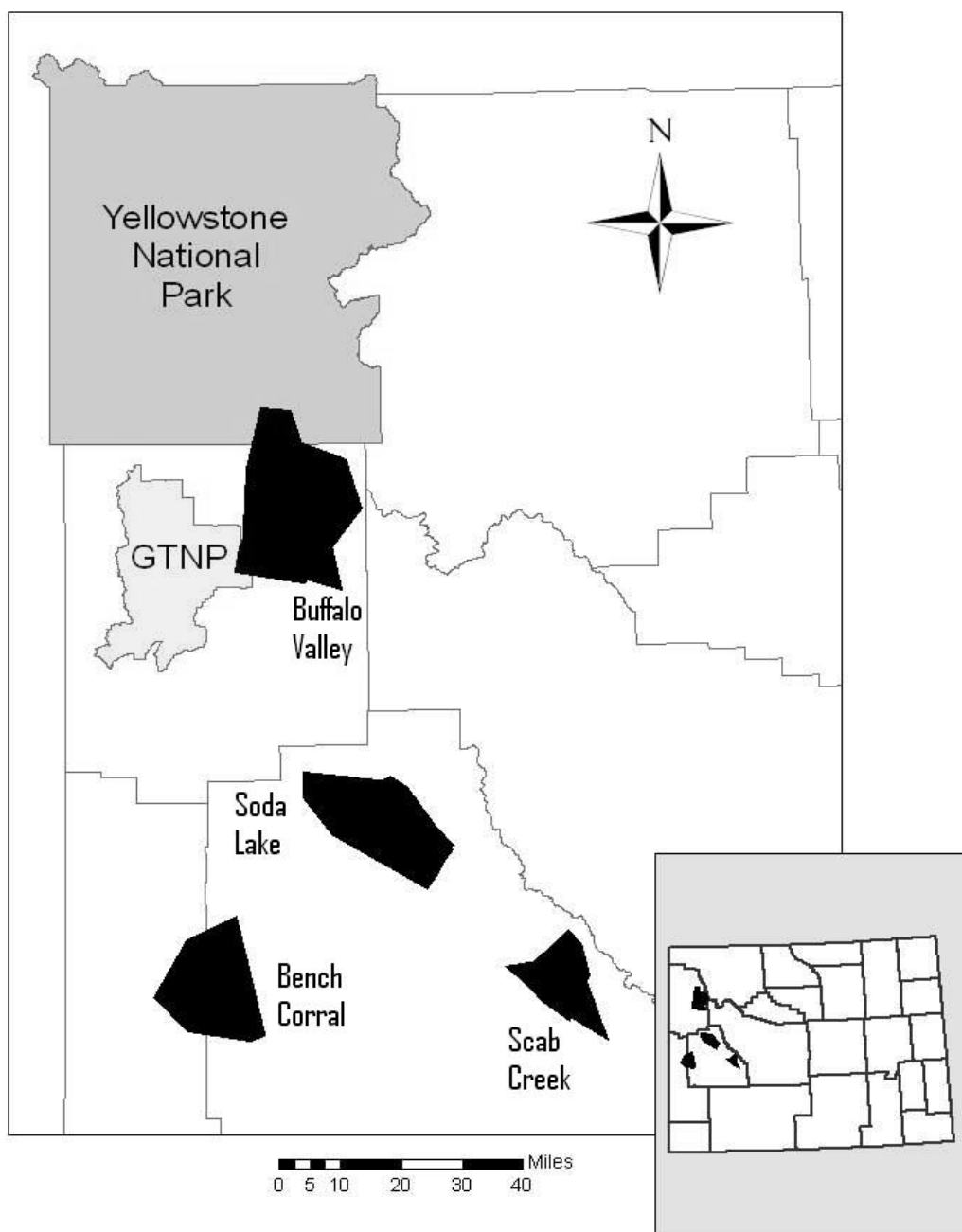


Figure 1. Map of the combined study areas with reference to Yellowstone and Grand Teton National Parks (YNP and GTNP). All study areas fell within the western Wyoming portion of the Greater Yellowstone Ecosystem.

This project was implemented as a collaborative study of elk on four sites in the brucellosis endemic area of western Wyoming (Figure 1). We defined winter free-ranging animals as those not using elk feedgrounds during the year of study, improved feedground animals as using those feedgrounds with shortened feeding season, habitat improvements, and larger feeding area, and unimproved feedground or feedground dependent animals as using feedgrounds having none of the improved feedground features. Our study sites were Scab Creek (42 ° 81' N, 109 ° 58' W) an unimproved feedground; Soda Lake (42°95' N, 109°81' W) and Bench Corral (42 ° 72' N, 110 ° 13' W), two improved feedgrounds; and Buffalo Valley (43°84' N, 110°45' W), an area used by a large population of winter free-ranging animals. Some Buffalo Valley animals were fed in the first year of this study and were classified as improved feedground animals during that year. Elevation ranged from 1500-4195 m in Teton and Sublette Counties. Vegetation communities existed on an elevational gradient from sagebrush (*Artemesia tridentata*) and riparian communities, transitioning to lodgepole pine (*Pinus contorta*), Douglas fir (*Pseudotsuga menziesii*), and aspen (*Populus tremuloides*), and finally high meadows interspersed with spruce (*Picea engelmannii*)/subalpine fir (*Abies lasiocarpa*) communities. The southern portion of the study area received slightly less precipitation than the north. Private land uses are primarily recreational and agricultural, but private lands exist in a dominant public land matrix made up of Bridger Teton National Forest, Grand Teton and Yellowstone National Parks, and areas administered by the Bureau of Land Management and the state of Wyoming.

THESIS ORGANIZATION

This thesis consists of five chapters, three of which are papers to be submitted to scientific journals. Chapter 1 is a general introduction to my research objectives and my

study area, while Chapter 5 is a general conclusion to my research and summarizes concurrent and future research plans. Chapter 2 examines the functionality of vaginal implant transmitters in locating elk parturition sites. Chapter 3 focuses on parturition habitat selection both across all study populations and with respect to winter feeding opportunities. Chapter 4 examines the spatial distribution of parturition sites with respect to winter feeding opportunities. Chapter 4 also addresses potential changes in parturition-related brucellosis transmission risk associated with winter feeding opportunities.

Chapters 2, 3, and 4 are intended for publication in peer-reviewed scientific journals and co-authors are listed at the beginning of each chapter. W. Sue Fairbanks, Jared Rogerson, and Eric Maichak contributed to project development, field research, and acted as editors on chapters. Laura Meadows and Brandon Scurlock assisted with field research and acted as contributing authors on several chapters.

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CHAPTER 2. EFFECTIVENESS OF VAGINAL IMPLANT TRANSMITTERS FOR LOCATING ELK PARTURITION SITES

A paper submitted to the *Journal of Wildlife Management*

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Meadows

ABSTRACT

Vaginal implant transmitters [VITs] may provide accurate abortion or parturition locations for elk and facilitate mapping of ranges, timing of these events, and determination of parturition-specific habitat. We assessed the success of vaginal implant transmitters for locating elk calving sites in western Wyoming in 2006 and 2007 as part of a study on abortion and habitat selection by parturient elk. Transmitters were deployed in 198 animals over the study period. We identified 60.3% of expelled VIT locations as definite/probable event markers and an additional 21.8% as possible event markers. The failure rate for VITs in this study was 10.6%, while an additional 7.3% were found in improbable/impossible parturition sites. Although the functional integrity of this relatively new technology is not perfect, it was very effective in facilitating location of calving and abortion sites and can ultimately facilitate definition of parturition habitat selection and parturition ranges of specific subpopulations.

INTRODUCTION

Much of the seminal literature on the parturition ecology of Rocky Mountain elk (*Cervus elaphus nelsoni*) was produced between the years of 1950 and 1970 (e.g. Johnson 1951, Troyer 1960, Dalke et al. 1965, Stevens 1966, Harper et al. 1967). In these studies, parturition locations were assumed to be those areas where high concentrations of neonatal

elk (within the first week of life but not necessarily at the parturition site) were first observed during aerial or ground surveys conducted during the spring. This may have introduced bias toward areas and habitat types where visibility of females with calves was greatest or areas used by females with slightly older, ambulatory calves and may have led to a misrepresentation of habitats associated with parturition events. In addition, the difficulty of locating neonatal calves often led to conclusions based on sample sizes of fewer than 15 animals, with the notable exception of 154 calf locations reported by Johnson (1951).

Vaginal implant transmitters [VITs] were developed in the early 1980s to assist in the detection of parturition (or calving) events and facilitate capture of neonates. Early versions of VITs were surgically sutured into the animal of interest causing local trauma and risk of infection and were not effective in locating calving events due to poor retention (Garrot and Bartman 1984). More recently, a carrier based on an intravaginal hormone delivery system used in cattle, which included flexible wings, was developed (Bowman and Jacobson 1998). This eliminated the use of sutures and related trauma and, after trials of various wing lengths (Johnson et al. 2006), greatly reduced premature expulsion.

Previous reports on the use of VITs in capturing neonatal ungulates suggest that VIT performance and effectiveness in locating neonatal deer (*Odocoileus* sp.) and elk has steadily increased with time (Garrott and Bartmann 1984, Bishop et al. 2007). VIT success as defined by neonate capture in deer has varied from 50% in Mississippi (Bowman and Jacobsen 1998) to 88% in Minnesota and Colorado (Cartensen et al. 2003, Bishop et al. 2007). Johnstone-Yellin et al. (2006) identified 63% of VITs as shed at bed sites but did not confirm any as parturition locations, as fawns were not located on the site. In elk, effectiveness of VITs in capturing neonates ranged from 5% in a translocated elk herd in

Kentucky (Seward et al. 2005) to 38% for a native elk herd in Montana (Vore and Schmidt 2001), although sample sizes were much lower than those reported for deer.

Although the use of VITs has increased in recent years, little work has been done to quantify specific parturition locations and associated habitat characteristics associated with calving or fawning events. Recently, 116 VITs were deployed in elk in Oregon for the purpose of capturing neonates and evaluating birth sites (Rearden 2005). Forty-nine VIT locations were used to identify calving habitat, but it is unclear whether these locations represented a subset of the parturition sites that were identified. While a primary use of VITs has been as an aid for capturing and radio marking neonates (Johnstone-Yellin et al. 2006) to quantify survival, precise locations of parturition events in space and time can enhance our existing knowledge of ungulate parturition ecology, especially in association with diseases (e.g. brucellosis, Barbknecht 2008) or changes in landscapes or management strategies. This paper reports on the effectiveness of using VITs to locate abortion and parturition sites of elk in northwest Wyoming.

STUDY AREA

The study was conducted in the western Wyoming area of the Greater Yellowstone Ecosystem on a free-ranging elk herd segment wintering in Buffalo Valley, Teton County, Wyoming (43°84'N, 110°45'W) and 3 Wyoming Game and Fish Department (WGFD) elk feedgrounds (Bench Corral: 42 ° 72'N, 110 ° 13'W, Soda Lake: 42°95'N, 109°81'W, Scab Creek: 42 ° 81'N, 109 ° 58'W) in Sublette County, Wyoming. Elevation ranged from 1500-4195 m in Teton and Sublette Counties. Vegetation on all study sites was typified by sagebrush (*Artemisia tridentata*) communities on dry sites, at low elevations and on southern slopes, transitioning to lodgepole pine (*Pinus contorta*), Douglas fir (*Pseudotsuga menziesii*),

and aspen (*Populus tremuloides*) interspersed with high meadows at higher elevations, and spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) communities above 2750 m in elevation (Whitlock 1993). Riparian areas were dominated by willow (*Salix* spp.) and sagebrush communities and cottonwood (*Populus* sp.) communities (Wigglesworth and Wachob 2004). There was some degree of climatic variation within the study area. The southern portion of the study area was drier, averaging 28 cm of precipitation annually, compared to 40 cm of precipitation in the northern range of the study area. Primary private land uses were agriculture and recreation with higher proportions of private lands and agricultural uses in the south than the north. The dominant public lands matrix used by elk included Bridger Teton National Forest, Grand Teton and Yellowstone National Parks, and areas administered by the Bureau of Land Management and the State of Wyoming.

METHODS

As part of a larger study of *Brucella abortus*-related abortions and parturition site selection in elk, we captured 118 animals and deployed 96 VITs [M3960, Advanced Telemetry Systems (ATS), Isanti, MN, USA] in pregnant adult female elk between 7 February and 14 March 2006. One-hundred thirty-four adult female elk were captured and 102 VITs were deployed from 5 January through 7 March 2007. We captured elk wintering on feedgrounds using a corral trap baited with hay or by chemically immobilizing elk using 1.5-ml darts loaded with carfentanil (0.01 mg/kg) and xylazine (0.1 mg/kg). Free-ranging elk were captured using net guns fired from a helicopter (Leading Edge Aviation, Clarkston, WA, USA), and were not chemically immobilized. We used a Bantam XLS portable ultrasound (E.I. Medical Imaging, Loveland, Colorado, USA) with a 5-MHz sector transducer in a gun-style rectal probe to transrectally image females to determine pregnancy.

Some free-ranging elk were tested for pregnancy by rectal palpation (Greer and Hawkins 1967) in 2007 due to weather-related breakdown of the ultrasound. All pregnant females were outfitted with VITs and numbered ear tags. We implanted VITs using a fabricated PVC applicator as described in Johnson et al. (2006). We cleaned and soaked applicators in 10% bleach solution between uses. Feedground elk were fitted with PVC cloth visibility collars with a unique color-letter-number combination (n=149) or Global Positioning System (GPS) collars (n=4) (Telonics, Mesa, AZ, USA), while free-ranging elk were equipped with either GPS collars (n=16) (Telonics, Mesa, AZ, USA) or Very High Frequency (VHF) collars (n=37) (ATS, Isanti, MN, USA). Collars with VHF beacons were part of separate studies, but were used in this study to facilitate location of individuals. Captures were performed in accordance with the approved Iowa State University Animal Care and Use Protocol # 8-05-5962, and approved University of Wyoming Animal Care and Use Protocols Rogerson 2005-2006 and Linn 2005-2006 and 2006-2007.

The basic design of the VITs we used has been described in detail elsewhere (Vore and Schmidt 2001, Johnson et al. 2006, Johnstone-Yellin 2006). We used 43-g VITs with an 80-mm flexible wing. Each implanted VIT contained a temperature-sensitive switch that switched from a 40 beats per minute (BPM) active pulse rate to an 80 BPM “mortality” pulse when its temperature dropped below 28° C (i.e. when expelled from the elk’s body). Antennas were pre-cut to 17 cm in length and the tips were encased in resin to prevent injury to the female. We used a precise event timing (PET) function that transmitted a binary coded time signal, pinpointing the time of expulsion in 30-min increments up to 5.3 days after expulsion. To prevent expelled VITs from returning to active signal when in direct sunlight, a locking mechanism program was installed in 22 VITs deployed in feedground elk (Soda

Lake and Bench Corral) in 2007. In all but three cases, a “bug” in the locking mechanism program (J. Roth, Advanced Telemetry Systems, pers. comm.) likely caused disappearance of the signal some time around parturition after several successful pre-parturition ground and/or aerial locations. These animals were censured from the analysis, leaving a sample size of 179 VITs.

VITs were monitored for expulsion on a daily basis from date of capture until females were no longer within ground telemetry range prior to calving season. Once females left their respective wintering areas, ground telemetry was supported by weekly telemetry flights with fixed wing aircraft (Sky Aviation, Worland, WY, USA). When we detected an expelled VIT, it was located and retrieved using ground telemetry. We recorded locations of expelled VITs in Universal Transverse Mercators (UTM) with a hand held Garmin E-trex Vista (Olathe, KS, USA) or Trimble GeoXT GPS unit (Sunnyvale, CA, USA).

We assessed VITs on the basis of function prior to expulsion, device- and human-related failure rates, and success in marking parturition or abortion events. When a VIT was expelled, we evaluated and categorized the location to determine if it was a birth or abortion site. Our classification system had four levels:

Definite/Probable – Sites were classified as definite/probable when we observed an abortion (expelled prior to the calving season with evidence of fetus or viable *B. abortus* colonies were cultured from the recovered VIT) or when we observed the birth, the calf and/or cow at the location, the placenta, or a site with the following characteristics: cleared spot on ground, strong odor, moistened soil, evidence of grazing/browsing, fresh fecal pellets.

Possible – We observed evidence of recent elk use, but one of the more definitive calving

site characteristics: cleared spot, odor, or moist soil, was not present.

Improbable/Impossible – There was no evidence of recent elk activity, unlikely habitat (rock outcroppings, surface water present, etc.), scavenger tooth marks on transmitter (wings were most often chewed), or in a place inaccessible to elk (in a tree, in a rodent/predator burrow, etc.).

Failure – We categorized as failed VITs that were retained in the female (failure of pregnancy diagnosis or fetus absorption), suffered mechanical failure, or did not maintain signal long enough for retrieval because of battery or mechanical failure after expulsion.

We recorded calving date as the Julian date prior to the first location of the expelled VIT from the ground, or the median Julian date between flight locations when the VIT was determined to have been expelled and the date when it was still in the female. Retrieval time from estimated birth date to date of retrieval was measured for all VITs dropped during the parturition season. Retrieval times were grouped by classification level and the retrieval time of definite/probable, possible, and improbable/impossible events were compared using a Student's t-test assuming equal variance [SAS 9.1 (SAS Institute Inc. Cary, NC, USA)].

RESULTS

VITs fitted in feedground elk were readily detected from distances up to 1.5 km. These animals were relatively sedentary during winter as compared to the free-ranging elk, and there was no difficulty monitoring animals without an additional VHF device during the feeding season, from capture through March. VHF collars were the primary means used to monitor free-ranging elk, as these animals were seldom close enough to roads or trails to allow direct checks of implanted VIT signals, although we were able to detect expelled VITs.

Expelled VITs could be heard at distances of up to 11 km depending upon topography and the position of the receiver relative to the VIT. The combined area used by study elk for calving on the four areas, defined by the summed area of minimum convex polygons, was 217,984 ha in 2006 and 179,167 ha in 2007.

The number of pregnant animals located from the ground in a given week declined from nearly 100% in the first week of parturition to less than 10% in the final weeks of monitoring. Thus, animals giving birth at the end of the calving season were most often detected from weekly aerial surveys. If an animal was located from the ground within a week it was generally located 3-7 times during that week. Our recovery time ranged from several hours to several weeks. Thirty-six percent of VITs were recovered within three days of detection, 56% within the first week, and 17% were recovered more than two weeks after detection. Longer recovery periods were necessary for VITs dropped in wilderness or otherwise inaccessible areas that required coordinated backcountry travel.

When VITs were recovered from potential abortion or parturition sites, 60.1% (119/198, SE = 3.5%) of total deployments were classified as definite/probable event locations. An additional 21.7% (43/198, SE = 2.9%) of VIT deployments were classified as possible event locations. Improbable/impossible classifications accounted for 7.6% (15/198, SE = 1.9%) of the total deployments and VIT failures accounted for 10.6% (21/198, SE = 2.2%) of VIT deployments. Events classified as definite/probable were located an average of three days earlier than events classified as possible ($t=2.22$, $p=0.02$) or improbable/impossible ($t=1.91$, $p=0.04$). Thus it appears that classification of definite/probable vs. possible events was dependent somewhat on how quickly the VIT could be retrieved, and both of these categories might arguably be identified as successful event

markers. Longer retrieval times likely provided more opportunity for scavengers to access expelled VITs as most of the improbable/impossible parturition events appear to have been moved from the parturition location by scavengers or other animals (Table 1). While it was possible to identify the majority of sites as definite/probable, only one event resulted in direct observation of abortion and five events resulted in direct observation of the calf.

Table 1. Reasons for improbable/impossible parturition site classification and vaginal implant transmitter [VIT] failures for elk in northwestern Wyoming for 2006 and 2007.

Improbable/impossible parturition reason	<i>n</i>
Moved by scavenger	6
Moved by other animal (i.e. in tree)	3
No evidence of elk activity	2
Inhospitable location (i.e. open water)	2
Total	13
Failure reason	<i>n</i>
Premature expulsion	2
VIT retention	7
Unknown mechanical or biological	10
Total	19

Failures were caused by biological or mechanical errors that precluded VITs being expelled at, or recovered from, abortion or parturition sites (Table 1). Biological reasons for failure included premature expulsion events which did not involve physical evidence of abortion or positive *B. abortus* cultures; animals that had not calved at the time of the final flight at the end of June or early July; or animals which left the flight radius prior to location from the air. Potential reasons for mechanical errors included battery life failure or other mechanical failure that caused the cessation of transmission. Because we were not able to

recover VITs that did not produce a telemetry signal, we could only know the cause of failure for premature expulsion or VIT retention where we could incorporate other sources of data into our assessment. Of animals that did not calve during the study, all instances were attributable to misdiagnosis of pregnancy in the field (revealed by subsequent blood tests). Although we could not differentiate between mechanical failure and animals moving beyond the search radius, this scenario is more likely for animals without radio collars which could only be located by using the much weaker VIT signal. The battery life of VITs appears to be variable. Some signals died when we attempted to retrieve them within the parturition season, while a retained VIT in 2006 continued functioning for the entire season the following year. An additional 2.8% of deployed VITs were not recovered at potential event locations not because of error, but because of the death of the implanted female. None of these mortalities were linked to problems with the transmitter or capture.

While they did not result in failures, some previously encountered difficulties with VIT function (Bowman and Jacobson 1998, Seward et al. 2005, Johnstone-Yellin et al. 2006, Bishop et al. 2007) were also present in this study. VITs expelled in sunny locations, when ambient temperatures were greater than 27° C, switched from a “mortality” signal to an active signal, creating confusion during checks that were not completed in the early morning or cool weather. This also reset the PET mechanism, often making it impossible to determine when the VIT was expelled based on the binary signal code. While this ambient temperature is below the switch threshold, direct sun and a clear plastic casing apparently contributed to a warmer internal temperature in the VIT. Switching to active mode after expulsion was less of a problem for radiocollared females because the female and VIT could be located independently.

Identifying parturition status of elk without collars was more difficult, especially when we commonly experienced signal flux. On several occasions, researchers attempted to collect a VIT that was thought to be expelled based on signal strength rather than signal mode only to find the animal still carrying the VIT or to not find the animal at all, necessitating aerial relocation of the VIT, often in a different area. This reduced research personnel retrieval efficiency and increased disturbance to the animals. It also caused confusion as to whether VITs had malfunctioned.

DISCUSSION

VITs were an effective tool for locating parturition and abortion sites in this study. We classified 82.1% of VITs as marking definite/probable (60.3%) or possible (21.8%) parturition events. In particular, VITs allowed accurate location of abortion and parturition sites independent of accessibility or cover type, eliminating any potential visibility bias in determining parturition habitat and ranges of elk from specific wintering areas. Detection and recovery timing potentially impacted our ability to recognize parturition areas. VITs with longer retrieval times were more likely to be classified as possible rather than definite/probable, or to be moved or adulterated and placed in the improbable/impossible category. If VITs are used for locating neonates for capture rather than just parturition locations, we suggest a more rigorous monitoring schedule, locating VITs daily during parturition season and having almost immediate access to parturition locations given the rarity of direct observations of calves during this study.

We suggest several improvements in the VIT technology that would likely increase effectiveness in marking parturition locations. We experienced a change in signal pulse rate with sun exposure and warm temperatures, a phenomenon experienced by the majority of

researchers using VITs (e.g. Seward et al. 2005, Johnstone-Yellin et al. 2006, Bishop et al. 2007) and often termed signal flux. This flux can delay retrieval and resets PET functions, rendering timing of events suspect in almost all cases. In the future, we recommend the development of a white or mylar transmitter, rather than transparent, to increase reflectance of solar radiation and potentially minimize signal flux. We also experienced uneven battery life, in some cases causing the VIT to cease transmitting before we were able to retrieve it. A 12-hr duty cycle has been used to reduce battery failures (Bishop et al. 2007). Using a 12-hr duty cycle eliminates the opportunity to use a PET function, but we would recommend incorporation of this measure in VITs to maximize battery life. We did not observe a decay in battery life related to storage (room temperature), so we suggest it is safe to store VITs at least one year prior to deployment. Premature expulsion was not a significant problem in this study, as it has been in earlier studies (Garrott and Bartmann 1984, Seward et al. 2005, Johnstone-Yellin et al. 2006). We found only two instances with no evidence of abortion at the location of transmitters dropped outside the calving season.

The retention of VITs by non-pregnant cows is a concern from an animal welfare standpoint. During this study we elected to monitor animals with retained transmitters until expulsion or battery failure based on the findings of Seward et al. (2005) that indicated females with retained VITs were able to conceive successfully in the following year. However, we found after the conclusion of the study period, if animals can be recaptured, VITs may be removed easily with no tissue damage as the internal temperature of the females greatly increases flexibility of the retaining wings. Several transmitters maintained active signals through the winter of the following year, but these were not radio-collared animals; the signals failed prior to the calving season for most retained VITs, and we were

unable to establish whether they had calved successfully. We did not observe a calving event for the one cow whose VIT maintained signal through the following calving season.

As a cost saving measure, feedground animals were not equipped with VHF collars to assist in location of the animals. This led to increased cost of aerial locations during the parturition season because of increased time spent locating active VITs or relocating questionable parturition events. We were often uncertain whether an animal had calved or not, as the female and VIT could not be located independently. This increased retrieval time for several VITs and the increased time to recovery could decrease the probability of detecting a parturition event. We recommend that VITs deployed on animals in non-captive populations always be deployed with a separate VHF transmitter to allow simultaneous location of the VIT and female, and increase the distance at which the female can be located. If possible, we also recommend more frequent overflights for VITs as this may increase efficiency of detection and retrieval and perhaps reduce the number of VITs encountered by scavengers and possibly moved prior to retrieval.

MANAGEMENT IMPLICATIONS

We suggest that VITs can be used to accurately mark abortion and birth sites of elk when care is taken to verify that there is evidence of parturition activity at the location. In our study, VITs recovered within approximately 7 days of parturition were more likely to successfully mark parturition locations. Retrieval efficiency will likely vary among study sites depending on species and abundance of scavengers, terrain, and method (ground or aerial) and schedule of monitoring. We suggest that failure rates of approximately 10% should be built into future management and research projects to ensure adequate sample sizes are met. Managers can use VITs in elk to revisit habitat requirements of parturient females

and to delineate calving areas used by specific groups of females. For species like elk, where the birth site is not used for an extended period and females may move great distances between wintering areas and parturition sites, this technology may be more successful in studies of parturition sites than for locating and capturing neonates.

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CHAPTER 3. ELK PARTURITION SITE SELECTION AT LOCAL AND LANDSCAPE SCALES IN WESTERN WYOMING

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ABSTRACT

We examined parturition-specific habitat selection of elk in western Wyoming. Although elk are one of the most studied wildlife species, there has been relatively little quantitative multivariate analysis of parturition site selection in elk. With vaginal implant transmitters we were able to accurately and precisely mark parturition locations and evaluate habitat variables at macrohabitat and microhabitat spatial scales. There was evidence for selection at both scales. We found the strongest support for cover/physical feature models at the macrohabitat scale and cover hypotheses at the microhabitat scale. Forage-based models were the least supported models at both scales. Our findings of weak/no selection for sagebrush habitat and selection against conifers contrasted with previous studies. This result may be evidence of bias introduced by variable sightability of cows/calves in early studies. We found no evidence of differences in parturition habitat selection with respect to winter feeding opportunity. The results of this study increase existing knowledge of elk calving ecology.

INTRODUCTION

Habitat selection by ungulates is often defined as driven by acquisition of food resources, avoidance of predation, minimization of thermal stress, and maintenance of social contacts (Collins and Urness 1983, Haskins et al. 1997, Mysterud and Ostbye 1999).

Situational habitat selection, such as during the mating season or related to reproduction, may alter the equation for the individual. Habitat selection relative to birth sites can be considered a special behavioral requirement, a subset of general habitat selection. Habitat related to birth and neonatal locations was one of the earliest aspects of ungulate natural history to be examined in a systematic and scientific manner (Johnson 1951, Troyer 1960).

The birth and early neonatal periods are important because neonatal ungulates are more susceptible to predation and other forms of mortality than older juveniles and healthy adults (Adams et al. 1995, Bertram and Vivon 2002). Reproduction and lactation also represent a high nutritional and behavioral demand on the female (Millar 1977, Wade and Schneider 1992). Therefore, an ecological tradeoff between maximizing energy intake and minimizing predation risk may exist (Bleich et al. 1997, Cote and Hamel 2007). Given that the cow-calf unit experience very high predation risk as well as high nutritional demands, areas with a strong component of both may be selected by cows. Alternatively, the risk of predation may strongly outweigh nutritional demands (Mysterud and Ims 1998) and use of areas with high quality forage may be delayed during this period.

Animals often respond to habitats in a spatially hierarchical manner (Johnson 1980, Poizat and Pont 1996, Johnson et al. 2002, McLoughlin et al. 2004). Selection of physical and biological habitat components may differ between, for example, the home range scale and the feeding site scales, and inferences about these mechanisms may also vary with scale (Weins 1989, Anderson et al. 2005). Thus, it is important to measure habitat selection at different scales in order to incorporate the range of selection thought to be biologically relevant. Our use of scale here is most closely aligned with the definition of spatial extent within a landscape ecology context. Temporal scales are also often implicit in definitions of

the spatial scale of availability of resources. Understanding the perception of heterogeneous landscapes at multiple scales allows for better comprehension of ungulate behavior.

Elk (*Cervus elaphus nelsoni*) parturition ecology has been investigated in the past with mixed results. Much of the literature on this topic was produced between the years of 1950 and 1970 (e.g. Johnson 1951, Troyer 1960, Dalke et al. 1965, Stevens 1966, Harper et al. 1967). More recent studies have looked at seasonal selection that roughly corresponds to the calving season (e.g. Irwin and Peek 1983, Witmer and deCalesta 1983, McCorquodale et al. 1986, Unsworth et al. 1998, Stewart et al. 2002), but relatively few have addressed the specific calving locations. There has also been relatively little quantitative analysis of parturition site selection in elk. Much of the published work in this area is descriptive in nature, based on observations of few individuals (a notable exception is Johnson (1951) with 154 calf locations), and was published before telemetry technology allowed for exact location of parturition sites and before multivariate methods allowed for more complex analyses. Early studies identified variables related to physical characteristics of the environment (Johnson 1951, Phillips 1974, Waldrip and Shaw 1979), vegetative characteristics related to nutritional quality, available cover, and landcover of locations (Johnson 1951, Troyer 1960, Dalke et al. 1965, Stevens 1966, Harper et al. 1967), and spatial characteristics such as amount of edge and distance to roads (Johnson 1951) as important in calving site selection. The general observations made in these studies were useful in focusing our study of parturition site selection in elk.

The goal of this research was to revisit elk calving site selection using modern field and statistical methodologies. Our first objective was to identify habitat selection related to parturition at the calving range (or macro-scale) and at the micro-scale, specifically

investigating the relationship between forage and cover needs for parturient elk. The study area was in western Wyoming, which has a history of winter feeding of elk beginning in 1911 on the National Elk Refuge and continuing with establishment of 23 state-run feedgrounds. One predominantly winter-free ranging subherd and 3 winter feedground subherds were studied. Thus, a second objective was to determine if there were any changes in selection behavior related to winter feeding opportunity. To accurately mark parturition locations, we used vaginal implant transmitter (VIT) technology. VITs have been used with growing frequency in the last ten years to locate and capture neonatal ungulates (Bowman and Jacobsen 1998, Cartensen et al. 2003, Bishop et al. 2007). VITs provide unbiased locations of parturition sites, eliminating the bias toward habitats with greater sightability that may have been a problem in previous studies. More than 82% of VITs deployed in this study were dropped at definite to possible parturition locations (Barbknecht et al. Chapter 2), validating this technology for use in habitat selection applications.

MATERIALS AND METHODS

The study was conducted in the western Wyoming area of the Greater Yellowstone Ecosystem on a predominantly free-ranging elk herd segment wintering in Buffalo Valley (BV), Teton County, Wyoming (43°84'N, 110°45'W) and 3 Wyoming Game and Fish Department (WGFD) elk feedgrounds (Bench Corral: 42 ° 72'N, 110 ° 13'W, Soda Lake: 42°95'N, 109°81'W, Scab Creek: 42 ° 81'N, 109 ° 58'W) in Sublette County, Wyoming. Bench Corral and Soda Lake have shorter feeding seasons, larger feeding areas, and are at lower elevations (closer to native winter range). Local habitat improvements have also been implemented on Soda Lake and Bench Corral feedgrounds in an effort to shorten the feeding season and reduce dependence on the feedground during the feeding season. Within the last

12 years, 2000 ha of prescribed burning and 16 ha of mechanical treatments have occurred on land surrounding Soda Lake feedground. Herbicide treatments were used on 216 ha surrounding Bench Coral feedground, as well as 233 ha of mechanical treatments during this period. These treatments have reduced feedground dependency to some extent (WGFD, unpublished data). Habitat improvements, mostly burn treatments, have also been implemented on more than 3000 ha of the range of the winter free-ranging herd segment in Buffalo Valley.

During the first year of the study, emergency feeding of elk was conducted in the free-ranging population. Telemetry locations allowed us to assign animals to fed and non-fed groups, although some animals could not be classified and were censored from analysis. We used a mean telemetry error to define a radius around the feedline and did one ground check for animals on the feedline. Animals located on the ground on the feedlines or having three or more telemetry locations within the error radius were defined as using the feedlines, animals with one or fewer locations within the error radius were defined as free ranging and we were not able to classify the remainder of the animals (these were censored from feedground-specific analyses). Eleven animals were classified as using the emergency feedline, 11 as winter free-ranging in that year, and 5 were not classified. We classified Soda Lake and Bench Corral as improved feedgrounds (reduced feeding seasons, habitat improvements, and larger feeding areas), and Scab Creek as an unimproved feedground (Scab Creek, Barbknecht et al. Chapter 4). Elk using unimproved feedgrounds we termed feedground-dependent. Elk identified as using the emergency feedline in Buffalo Valley were grouped in the improved feedground category.

We captured 118 animals and deployed 96 vaginal implant transmitters (VITs,

M3960, Advanced Telemetry Systems [ATS], Isanti, MN, USA) in pregnant adult female elk between 7 February and 14 March 2006. One-hundred thirty-four adult female elk were captured and 102 VITs were deployed from 5 January through 7 March 2007. We chemically immobilized elk wintering on feedgrounds using darts loaded with carfentanil (0.01 mg/kg) and xylazine (0.1 mg/kg). Free-ranging elk were captured using net guns fired from a helicopter (Leading Edge Aviation, Cody, WY, USA) and were not chemically immobilized. We collected blood from all captured animals and tested them for exposure to *Brucella abortus*. We used a Bantam XLS portable ultrasound (E.I. Medical Imaging, Loveland, Colorado, USA) with a 5-MHz cepter transducer in a rectal probe to transrectally image females to determine pregnancy. Some free-ranging elk were tested for pregnancy by rectal palpation (Greer and Hawkins 1967) in 2007 due to weather related ultrasound malfunctions. All pregnant females were outfitted with VITs and numbered metal ear tags (Table 1). We implanted VITs using a fabricated PVC applicator as described in Johnson et al. (2006). Applicators were pre-sterilized and we used sterile lubricating jelly during the insertion process. Feedground elk were fitted with PVC cloth visibility collars with a unique color-letter-number combination (n=149) or Global Positioning System (GPS) collars (n=4) (Telonics, Mesa, AZ, USA), while free-ranging elk were equipped with either GPS collars (n=16) (Telonics, Mesa, AZ, USA) or Very High Frequency (VHF) collars (n=37) (ATS, Isanti, MN, USA). Collars with VHF beacons were part of separate studies, but were used in this study to facilitate location of individuals. Captures were performed in accordance with the approved Iowa State University Animal Care and Use Protocol # 8-05-5962 and approved University of Wyoming Animal Care and Use Protocols Rogerson 2005-2006 and Linn 2005-2006 and 2006-2007.

Table 1. Distribution of vaginal implant transmitters in elk among study sites in western Wyoming in 2006 and 2007.

Study Area	Year	
	2006	2007
Buffalo Valley	26	27
Bench Corral	29	9
Scab Creek	12	33
Soda Lake	29	33

The basic design of the VITs we used has been described in detail elsewhere (Vore and Schmidt 2001, Johnson et al. 2006, Johnstone-Yellin 2006). We deployed 43-g VITs with an 80-mm flexible wing containing a temperature-sensitive switch that went from a 40 beats per minute (BPM) active pulse rate to an 80 BPM “mortality” pulse when its temperature dropped below 28° C (i.e., when expelled from the elk’s body). The antennas were pre-cut to 17 cm in length and the tips were encased in resin to avoid injury to the female.

VITs were monitored for expulsion on a daily basis from date of capture until females were no longer within ground telemetry range prior to calving season. Once females left their respective wintering areas, ground telemetry was supported by weekly telemetry flights with fixed wing aircraft (Sky Aviation, Worland, WY, USA). When we detected an expelled VIT, it was located and retrieved using ground telemetry. We recorded locations of expelled VITs in Universal Transverse Mercators (UTM) with a hand held Trimble GeoXT GPS unit (Sunnyvale, CA, USA). When a VIT was expelled, we evaluated the location to determine the potential that it was a birth site (Barbknecht et al. Chapter 2). We identified sites used in analysis based on observation of birth, calf, or placenta, or the presence of at least some common parturition site characteristics. A cleared area, moist soil, characteristic odor,

evidence of browsing activity, tracks, and fresh fecal pellets were characteristic of calving locations.

Habitat Data Collection

Parturition site selection was evaluated at the microhabitat, or local scale, and at the macrohabitat, or parturition range scale. Habitat selection processes have been described as naturally ordered and hierarchical in nature (Johnson 1980), thus it is important to investigate selection at multiple scales. We selected the parturition range and local scales corresponding to Johnson's (1980) third order and fourth order selection, respectively. We examined selection at the parturition range scale not only because of its ecological significance, but because this scale represents the level at which many management decisions are made and Geographic Information System (GIS) coverages are available and transferable to habitat maps. The microhabitat, or local scale, represents a biologically important scale at which short term behavioral decisions are made and a scale at which behavioral plasticity may be more evident (Bellows et al. 2001, Asbury and Adolph 2007).

Parturition sites were compared to available habitat points at a macrohabitat scale using GIS technology. Minimum convex polygons were created around all parturition locations for each study site in each year, defining available habitats and parturition ranges at the landscape scale. We used GIS coverages to extract physical and vegetative characteristics for parturition sites and for randomly generated points within the parturition ranges. We created 200-m buffers surrounding parturition and random locations and assessed the percent cover of six vegetation classes within the buffered area, as treating use as a point may increase bias (Rettie and McLoughlin 1999). There was not a single comprehensive vegetation map that covered the entire study area. Instead, features from

Bridger-Teton National Forest (2007), Utah State Region Four (1998), and Grand Teton National Park (2006) vegetation coverages were compared and classified as deciduous (aspen and aspen mix), coniferous, riparian, herbaceous, shrubland (predominantly sage), or non-vegetated. Because all vegetation classes summed to 100%, we did not enter more than three vegetation classes into any candidate model to avoid violating the unit sum constraint (Aebischer et al. 1993). Elevation values for locations were extracted from a 90-m resolution digital elevation model (DEM). We used the spatial analyst toolbox in ArcGIS 9.1 (ESRI, Redland, CA, USA) to create 90-m resolution slope and aspect rasters from the DEM. Aspect was divided into four classes representing 90° increments centered on the four cardinal directions. Distance from roads was calculated using the nearest feature function in ArcView 3.3 (ESRI, Redland, CA, USA). We did not differentiate between high and low traffic roads in the distance measures.

Microhabitat variables were measured at parturition sites and at 2 reference sites located 200 m from the parturition location in random directions. Elk move an average of 1759 m/day for the 4 days prior to parturition (Vore and Schmidt 2001) and a 200-m radius represents a portion of this distance that elk may move in a few hours before parturition and thus may be making local habitat decisions. At each site, we used a spherical densiometer to measure canopy cover at the location and averaged it over the four cardinal directions. We used a Robel pole (Robel et al. 1970) with 10-cm increments to measure concealment cover. The pole was placed 10 m from the location of the VIT or reference site in the four cardinal directions and the number of clear (<50% covered) sections was observed from a height of 1 m. Percentages of obscured segments were averaged across the cardinal directions. Woody vegetation density was assessed by counting above ground individual plants rooted within a

1-m wide shrub belt along a 50-m transect. The transect was placed in a random direction and centered on the VIT or reference location. We divided woody vegetation densities into browse, sage, and total shrub categories. We visually estimated percent cover of grasses and forbs in 5, 50 x 100-cm quadrats placed at random points along the 50-m transect, and averaged them for each VIT or reference location. Distance from the location to the nearest tree, defined as woody vegetation greater than 2 m in height, was measured, and dominant species of woody overstory and understory vegetation within a 25-m radius were recorded. We measured distance to nearest edge on the ground when it was within 200 m of the location and used a GIS vegetation coverage when the nearest edge was greater than 200 m. We defined an edge as a change in vegetation cover type where the second cover type was > 50 m in diameter to exclude small islands in otherwise homogeneous cover types. If they were present, aspen, serviceberry (*Amelanchier arborea*), willow (*Salix* spp.), chokecherry (*Prunus virginiana*) and bitterbrush (*Purshia tridentata*) were sampled from within 25 m of the location for nutritional analyses. A sample consisted of 10-20 sub-samples clipped from individual plants of the same species. Samples were analyzed at the University of Nebraska Plant and Soil Analytical Laboratory (Lincoln, NE, USA) for nutritional content. Total digestible nutrients (TDN) and protein levels were included in analyses of microhabitat selection.

Statistical Methods

All statistical analyses were performed using SAS 9.1 (SAS Institute Inc. Cary, NC, USA). We visually examined variables for approximate normal distributions. Although there were some variables that obviously deviated from normality, most often associated with large numbers of zeros in the dataset, our efforts to transform these variables resulted in little

improvement. Thus, we did not transform variables to simplify model interpretation. This represents a statistical shortcoming in our data, but ecological data rarely conform to all assumptions. We created bivariate correlation matrices to test for collinearity and used only the member of any pair of highly correlated variables ($|r| > 0.50$) that we believed most biologically relevant.

Using a use-availability design, we created resource selection functions (RSF) for the macrohabitat scale. Resource selection functions are models that approximate, and are proportional to, the probability of use of an area (Manly et al. 2002). We created models of selection at the local and landscape scales and tested them using an information theoretic approach. We computed models and estimated beta values for variables using logistic regression (proc LOGISTIC) with parturition/random point being the response variable. We created a suite of *a priori* macrohabitat models based on biologically plausible hypotheses that forage availability, cover availability, physical characteristics of the landscape, proximity to roads, or some combination of these were driving selection of parturition sites (Table 2). The effect of year was also considered. Models were ranked based on Akaike's Information Criterion (AIC) with the lowest AIC value representing the most parsimonious (best) model. Models within two AIC units of each other were considered competitive. We created four models relating to macro-scale selection of forage and cover as well as three models relating to the physical characteristics of the landscape. The models with the lowest AIC values from both classifications were combined to test if a combination of vegetative and physical characteristics created a better model. We then added the spatial variable distance to roads to the best model of the vegetative, physical, and combined model to see if this improved the model. Finally, although a year effect was expected, we tested model

performance without the year effect to determine to what extent this factor improved the model. Upon selection of a best model, we tested for influential points, and assessed goodness of fit using the Hosmer-Lemeshow goodness of fit test. The amount of variance explained by the best model was assessed using the R^2 value. We also used odds-ratios and a cut-off point of 0.50 to examine model fit.

At the microhabitat scale, we created resource use risk functions. These functions are similar in nature to resource selection functions, but cannot be directly compared because of the paired nature of the analysis. A best model of selection was identified using conditional logistic regression (proc PHREG), pairing each parturition site with its reference sites to identify habitat available to the individual and because habitat variance is likely to be greater across the study area than at a local scale. We generated *a priori* models based on hypotheses that forage availability and quality, cover availability, proximity to edge, or a combination of these factors was driving selection at this scale (Table 5). We created three models representing overall forage availability, graze, and browse availability and two models representing overall cover, ground cover, and overhead (canopy) cover. The models with the lowest AIC values for cover and forage were combined to test the hypothesis that both processes are important in parturition site selection. Edge was added to the best model in this process to test whether this spatial variable had an appreciable effect. Finally, the year effect was removed to determine the importance of inter-year variability in the process. The microhabitat risk function was scaled to one and then parturition sites were classified to give a rough estimate of model fit for the study area. We used odds-ratios and a cut-off point of 0.50 to examine model fit.

In order to test the hypothesis that habitat selection differed among winter feeding opportunities, we conducted univariate logistic regressions on macrohabitat-scale variables for each location. We conducted univariate conditional logistic regressions on microhabitat-scale variables, pairing each parturition site with its reference sites to better evaluate local-scale selection. The β values for each variable at each location were entered into a new dataset. For each variable, we conducted a one-way ANOVA to test for differences in selection coefficients among feeding opportunities. *Post hoc* Tukey tests were used to determine differences among treatment groups.

Due to limited sample size of parturition locations in a given study area, univariate analyses were necessary to avoid overfitting the data. Multiple univariate tests (ANOVAs in this case) have the potential to detect spurious results, but we considered this the lesser of statistical evils. Given that the study area was the experimental unit in this analysis, we were somewhat limited in our statistical power in detecting differences in selection among feeding opportunities.

RESULTS

Of the 198 VIT deployments, 153 successfully marked parturition sites with complete microhabitat datasets and were included in analysis of calving site selection at the microhabitat scale; 169 (16 were not used in microanalysis because we could not confirm that they were at the exact parturition site) were included in analysis at the macrohabitat scale (Barbknecht et al. Chapter 2). The median calving date was 31 May in both years with calving dates ranging from 17 May to 11 June in 2006 and 22 May to 20 July in 2007. Mean parturition range size in each year was largest for free-ranging animals, intermediate for

improved feedground animals, and smallest for feedground-dependent animals (Barbknecht et al. Chapter 4).

Elk were selective at both spatial scales when choosing parturition sites. At the macrohabitat scale, the most supported hypothesis was a combination of cover and physical characteristics (Table 2). The resource selection function at this scale included percent cover of coniferous, deciduous, and shrub habitats, as well as aspect (as a categorical variable referenced to west) and elevation. A model including distance to road was competitive, but we opted for parsimony in selecting the best model. Distance to road was also dropped from the final model because the β value was vanishingly small (Table 3), so we felt secure in dismissing its biological significance. Adding distance to road did not appreciably change other variables. Elk across the study sites selected for southerly aspects and against northerly aspects, for less conifer cover, greater deciduous cover, and greater shrub cover (Table 4) although some of these variables were not significant in the final model (Table 3). Selection for southern aspect appears to have the largest influence, with deciduous, and shrub cover also likely biologically significant. The Hosmer-Lemshow goodness of fit test indicated good overall model fit ($p=0.11$). Our best model did not, however, account for much of the variation in the dataset ($R^2=0.14$). When we classified scaled probability of use for parturition sites, 45.7% of parturition locations had resource selection function scores above 0.50.

Table 2. AIC and Δ AIC values for candidate models of macrohabitat parturition site selection by elk in western Wyoming.

Hypothesis	Model	AIC	Δ AIC
Cover, Physical, and Road	Elevation, Aspect, Conifer, Deciduous, Shrubland, Distance to Road	520.18	0
Cover and Physical No Year	Elevation, Aspect, Conifer, Deciduous, Shrubland	521.10	0.92
Cover, Physical, and Year	Elevation, Aspect, Conifer, Deciduous, Shrubland, Year	522.84	2.67
Physical 2	Elevation, Aspect, Year	542.63	22.45
Physical 1	Slope, Elevation, Aspect, Year	544.62	24.44
Physical 3	Aspect, Year	547.95	27.77
Cover	Conifer, Deciduous, Shrubland, Year	551.48	31.30
Shrub Cover	Shrubland, Year	564.27	44.09
Cover and Forage	Deciduous, Year	567.40	47.22
Forage	Deciduous, Herbland, Riparian, Year	568.20	48.02

Table 3. Parameter estimates and standard errors for best model of macrohabitat parturition site selection by elk in western Wyoming.

Parameter	β Estimate	SE	$P > \chi^2$
Intercept	-0.0137	1.1829	0.991
Aspect N	-0.2670	0.2540	0.293
Aspect S	0.4756	0.1710	0.005
Elevation	-0.0003	0.0004	0.483
Conifer	-0.0057	0.0039	0.138
Deciduous	0.0127	0.0063	0.044
Shrubland	0.0097	0.0048	0.043
Road Dist	0.000017	0.000017	0.310

Table 4. Mean habitat variable values for elk parturition and random sites at the macrohabitat scale. Proportion is the proportion of parturition or reference sites that had this aspect.

Variable (Units)	Parturition (SD)	Random (SD)
Elevation (m) ^a	2608 (303)	2686 (280)
Aspect N (proportion) ^a	0.09 (0.29)	0.17 (0.38)
Aspect S (proportion) ^a	0.44 (0.50)	0.29 (0.46)
Aspect E (proportion)	0.17 (0.37)	0.22 (0.41)
Slope (%)	15.04 (12.48)	15.35 (12.93)
Conifer (%) ^a	42.18 (37.09)	61.26 (39.85)
Deciduous (%) ^a	12.19 (24.67)	4.58 (14.30)
Herbland (%)	11.57 (22.98)	14.54 (27.27)
Non-Vegetated (%)	0.63 (2.46)	1.92 (10.09)
Riparian (%)	6.74 (9.02)	4.50 (13.46)
Shrub (%) ^a	26.55 (32.57)	13.19 (27.56)
Distance to Road (m) ^a	4322 (6898)	4826 (6150)

^a Variables appeared in best macrohabitat model of parturition site selection

At the microhabitat scale, sage density, total shrub density, canopy cover, concealment cover, and distance to the nearest tree (Table 5) were included in the best model of elk parturition site selection. Models including distance to edge and year were competitive with the best model, but we again sided with parsimony in selecting a best model. Conditional logistic regression represents a risk assessment which yields coefficients similar, but not entirely comparable, to traditional logistic coefficients. The effect of distance to edge when all other variables were held constant may be of questionable biological relevance. Adding edge to the model did not appreciably change the selection values of other variables. Elk exhibited strong selection on the basis of canopy and concealment cover (Table 6), selecting for areas with higher levels of both (Table 7). They also selected for areas with higher overall shrub density, but lower sage density, and closer to trees (Table 7) although these variables had $p > 0.10$. Conditional logistic regression has a model structure

that does not facilitate calculation of traditional model fit statistics. When we classified parturition observations, 79.7% of parturition sites were at or above a scaled risk of use for parturition of 0.50.

Table 5. AIC and Δ AIC values for candidate models of microhabitat parturition site selection by elk in western Wyoming.

Hypothesis	Model	AIC	Δ AIC
Total Cover	Sage, Shrub, Canopy, Concealment, Tree Distance	256.308	0
Total Cover -Year	Sage, Shrub, Canopy, Concealment, Tree Distance, Year	256.308	0
Total Cover and Edge	Sage, Shrub, Canopy, Concealment, Tree Distance, Edge, Year	258.021	1.713
Cover and Forage	Sage, Shrub, Canopy, Concealment, Tree Distance, Forb, Grass, Browse, Protein, Year	259.626	3.318
Concealment Cover	Sage, Shrub, Concealment, Year	261.998	5.690
Tree Cover	Canopy, Tree Distance, Year	272.058	15.750
Forage	Browse, Forb, Grass, Protein, Year	288.964	32.656
Graze	Forb, Grass, Year	290.684	34.376
Browse	Browse, Protein, Year	295.251	38.943

Table 6. Parameter estimates and standard errors for best model of microhabitat parturition site selection by elk in western Wyoming.

Parameter	β Estimate	SE	$P > \chi^2$
Sage	-0.01023	0.00877	0.243
Shrub	0.00307	0.00357	0.390
Canopy	0.01287	0.00444	0.004
Concealment	0.02434	0.00637	<0.001
Tree Distance	-0.00022	0.00821	0.978
Distance to Edge	0.00090	0.00168	0.590

Table 7. Mean variable values for elk parturition and random sites at the microhabitat scale.

Variable (Unit)	Parturition (SD)	Reference (SD)
Canopy Cover (%) ^a	52.03 (35.95)	32.43 (35.48)
Concealment Cover (%) ^a	49.27 (22.64)	36.58 (23.30)
Shrub Density (50m ⁻²) ^a	50.00 (53.79)	46.27 (48.14)
Sage Density (50m ⁻²) ^a	9.87 (17.80)	16.02 (27.95)
Browse Density (50m ⁻²)	16.39 (30.67)	12.32 (26.87)
Distance to Tree (m) ^a	11.16 (20.74)	16.45 (21.22)
Grass (%)	13.72 (11.51)	14.59 (13.65)
Forb (%)	8.85 (8.71)	11.88 (13.76)
TDN (%)	32.11 (35.89)	27.65 (35.46)
Protein (%)	6.77 (7.91)	5.77 (7.74)
Distance to Edge (m) ^a	78.34 (115.51)	84.88 (125.40)

^a Variables appeared in the best model of parturition site selection.

At both scales of selection, hypotheses relating to selection for cover were supported over those relating to selection for forage. Parturient elk selected for attributes related to physical features of the environment and landscape classes related to cover, but not those related to forage. At the microhabitat scale, forage models were the least supported models and did not synergistically improve models based on cover.

There was weak evidence of altered habitat selection with respect to feedgrounds at both scales. At the macrohabitat scale, only use of shrub cover differed marginally ($F_4=8.11$, $p = 0.10$) among winter feeding opportunities. Selection against shrub landcover was nearly 4 times greater in winter free-ranging animals than feedground-dependent animals and nearly 6 times greater than animals on improved feedgrounds (Figure 1), although *post hoc* Tukey tests were not able to differentiate statistically among groups. At the microhabitat scale, use of sage cover differed significantly ($F_4=123.33$, $p = 0.008$) and use of shrub cover differed marginally ($F_4=12.13$, $p = 0.076$) among winter feeding opportunities. Feedground-dependent animals selected more strongly against sage density than free-ranging or improved

feedground animals, which were grouped together by Tukey tests (Figure 2A). Free-ranging animals had a slightly positive relationship with local-scale shrub density, while improved feedground animals had a smaller positive relationship, and feedground-dependent animals had a slightly negative relationship. Post hoc tests were not able to differentiate among the feeding regimes (Figure 2B).

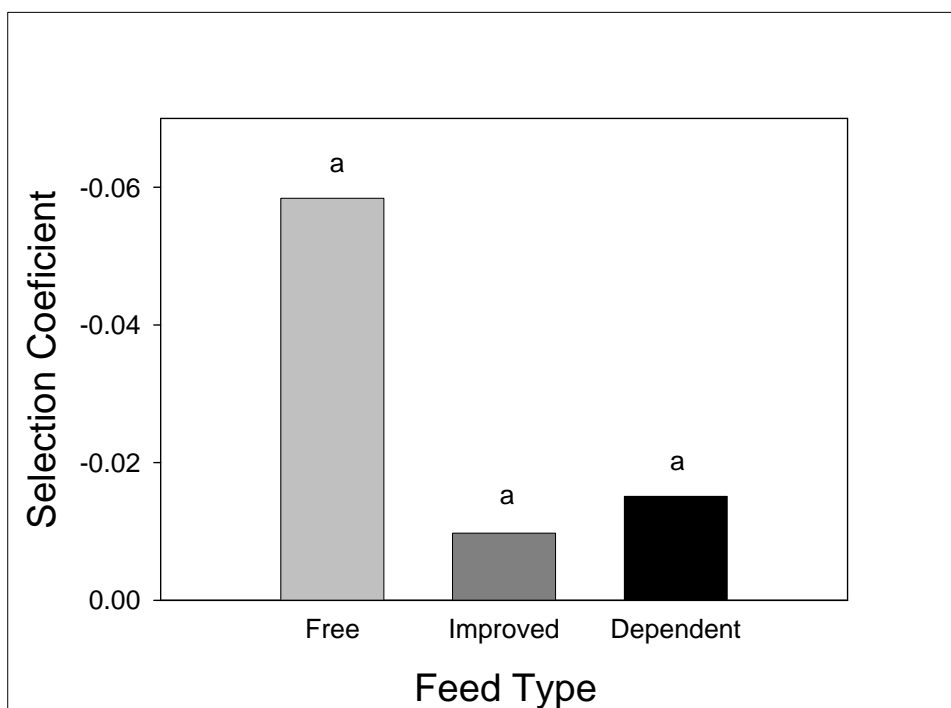


Figure 1. Mean univariate selection coefficients (β 's) for macro-scale elk parturition site selection with respect to shrub cover in western Wyoming. Lower case letters above bars indicate post hoc Tukey groupings.

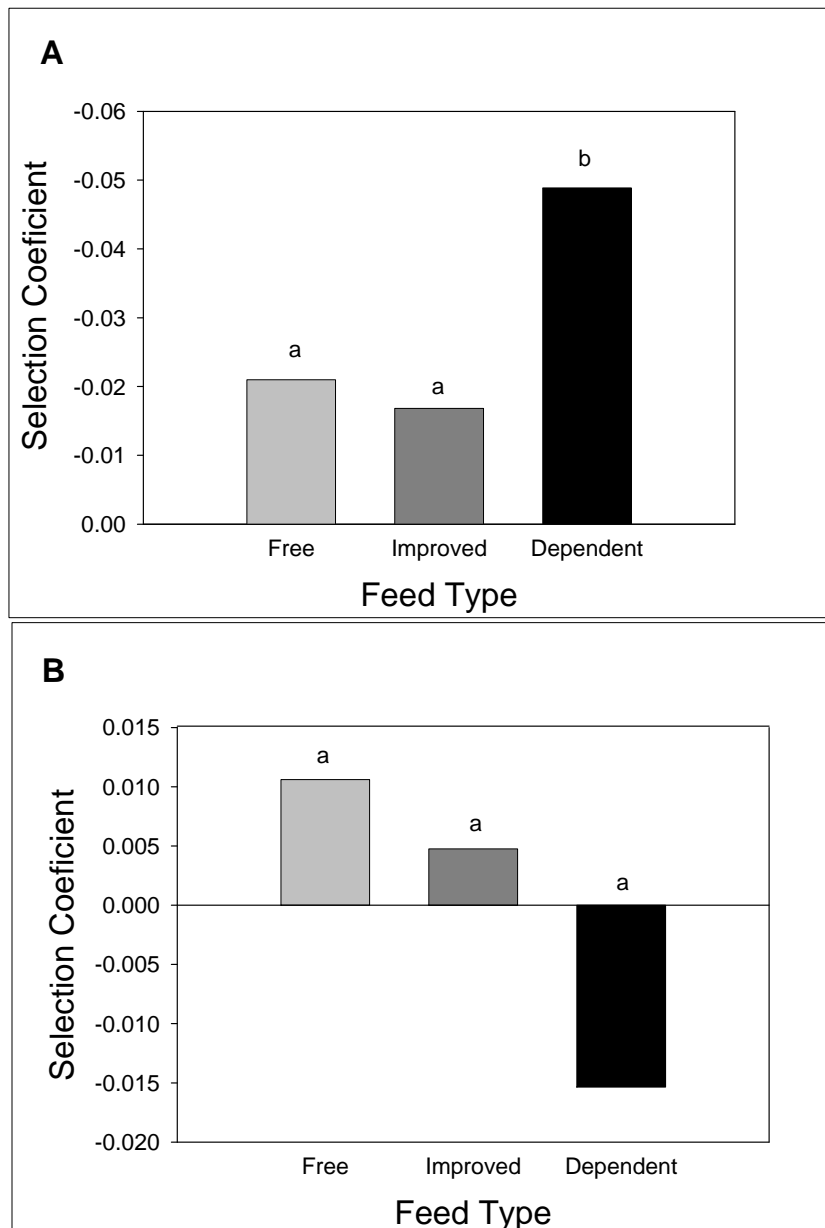


Figure 2. Mean univariate selection coefficients (β 's) for micro-scale elk parturition site selection with respect to sage (A) and shrub (B) densities. Lower case letters above bars indicate post hoc Tukey groupings.

DISCUSSION

Elk appear to be more selective for cover components of the environment at macrohabitat and microhabitat scales, while hypotheses based on selection for a forage component were the least supported. Given that deciduous landcover, which potentially

produces both cover and forage, was more supported in cover models than with other forage components or alone, this also seems to point to stronger selection for cover than forage. We did not see evidence that hypotheses representing combinations of cover and forage variables were stronger than cover models alone at either scale, indicating that elk were not selecting for forage in addition to cover components. A possible reason for this is that high quality forage was nearly universally available at both scales so that animals may maximize selection for cover without sacrificing foraging ability. More intensive investigation would be necessary in order to vet this hypothesis.

Other studies of parturition-related habitat selection in ungulates have been equivocal on the subject of selection for forage versus cover. We are aware of only one other study to date that used VITs to investigate elk parturition site selection. Reardon (2005), in his study of elk calving behavior in Oregon, concluded that nutritional considerations were more important than cover when selecting parturition sites. Other studies have noted that elk cows use areas of heavy brush and canopy cover, although evidence for selection was equivocal (Skovlin 1979). Parturient pronghorn (*Antilocapra americanus*) also selected for vegetation cover (Alldredge et al. 1991), but this open habitat species did not select the areas of highest cover density. Caribou (*Rangifer tarandus*) calving sites in Alaska were linked to lower predator densities and lower forage quality (Barten et al. 2001), a finding similar to our own in suggesting that avoidance of predators may be more important than food availability during the several hours that the female occupies the parturition site. In another study on caribou, however, calving sites and survival of calves were strongly tied to shrub cover, but also to indices of vegetation quality (Gustine et al. 2006). Some populations of caribou are frequently in a negative protein balance, so we would expect the importance of forage to be

greater for these animals. Thus, regional differences in forage availability and nutritional status of females may affect strength of selection for forage availability at parturition sites.

Predation risk and life history characteristics also appear to interact to affect strength of selection for forage and cover. Female moose (*Alces alces*) make tradeoffs, selecting for viewscapes and forage in a landscape where increased forage value is linked to increased predation risk (Bowyer et al. 1999). The importance of forage at or near parturition sites of moose may be explained in part because moose remain close to the birth site for a prolonged period, contrary to elk behavior. On the other hand, neonatal black-tailed deer (*Odocoileus hemionus columbianus*) differ from elk in that they generally follow the female soon after birth, but neonates still selected for both forage and cover components at bed sites (Bowyer et al. 1998). There was, however, no evidence for a tradeoff between foraging efficiency and predator avoidance, and selection appeared to be more strongly driven by forage. In situations where predation risk increases with increasing forage value, tradeoffs are inherent in habitat selection patterns (Lima and Dill 1990, Seip 1992, Miller 2002, Pierce et al. 2004). Caribou, like elk, use the parturition site for a very limited time period and life history and regional differences in forage availability may interact to affect selection for forage and cover components (Barten et al. 2001, Gustine et al. 2006).

Calf locations during the neonatal period, as measured in previous studies of elk calving behavior, may differ from actual birthsites. Lactation requires a great deal of protein and energy, and changes in habitat use have been associated with lactational needs (Rachlow and Bowyer 1998). The neonatal period is also the time of highest predation risk (Adams et al. 1995), and parturition areas are only used by elk for a several hours following calving. It is likely then that the fitness consequences of greater predation exposure outweigh those of

short term nutritional benefit.

Our results contrast with many previous studies on parturient elk use of vegetation cover type during the calving season. Johnson (1951) reported that sage was the most important calving habitat, accounting for 42% of observations. Elk calves were also found predominantly in sagebrush habitats in eastern Idaho, but it was acknowledged that differential ability to sight calves in different habitats and small sample size may have created bias (Davis 1970). Using radio-tracking data, elk movements during spring were associated with sage, but use of riparian areas was preferred during the calving season in Washington (McCorquodale et al. 1986). Thus, elk have been associated strongly with sage, but not necessarily specific to calving behavior. We found some evidence that elk selected against sage cover for parturition sites at the microhabitat scale and selected only weakly for shrub (sage) in the global model at the macrohabitat scale. When we looked at microhabitat selection stratified by feeding opportunity, all feeding types select against shrub habitat (predominantly sage) cover.

Other studies identified conifer as heavily used by females during the calving season and with neonates (Troyer 1960, Stevens 1966, Witmer and deCalesta 1983). We showed selection against this cover type, as well, at the macrohabitat scale, although elk did select for canopy cover at the microhabitat scale. The most common method of finding calves in early studies involved observation of cow behavior or searching for neonatal locations introducing a sightability bias toward more open habitats such as sage, or conifer patches with greater canopy closure and less ground cover. Our location of parturition sites was not dependent on visibility and thus gives a more accurate picture of calving site selection with respect to sage and conifer cover.

Roads have often been implicated in disturbances to elk habitat use (Lyon 1979, Lyon 1983, Rowland et al. 2000). Distance to road was maximized by elk during the late spring and early summer calving season in Oregon (Ager et al. 2003). Bian and West (1997) found that, in a prairie population, elk that had calved in that season were nominally further from roads than elk that had not calved. We found only minimal evidence for an effect of roads on calving site selection and, in fact, several animals calved within 100 m of a heavily trafficked state highway. Our lack of support for distance to road as an important variable when it has been implicated as a strong driver of elk use could be due to our road classification system. Although it would have been possible to subdivide roads by degree of traffic, we opted not to add another variable to a dataset already approaching excessive dimensionality, so road categories were grouped regardless of use level.

This study was conducted across four study areas covering a wide geographic range. Although cover types and climate were generally similar, there were differences that increased variability in measured parameters, especially at the macrohabitat scale. At the microhabitat scale, parturition sites were compared to local availability, mediating this effect to some extent. The result of covering such a large range is that our inference space is regional. Rarely are studies coordinated such that standardized methodologies are used across a region over the same time period so that behavioral decisions can be measured at this scale. While we probably sacrificed some ability to explain variance in the dataset, evidenced by the low R^2 value at the macrohabitat scale, we did find evidence of selection at both scales. The ability to detect selection across these areas speaks to an underlying behavioral pattern perhaps more likely to be common across elk populations.

At the time of this study there were at least six wolf (*Canis lupus*) packs using all or

part of the Buffalo Valley study area. Grizzly bears (*Ursus arctos*) are also relatively common in the northern portion of the study area. While members of both species have made exploratory movements into the southern parts of our study area, they are not as common. Other predators, such as mountain lions (*Felis concolor*), black bears (*Ursus americanus*), and coyotes (*Canis latrans*) are present throughout the study area. Despite differences in density and diversity of predators, selection for cover still appeared to be the most important factor in selection at both scales. A possible factor increasing cover needs for elk in the southern portion of the study area is higher human population density and accompanying greater proportions of private lands. Disturbance by humans can reduce elk calf survival (Shively et al. 2005), and thus humans potentially serve a similar role to predators.

Our models at the macrohabitat level covering all study sites did not explain the majority of variation in the dataset, suggesting that we did not measure one or more habitat components that strongly influence selection of parturition locations. A second possibility is that elk have a broad range of acceptable habitats at this scale and are therefore not as selective in choosing calving locations. While we were unable to describe the majority of variation, our study represents the most comprehensive view of elk calving site selection to date.

A potential consequence of winter feeding of elk is a movement towards domestication. Animals can be viewed to exist on a continuum of wild to domestic, and from completely unimpacted to completely human dependent. Supplemental feeding and captive breeding of wild animals fall somewhere in between these two extremes of management intensity. Some of the potential negative consequences of supplemental feeding are the

alteration of foraging behavior, altered reproduction, and dependency or habituation (Orams 2002). The effects of seasonal feeding on behaviors outside of the feeding season are not well known.

We found no strong evidence for detrimental differences in parturition habitat selection associated with winter feeding opportunity. We expected to see lower selectivity for fed animals if feeding was having a negative effect on parturition site selection behavior. At the macrohabitat scale, the free-ranging animals were the most selective, as would be expected if feeding were limiting choices for elk using feedgrounds or altering behavioral patterns specific to calving site selection. At the microhabitat scale, feedground-dependent animals were the most selective with respect to avoidance of sage. However, this could be due to the greater proportional abundance of this element on the calving range used by animals fed on the unimproved feedground.

While behavior of elk on feedgrounds is altered from normal winter migration and foraging patterns, winter feeding does not appear to be contributing to domestication and loss of behavioral adaptations to the environment during the calving season. The scope of this study was broad, and included a large sample size of individuals, but we were not able to have replicate sites for winter free-ranging and feedground-dependent elk, limiting our ability to find any differences among feeding opportunities, if they exist. Effects of winter feeding on the spatial arrangement of parturition sites are reported as a separate part of this study (Barbknecht et al. Chapter 4).

Accurate definition of parturition locations allows for better-informed management of this important component of elk habitat. Identification of parturition habitat also has implications for disease management in western Wyoming. Brucellosis, causative agent

Brucella abortus, is endemic in elk populations in western Wyoming. This disease can be spread by contact with fluids and tissue associated with parturition events of infected females and thus identifying the areas potentially used more often for parturition can be useful in managing intra- and interspecific transmission.

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**CHAPTER 4. RELATIONSHIPS OF WINTER FEEDING OF ELK TO SPATIAL
PATTERNS OF PARTURITION SITES WITH IMPLICATIONS FOR DISEASE
TRANSMISSION RISK**

A paper to be submitted to the *Journal of Wildlife Diseases*

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ABSTRACT

The potential for calving ecology to influence intra- and interspecific spread of brucellosis, and the effect that winter feeding of elk has on this transmission potential, have not been well studied. Brucellosis is a disease causing abortion in elk (*Cervus elaphus nelsoni*), bison (*Bos bison*), and cattle (*Bos spp.*). The most common transmission route is through oral contact with aborted fetuses or parturition tissues/fluids. We used vaginal implant transmitters to mark calving locations for free-ranging elk and winter-fed elk on improved and unimproved feedgrounds. We investigated spatial characteristics of calving sites to make inferences about the potential effects of winter feeding on brucellosis transmission risk during the calving season. Winter-fed animals were closer to winter range and more aggregated on parturition ranges than free-ranging animals, although improved feedgrounds mitigated this effect to some extent. Both of these findings indicate that winter feeding of elk potentially increases contact rates associated with parturition events, and thus may increase transmission risk for the parturition period. Changes in feedground management policy may allow for risk reduction.

INTRODUCTION

The importance of disease ecology and its role in wildlife populations is increasingly recognized. Disease can dramatically affect the population dynamics of a species (Anderson and May 1979) and can also play a role in interspecific interactions (Holt and Pickering 1985). When one or more of the species involved is of economic value, such as cattle (*Bos taurus*) and elk (*Cervus elaphus nelsoni*) in the case of brucellosis, or is threatened or endangered, such as canine distemper in black-footed ferrets (*Mustella nigripes*, Thorne and Williams 1988), understanding particular aspects of disease ecology is of paramount importance to management decisions. The importance and prevalence of interspecies disease transmission has been acknowledged (Begon et al. 1999, Woodroffe 1999, Holt et al. 2003, MacDonald et al. 2006, Morgan et al. 2006), but many unknowns remain in our understanding of disease transmission risk factors. Therefore, interactions of the host, pathogen, and environment in multi-species systems require greater scrutiny.

Contact patterns are often important in disease transmission processes (McCallum et al. 2001). Contact rates are most often associated with social interactions of individuals (Ramsey et al. 2002, Totton et al. 2002), but animals whose ranges overlap, especially in multispecies systems may also have contact with infective biotic or abiotic vectors. Direct contact rates among individuals are very difficult to quantify and this is an emerging field of research (Weihong et al. 2005). However, the spatial attributes of potentially infectious materials may be easier to quantify and also have implications in disease transmission risk, especially in disease systems such as brucellosis in elk, bison, and domestic cattle.

Using an elk/brucellosis study system, we looked at spatial arrangement of parturition sites to make inferences about the potential of spatial patterns to influence disease

transmission. Brucellosis is a zoonotic bacterial infection caused by *Brucella abortus*. Infection results in reproductive failure in ungulates, typically abortion, which occurs most often the first year after infection (Thorne et al. 1978). It has become endemic in elk and bison (*Bos bison*) of the Greater Yellowstone Ecosystem (GYE), which are now some of the last reservoirs of the disease in the United States. The prevalence of brucellosis in wild ungulate populations threatens eradication of the disease in domestic livestock. Various outbreaks in cattle in the last decade have been linked to elk feedgrounds (Kreeger 2002, Wyoming Brucellosis Coordination Team 2005). These outbreaks led to increased efforts to better understand and control brucellosis in wild ungulates. The primary mode of brucellosis transmission is thought to be oral contact with fetal tissues or fluids associated with abortion or parturition events (Thorne et al. 1978) that typically occur from February through June (Thorne et al. 1991, Roffe et al. 2004). Intraspecific transmission risk among feedground elk during the abortion period has received much scrutiny (Cross et al. 2007, Maichak et al. in preparation), but contact associated with term pregnancies in the first year of infection and in subsequent years has not been previously studied. It is unknown how spatial distribution and transmission risk differ between free-ranging and feedground elk during the parturition season.

The importance of calving ecology to the risk of intra- and interspecific (elk to cattle) transmission of brucellosis has generally been discounted. However, there is potential for disease transmission through full term births of weak or nonviable calves in the first year of infection, or successful pregnancies in subsequent years. In cattle, some individuals can remain carriers for life, with re-infection of the placenta occurring for subsequent pregnancies (Ficht 2003) and active infection has been reported in captive elk for at least

4.67 years (Thorne et al. 1978). About 60% of infected elk abort in their first year of infection (Thorne et al. 1997). Viable births or birth events occurring within the calving season (May to June, Murie 1951), as well as stillbirths (8%) and weak calves (4%), may constitute a substantial transmission risk (Etter and Drew 2006). A study of captive elk demonstrated that elk may shed the bacteria through June (Roffe et al. 2004).

Supplemental feeding of elk in the GYE has been linked to the persistence of brucellosis in elk populations (Smith 2001, Kreeger 2002) because feedgrounds concentrate elk during the abortion period of February and March (Thorne et al. 1991). The effect of elk feedgrounds outside of the feeding season has not been previously studied. The history of winter feeding of elk in Wyoming goes back nearly 100 years. The influx of agriculture to western Wyoming at the turn of the century cut off traditional migration routes (Anderson 1958) and reduced available winter range. This led to starvation of elk in winter and depredations on hay supplies. Winter feeding of elk to mitigate these concerns began on the US Fish and Wildlife Service National Elk Refuge in 1911 (Preble 1911) and continued with the establishment of state feedgrounds through the 1970's (Clause et al. 2002). There have been up to 50 feeding locations, but this has been reduced to 23 state-run feedgrounds, in addition to the National Elk Refuge today. The fed elk in Wyoming represent 75% of the fed elk population in North America (Smith 2001).

Although winter feeding of elk increases intraspecific risk of brucellosis transmission, elk are generally spatially separated from cattle and interspecific risk is managed, to some extent. During the parturition season, infective events are likely more spatially separated, and may result in a lower intraspecific transmission risk, but they may also be more likely to occur in areas where there is potential contact with cattle, and thus they may increase

interspecific transmission risk. Further, the use of feedgrounds may directly or indirectly influence elk calving locations and thereby affect the potential for contact by cattle. Winter feeding of elk may cause previously unobserved spatial and behavioral changes to elk ecology beyond the feeding season. The effects of feedground management and habitat improvements are also of interest, because initiating or altering these practices may mitigate changes associated with winter feeding of elk. We initiated this investigation to determine the effects of winter feeding on the spatial distribution of parturition sites with respect to winter range and with implications for brucellosis transmission risk.

METHODS

Study Areas

The study was conducted on free-ranging and feedground elk in the western Wyoming area of the Greater Yellowstone Ecosystem. The free-ranging elk herd segment wintered in Buffalo Valley, Teton County, Wyoming (43°84'N, 110°45'W, 2069 m). Another study population, wintered on the Scab Creek Wyoming Game and Fish Department (WGFD) feedground (42° 81'N, 109° 58'W, 2455 m) in Sublette County, Wyoming. This population was fed during the winter, and no management actions were implemented to reduce feeding length or density on the feedground. Two elk feedgrounds, Soda Lake (42°95'N, 109°81'W, 2314 m) and Bench Corral (42° 72'N, 110° 13'W, 2169 m), had adjacent habitat improvements implemented within the last 12 years in an effort to shorten the feeding season and reduce dependence on the feedground during the feeding season. Prescribed burning has been done on about 2000 ha of land surrounding the Soda Lake feedground. Herbicide treatments were used on 216 ha and mechanical treatments on 233 ha surrounding the Bench Coral feedground. More than 3000 ha of habitat improvements,

primarily prescribed burn treatments have also been implemented for the winter free-ranging herd segment in Buffalo Valley.

Elevation ranged from 1500-4195 m in Teton and Sublette Counties. At low elevations, vegetation was typified by sagebrush (*Artemisia tridentata*) communities on xeric sites and willow (*Salix* spp.)/sagebrush communities and cottonwood (*Populus* spp.) communities in riparian areas (Wigglesworth and Wachob 2004). Higher elevations were typified by lodgepole pine (*Pinus contorta*), Douglas fir (*Pseudotsuga menziesii*), and aspen (*Populus tremuloides*) interspersed with high meadows, and spruce (*Picea engelmannii*)/subalpine fir (*Abies lasiocarpa*) communities above 2750 m in elevation (Whitlock 1993). The northern portion of the study area received more moisture, averaging 40 cm of precipitation annually, compared to 28 cm of precipitation on the southern ranges of the study area. Primary land uses were agriculture and recreation with increasing proportions of private lands and agricultural uses moving from north to south. Elk used many lands under public management including Bridger Teton National Forest, Grand Teton and Yellowstone National Parks, and areas administered by the Bureau of Land Management and the State of Wyoming.

We assigned winter feeding opportunity designations to each study site. Supplemental food was made available for elk in the Buffalo Valley from 4 February to 17 April during the first year of study due to emergency, weather-related conditions. The WGFD has fed elk in Buffalo Valley on rare occasions (such as 2006) during winters with above normal precipitation (Bill Long, WGFD, pers. comm.). We assigned Buffalo Valley animals to fed and non-fed groups in 2006 based on telemetry locations (Barbknecht et al. Chapter 3), although some animals could not be classified and were censored from analysis.

We classified animals with at least three telemetry locations within the telemetry error radius (1100 m) of the feedground or with ≥ 1 on-the-ground location at the feedline as fed while animals with one or fewer locations within the error radius of the feedline we classified as free-ranging. Eleven animals were identified as using the feedline, 11 as free-ranging in the year of study, and 5 could not be classified. We refer to the elk using Bench Corral and Soda Lake feedgrounds, with shorter feeding seasons, habitat improvements, and larger feedground areas, and the fed animals in the free-ranging herd (in 2006 only) as using improved feedgrounds. Scab Creek we termed an unimproved feedground and animals using this feedground as feedground-dependent. In 2007, no supplemental winter feeding occurred in Buffalo Valley, and all elk using the area as winter range were considered free-ranging.

Capture

We captured 118 animals between 7 February and 14 March 2006 and 134 animals from 5 January through 7 March 2007. We deployed 96 vaginal implant transmitters (VITs, M3960, Advanced Telemetry Systems (ATS), Isanti, MN, USA) in pregnant adult female elk in 2006 and 102 VITs in 2007. Variable capture success led to somewhat unequal sampling between areas and years (Barbknecht et al., Chapter 2). We captured feedground animals by use of chemical immobilization for feedground animals and helicopter and net gun (Leading Edge Aviation, Cody, WY, USA) for free-ranging animals and tested all captured females for pregnancy (Barbknecht et al. Chapter 2). All pregnant females were outfitted with VITs, numbered metal ear tags and either a VHF (ATS, Isanti, MN, USA, n=37), GPS (Telonics, Mesa, AZ, USA, n=20), or visibility collar (n=149). Collars with VHF beacons were used in this study to facilitate location of VITs. We drew blood from all captured animals and tested them for exposure to *B. abortus* at the Wyoming Game and Fish Laboratory (Laramie, WY,

USA). Captures were performed in accordance with the approved Iowa State University Animal Care and Use Protocol # 8-05-5962, and approved University of Wyoming Animal Care and Use Protocols Rogerson 2005-2006 and Linn 2005-2006 and 2006-2007.

VITs are expelled during abortion or parturition events, marking the location of the event. We used fabricated, pre-disinfected PVC applicators as described in Johnson et al. (2006) to implant VITs. The basic design of the VITs we used has been described in detail elsewhere (Vore and Schmidt 2001, Johnson et al. 2006, Johnstone-Yellin 2006). We used 43-g VITs with an 80-mm flexible wing and a temperature-sensitive switch that switched from a 40-beats-per-minute (BPM) pulse rate to an 80-BPM pulse rate when its temperature dropped below 28° C (elk body temperature). VIT antennas were pre-cut to 17 cm in length and the antenna tips were resin encased to avoid injury to the female.

We monitored VITs for expulsion on a daily basis from date of capture until females were no longer within ground telemetry range. Once females left their respective wintering areas, ground telemetry was supported by weekly telemetry flights with fixed-wing aircraft (Sky Aviation, Worland, WY, USA). We located and retrieved expelled VITs using ground telemetry and recorded the locations in Universal Transverse Mercators (UTMs) with a hand-held Trimble GeoXT (Sunnyvale, CA, USA) or Garmin E-trex Vista (Olathe, KS, USA) GPS unit. Expelled VITs were evaluated to determine the likelihood that they were expelled at a birth site (Barbknecht et al. Chapter 1). We identified sites used in analyses based on observation of birth, calf, or placenta, or the presence of at least the majority of common parturition site characteristics such as a cleared area, moist soil, distinctive odor, evidence of browsing activity, tracks, and fresh fecal pellets. Calving date was recorded as the Julian date prior to the first location of the expelled VIT from the ground, or the median Julian date

between flight locations when the VIT was determined to have been expelled and the date when it was still in the female.

We collected data on the spatial attributes of parturition locations and covariates. We used the Nearest Feature function in ArcView 3.3 (ESRI, Redland, CA, USA) to calculate distance moved between winter range and the parturition location. We defined winter range as the feedground location or the centroid of winter locations for all free-ranging elk. Spatial relationships between parturition locations were represented by mean interpoint distances between parturition locations. Mean interpoint distance is the average distance between parturition locations for a given study area. We used mean interpoint distances rather than a simple density measure because parturition sites were not distributed evenly across the landscape and the interpoint distance measure captures that variability better and represents a parameter more meaningful to theoretical modeling of disease transmission (Cook 1999). Additional covariates were winter range location and elevation, calving date, proportion of available calving habitat, length of time elk were fed, and end date of feeding for the year of study, as well as ten-year averages of feeding length and end date (Table 1). The elevation of the winter range location was extracted from a 90-m resolution digital elevation model (DEM) using ArcGIS 9.1 (ESRI, Redland, CA, USA). Elevation of winter range served as a surrogate for relative snow depth because this information was not available at an appropriate spatial scale. Feeding length and end date are somewhat arbitrary and can be quite variable, so 10-year averages were included to account for the effects of habituated behavior. We calculated potential calving habitat by using a macrohabitat scale calving resource selection function (Barbknecht et al. Chapter 3) to generate a GIS calving probability layer and defined calving probability contours using this layer (Appendix).

Table 1. Characteristics of elk parturition study sites in western Wyoming.

	Year	Feeding Length (days)	Mean Length (days)	Feeding End Date (Julian day)	Mean End Date (Julian day)	Proportion Calving Habitat (%)
Bench	2006	110	97.5	90	85.5	60.1
Corral	2007	117	97.1	87	82.2	
Buffalo	2006	0/73 ^a	0	NA/107 ^a	NA	36.8
Valley	2007	0	0	NA	NA	39.9
Scab	2006	131	141.9	103	106.8	59.9
Creek	2007	98	134.6	102	102.3	
Soda	2006	88	88.0	68	92.9	63.6
Lake	2007	82	84.4	92	89.8	

a- Some Buffalo Valley animals used an emergency feedline in the first year of the study.

Statistical Methods

All statistical analyses were conducted using SAS 9.1 (SAS Institute Inc. Cary, NC, USA). Variables were evaluated prior to analyses with respect to normality and correlations. We used multiple regression (proc REG) and an information-theoretic model selection approach to investigate the effect of winter feeding opportunities on the distance animals traveled from winter range to parturition areas. We first modeled the response variable distance from parturition site to winter range, accounting for the effects of winter range elevation (representing impediment to movement and effective foraging in spring), and calving date (because many elk are migratory during the late spring and later calving animals are likely to be further from winter range). This model was then compared to those incorporating feeding opportunity or feeding length using Akaike's Information Criterion (AIC). Lower AIC values represented better models; those within 2 AIC values were

considered competitive and those within 4 units were considered plausible. To investigate the effects of feedground management on distance traveled from winter range, we omitted free-ranging animals and regressed distance between winter range and parturition area on unimproved and improved designations and current year and historic measures of feedground-specific management, such as length of feeding season and feeding end date. Free-ranging animals were omitted from this analysis because they did not have end date values and because the specific effects of feedground management were of interest. Multiple regression and AIC methods were again used in this analysis.

A separate analysis was conducted on calving dates of females in the free-ranging population utilizing emergency feedlines and those that remained free-ranging in the first year of study. Student's t-tests were used to compare calving dates of fed and free-ranging females and the distances traveled from winter range to parturition site. This analysis allowed a comparison of fed and free-ranging animals on the same study area and in the same year.

To determine the importance of site differences on our results, we conducted a *post hoc* analysis, adding the amount of available calving habitat surrounding each of the study sites to the previous models. We summarized the proportion of potential calving habitat available within a radius equal to the average distance from calving location to winter location (22.1 km) over all study sites, for each wintering area. This variable was added after the initial analysis because we suspected that elevation might not adequately account for inter-site variability and that animals with greater proportions of suitable calving habitat available in proximity to wintering areas would not travel as far to calve. We added available calving habitat to the analysis to further control for the effect of study area because

the study covers a large geographic range. The addition of variables after the initial analysis risks the appearance of a fishing expedition, but we felt that the potential effects of the amount of available habitat warranted additional analysis.

We used simple linear regression to estimate the relationship between mean interpoint distance of parturition sites and feeding period. Current year and 10-year averages of feeding period were used to parse out the effects of feeding in the year of study and feeding in previous years, which may have led to habituation. Fed animals in Buffalo Valley were included in the current year analysis because feeding during the study likely affected movement patterns. However, they were not included in the 10-year average analysis as there was no documented history of regular feeding for these animals.

RESULTS

We collected data on 169 successfully marked parturition sites (Barbknecht et al. Chapter 2). Calving dates ranged from 17 May to 11 June in 2006 and from 22 May to 20 July in 2007. Median calving date was 31 May in both years. Mean parturition range size was 84,454 ha (SD=486, n=2) for free-ranging animals, 56,617 ha (SD=13,702, n=4) for improved feedground animals and 26,174 ha (SD=318, n=2) for feedground dependent animals. The minimum distance traveled by a female from winter range to parturition site was 857 m; maximum distance traveled was 53×10^3 m (53 km). Both of these animals were in the free-ranging Buffalo Valley population. Although there is some historical indication that feedground elk do not make patterned migrational movements in the manner of free-ranging elk (Anderson 1958), we observed that parturition ranges of fed animals were located in one direction from the feedground rather than a radial pattern surrounding the feedground, as would be expected with unpatterned movements. Exposure to brucellosis varied among

years and among study sites, but was generally consistent with greater seroprevalence levels with greater feedground attendance.

The best model for distance traveled from winter range to parturition sites, when the amount of available calving habitat was not included, was associated with feeding type (Table 2). Free-ranging and improved feedground animals were not significantly different in the distance traveled to parturition sites ($t=0.23$, $p=0.82$), but feedground-dependent animals were 21.7 km (SE 6.1 km) closer to winter range than free ranging animals ($t=3.58$, $p<0.001$) when calving date and winter range elevation were held constant (Figure 1). Model fit was relatively good ($R^2 = 0.31$, $F=17.43$, $p<0.001$). In examining the effects of feedground management on distance traveled to calving sites (excluding free-ranging animals from analysis), we found that the strongest model again was associated with feeding type (Table 3), with feedground-dependent animals calving 11.4 km (SE 3.4 km) closer, on average, from winter range than improved feedground animals ($t=3.34$, $p=0.001$). Model fit was good ($R^2=0.55$, $F=35.17$, $p<0.001$). Later calving dates were associated with more distant calving sites ($\beta= -43.7$, SE 9.35, $p<0.001$) while higher winter range elevations were associated with closer parturition locations ($\beta= 332.2$, SE 95.1, $p<0.001$), as would be expected if this variable acted as an appropriate surrogate for relative snow depth. For emergency fed and free-ranging animals in Buffalo Valley in 2006, animals using emergency feed calved 6.7 (SD 6.9) days earlier than animals avoiding feedlines ($t=2.17$, $df=18$, $p=0.04$). These animals were also 7.0 km (SD 10.3 km) closer to winter range at the time of calving, but not significantly so ($t= 1.50$, $df=18$, $p=0.14$).

Table 2. AIC and Δ AIC values for candidate models for distance between wintering areas and parturition sites for elk in western Wyoming 2006 and 2007.

Hypothesis	Model	AIC	Δ AIC
Feed Type	Elevation, Calving Date, Free v. Improved, Free v. Fed	2738.69	0
Multi-Year Mean Length of Feeding	Elevation, Calving Date, 10-yr Mean Length of Feeding	2759.53	20.84
Current Year Feeding Length	Elevation, Calving Date, Feeding Length	2767.57	28.88
Base - Year	Elevation, Calving Date	2775.91	37.22
Base + Year	Year, Elevation, Calving Date	2777.33	38.64

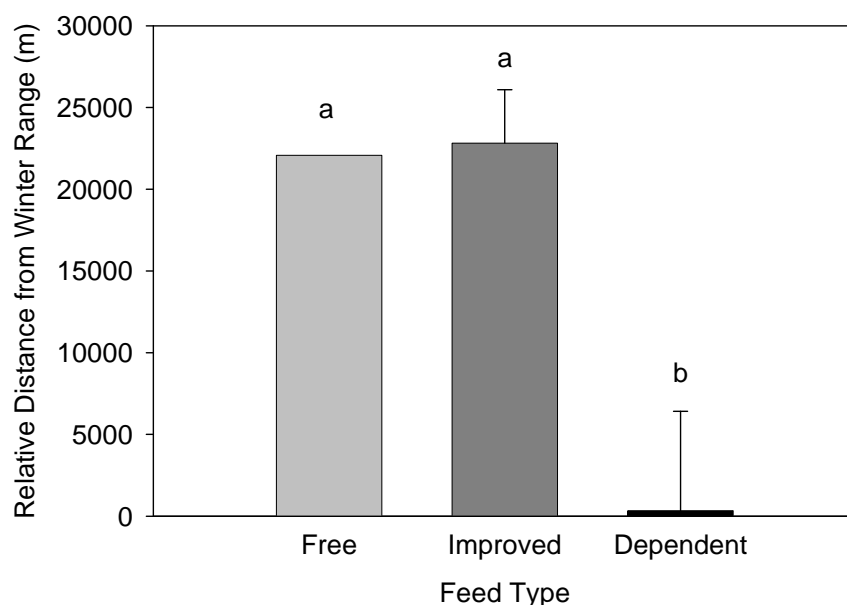


Figure 1. Relative distance traveled from winter range to parturition location by elk in western Wyoming. Results represent response in distances traveled when calving date and base elevation of winter range are held constant. Comparisons are to free-ranging animals and results are scaled to mean distance traveled by free-ranging animals. Lower case letters represent statistically significant groupings.

Table 3. AIC and Δ AIC values for candidate models for feedground-specific management effects on distance between wintering areas and parturition sites for improved and unimproved feedground elk in western Wyoming 2006 and 2007.

Hypothesis	Model	AIC	Δ AIC
Feed Type	Elevation, Calving Date, Fed v. Improved	1848.49	0
Mean Length	Elevation, Calving Date, 10 yr Average Length	1851.41	2.92
Feeding Length	Elevation, Calving Date, Feeding Length	1853.39	4.90
Feeding End	Elevation, Calving Date, End Date	1855.79	7.30
10-Yr Mean End	Elevation, Calving Date, Mean End Date	1857.18	8.69
Base - Year	Elevation, Calving Date	1857.47	8.98
Base + Year	Year, Elevation, Calving Date	1859.29	10.80

The amount of available calving range within the 22.1 km radius varied between study areas (Buffalo Valley = 36.8%, Bench Corral = 60.1%, Soda Lake = 63.6%, Scab Creek = 59.9%). Adding proportion of available calving habitat to models of distance traveled from winter range to parturition sites improved the models, but the effect was one of increasing distance traveled when a greater proportion of calving habitat was nearby. The magnitude of the effect was 1.10 km of travel from winter range for every 1% increase in proportion of available habitat nearby ($p < 0.001$). With available calving habitat incorporated, distance traveled from winter range was predicted best by length of feeding period in the year of study and by feeding type (Models 1 and 2; Table 4). Model fit was good ($R^2 = 0.44$, $F = 29.91$, $p < 0.0001$) for the best model of feeding length. Both improved feedground animals and feedground dependent animals calved closer to winter range than free-ranging animals (Figure 2). There was also a negative relationship between distance to winter range and length of feeding season, such that animals were 87 m closer to winter

range for every day of winter feeding ($p=0.01$). Adding proportion of available calving range to feedground specific models did not improve model performance.

Table 4. AIC and Δ AIC values for candidate models for distance between wintering areas and parturition sites for elk in western Wyoming 2006 and 2007. These models include proportion of available calving habitat.

Hypothesis	Model	AIC	Δ AIC
Current Year	Elevation, Calving Date, Feeding Length, Available Habitat	2707.58	0
Feeding Length	Elevation, Calving Date, Free v. Improved, Free v. Fed, Available Habitat	2707.81	0.23
Feed Type	Elevation, Calving Date, Available Habitat	2712.08	4.50
Base - Year	Elevation, Calving Date, 10-yr Mean Length of Feeding, Available Habitat	2712.68	5.10
Multi-Year Mean Length of Feeding	Year, Elevation, Calving Date, Available Habitat	2713.50	5.92
Base + Year			

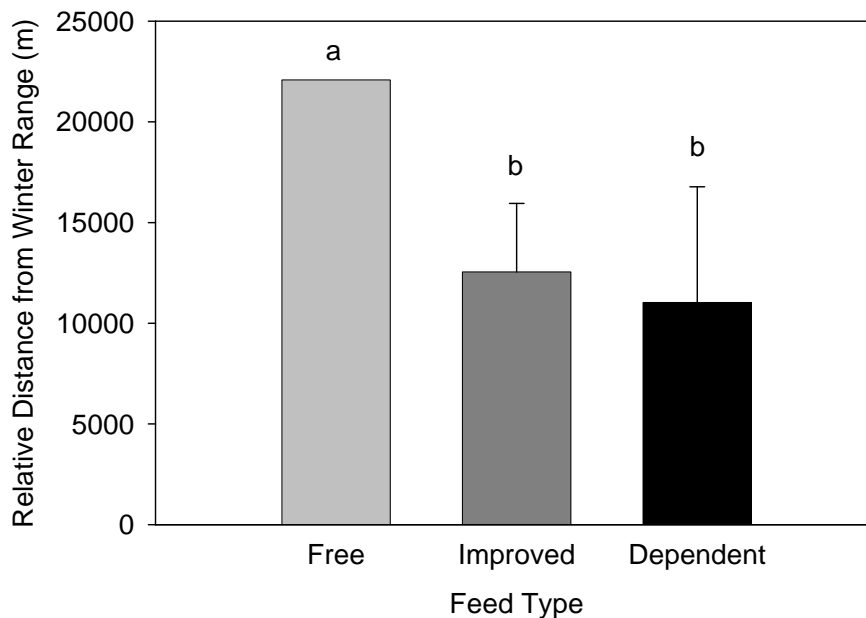


Figure 2. Relative distance traveled from winter range to parturition location by elk in western Wyoming. Results represent response in distances traveled when calving date, proportion of available calving habitat nearby, and base elevation of winter range are held constant. Comparisons are to free-ranging animals and results are scaled to mean distance traveled by free-ranging animals. Lower case letters represent statistically significant groupings ($p<0.05$).

Mean interpoint distance between parturition sites tended to decrease with longer feeding periods in the year of study (Figure 3), although the relationship was weak ($p=0.09$, $R^2=0.40$, Figure 3A). The effect of the 10-year average feeding length on interpoint distance was significant, however ($p=0.02$, $R^2=0.70$, Figure 3B). Females calved, on average, 67 m closer to other parturition sites with each additional day of winter feeding.

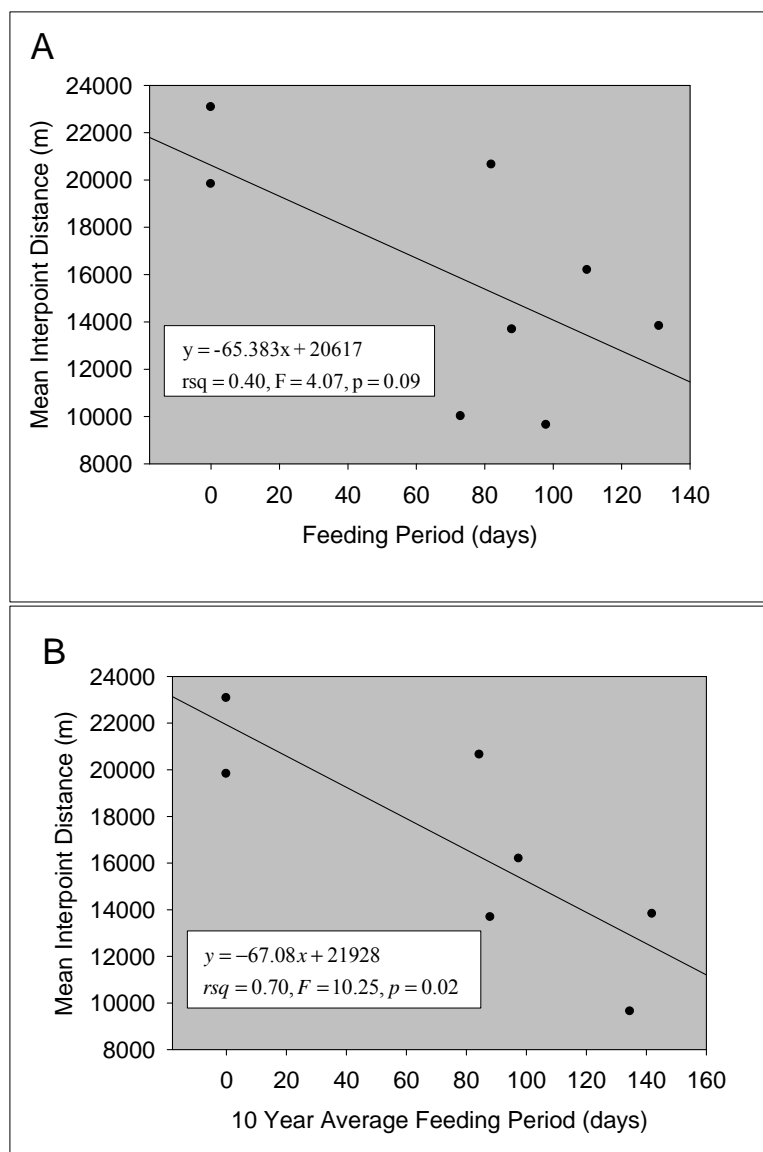


Figure 3. Effects of feeding period in the year of study (A) and historic feeding period (B) on mean interpoint distance.

DISCUSSION

Our results provide evidence for differences in spatial patterns of parturition sites associated with differences in winter feeding opportunity. We documented a pattern of greater aggregation on parturition ranges of elk with greater average length of supplemental feeding. Qualitative observations of elk calving behavior led to previous estimates of elk parturition ranges (WGFD unpublished data) that were approximately 50% smaller for winter-fed animals than for free-ranging animals in western Wyoming. This finding of altered space use following supplemental feeding also agrees with other studies on the direct effect of feeding on space use. Estimates of white-tailed deer (*Odocoileus virginianus*) winter ranges were up to 50% smaller for winter-fed deer than for free-ranging deer in Texas (Brown and Cooper 2006). Similarly, 19 of 23 studies in a review of supplemental feeding experiments indicated a decrease in home range size associated with supplemental feeding (Boutin 1990). These studies encompassed experimental food additions in a wide variety of taxa ranging from birds to mammals to reptiles, specifically assessing changes in behavior and space use associated with food addition. While the pattern of aggregation directly related to supplemental feeding has been established in the past, the potential for indirect effects on aggregation associated with feeding was less obvious until this study. We can establish that winter ranges are smaller for feedground animals, but that this would result in smaller parturition ranges after the conclusion of feeding activities is somewhat less intuitive.

Increased aggregation on parturition ranges for animals fed for longer periods during the winter has implications for parturition-specific brucellosis transmission risk. Although we do not have the capability to directly calculate transmission risk, greater spatial association potentially increases intraspecific contact rates, an important factor that can

increase transmission risk (Mollison 1977). If elk calving ranges with higher aggregation overlap early summer cattle calving and grazing areas, greater aggregation may also lead to areas of more concentrated inter-specific transmission risk. Elk transmission of brucellosis was originally thought to be simply density-dependent (Thorne et al. 1979). Recent studies of brucellosis seroprevalence, however, did not find strong connections between disease exposure rates and population size or density (Cross et al. 2007). Instead, they linked seroprevalence more closely to the duration of aggregation on the feedgrounds. We show here that aggregations of longer duration in supplementally fed animals during the feeding season are then extended into greater aggregation during the calving season. Thus, feeding likely impacts spatial dynamics of elk throughout the entirety of the brucellosis transmission period. We cannot say to what extent this additional aggregation plays a role in increasing prevalence, but it may be a contributing factor. Some degree of seasonal aggregation will always be expected and can have an impact on the dynamics of disease transmission (Altizer et al. 2006), but artificial feeding exacerbates the impact of these periods on persistence of disease in the population.

We presented results for distance traveled from winter range to calving site both with and without *post hoc* analyses, because, although adding amount of available calving range as an explanatory variable improved the model from a statistical standpoint, the effect was in the opposite direction expected. Our conclusions do not alter significantly following *post hoc* analyses, indicating differences in parturition ranges and spatial patterns with respect to winter feeding opportunity when we controlled for potentially confounding factors, such as elevation, proportion of available calving habitat, and calving date. Fed animals gave birth

significantly closer to winter range than free-ranging animals and feedground-dependent animals were closer than improved feedground animals.

Parturition ranges, and presumably migration routes, tend to be fan-shaped with their origin in the winter range. Thus, movements that are shorter considerably reduce the potential area of the parturition range and may contribute to the observed patterns of aggregation. Distance traveled from winter range may have additional implications for inter-specific transmission risk. Feedgrounds, in order to be effective, need to be on traditional winter range or, more commonly, on strategic locations designed to collect elk from summer range and prevent movement onto private lands where they can commingle with cattle. These areas are primarily agricultural, and as such they are generally in fairly close proximity to cattle calving areas. By contrast, summer ranges tend to be more remote and located in areas used as public grazing allotments after the bulk of the transmission period has passed or not used by cattle at all. This suggests that animals that are closer to winter range when calving are also potentially closer to areas of higher cattle density. Additional data regarding seasonal cattle and elk distributions are needed to accurately quantify this potential, and this would be a worthwhile avenue for future investigations.

The degree to which increased spatial association is an issue will depend not only on whether there are overlapping parturition ranges for cattle and elk, but the potential for contact within these ranges. Parasite (disease) establishment can be enhanced by the presence of multiple host species, but can be lowered if the hosts are weakly interacting (Holt et al. 2003). Elk tend to shift their diet somewhat from browse to grassy and herbaceous species following green-up (Harper 1967), increasing dietary overlap, and potentially habitat overlap, with cattle. Elk and bison have up to a 76% habitat overlap during the spring

(Ferrari and Garrott 2002) and bison share a significant portion of their niche with cattle (Schwartz and Ellis 1981, Van Vuren 1984) and may represent the maximum potential habitat overlap of cattle and elk. There is a tendency for elk to spatially segregate from cattle when possible (Frisna 1992, Coe et al. 2001, Stewart et al. 2002, Coe et al. 2004), however, transmission may occur by contact of cattle with an infected elk parturition site in the absence of direct contact with the elk calf.

Interpretation of our results for distance traveled from winter range must be made with caution. We had relatively few study sites and, although they were all within the same system and are all generally comparable, there are local differences in topography and vegetation cover types among study sites. Our findings were based on comparisons between these sites and may reflect, to some extent, the effects of location rather than treatment. We have attempted to control for as many of the biologically important components of local variability as possible to maximize the reliability of our results, but we cannot completely discount the confounding effect of study site.

The use of emergency feeding in the free-ranging population complicated our analyses, but also provided the opportunity to examine calving date and distance traveled from winter range to parturition site for animals using or not using feedgrounds on one study area. We found earlier calving dates for animals using the emergency feedline. Research on elk calving date relative to feeding indicates that nutritional condition in the previous year affects estrus timing and changes parturition dates (Cook et al. 2004). This indicates that gestation length is relatively insensitive to current-year winter nutrition for elk. The free-ranging elk in this study may have used livestock feedlines in previous years, although attempts are made to minimize use of horse lines and to actively move elk away from cattle

lines (Bill Long pers. comm.). These animals also may have low wintering location fidelity and used state run feedgrounds or the National Elk Refuge in previous years. It is thought that the Buffalo Valley population has relatively high winter range fidelity, but heavy early snows in 2006 may have prevented some animals from moving toward feedgrounds. In fact, three radio-collared animals that wintered in the Buffalo Valley in 2006 used the National Elk Refuge for at least a portion of the 2007 winter feeding season. We did not find evidence that the fed animals were significantly closer to winter range when calving although they were closer than completely free-ranging animals. This partially matched our finding in the multi-site analysis.

While there are some apparent behavioral effects of feeding on elk, our results also quantify, to some extent, the effectiveness of current strategies to reduce this effect. The results suggest that management techniques on improved feedgrounds, including habitat improvements and shortened feeding season, may be at least somewhat effective in reducing density on parturition ranges and increasing the distance traveled from winter range, either directly or indirectly. Habitat improvements are intended to increase available winter forage, enticing animals off of feedlines during the feeding season, and ultimately can shorten the length of the feeding season (Rogerson et al. in preparation). Our results agree with brucellosis disease transmission model predictions indicating that habitat improvements alone were not likely to eliminate disease, but they could have a strong effect on prevalence (Cook 1999, Gross et al. 2004) through their effect on feeding length. We suggest that directly or indirectly reducing the length of the feeding season may contribute to reducing calving-related brucellosis transmission risk in addition to the direct effects that were modeled in previous studies.

MANAGEMENT IMPLICATIONS

Brucellosis is thought to have relatively little impact on elk populations (Kreeger 2002) and it is the potential for transmission to cattle that makes this disease controversial. Risks of transmission, especially to cattle, in any one season are probably small, but even minimal increases in these risks can considerably increase the chances of a transmission event over a longer time period (Cook 1999).

Eradication of brucellosis in elk will be dependent on much more than feedground management, but our study suggests that there are some options for managing risk within the current management paradigm. Our study suggests that a shortened feeding season would mitigate, to some extent, the effects of feeding on distribution of parturition sites. Habitat improvements may contribute to decreasing length of feeding and could be implemented in a supportive role to other feedground management practices. Creating a decision-making matrix based on these recommendations would allow managers to better control outcomes and make effective changes in feeding policy.

Large-scale rotational grazing systems in Montana have been successful in creating spatial and temporal separation between elk and cattle during the critical abortion and parturition periods while maintaining multiple use doctrines and protecting habitat (Aune et al. 2002). Community-supported interagency habitat projects have also been successful in the GYE, and have increased winter foraging opportunities for elk and may have reduced the attractiveness of cattle feedlines. Ultimately, mitigating risks of interspecific transmission, while simultaneously eliminating brucellosis in feedground elk, will require cooperation and understanding among all elk and cattle stakeholders, in addition to continued research focused on ecological aspects of brucellosis.

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CHAPTER 5. GENERAL CONCLUSIONS

We were successful in meeting our research objectives and have evaluated both the technology and the ecology associated with elk parturition in western Wyoming. We were able to determine that VITs are effective in accurately marking elk parturition locations. We classified 82.1% of VITs as marking definite/probable or possible parturition events. In particular, VITs allowed location of abortion and parturition sites independent of accessibility or cover type, eliminating any potential bias in determining parturition habitat and ranges of elk from specific wintering areas. Although the functional integrity of this relatively new technology is not perfect, it was very effective in facilitating location of calving and abortion sites and will ultimately help define parturition habitat selection and parturition ranges of specific subpopulations.

We found evidence that elk are selective at both local and landscape scales with respect to parturition habitat. At both scales hypotheses based on cover were more supported than hypotheses based on forage. Areas used for calving in this study roughly matched other records in the area (Anderson 1958, North 1990), but did not match well with WGFD calving area designations. Our results showed somewhat different selection patterns than previous studies. While these studies found sage and conifer components to be the most important (Johnson 1951, Davis 1970), we did not find support for this in our results. This may be due to our use of parturition rather than neonatal locations and the fact that our study was not biased towards vegetation cover types with greater visibility of cows and calves.

Using the parameters identified in our best models of calving habitat selection, we were able to define likely parturition ranges. This knowledge means that habitat improvements directed at enhancement of parturition ranges may be more strategically

implemented in order to increase the value of existing parturition ranges. Knowledge of parturition habitat can also guide future land acquisitions, as the quality of this habitat can have disproportionate effect on neonate and parturient female survival.

We did not find any evidence for detrimental effects of winter feeding opportunity on habitat selection behavior relative to parturition sites. Many progressive management practices follow from a concept of natural management, or using methodologies that meet management objectives but minimize interference with natural processes. To some extent, wildlife management theory can be seen as progressing from a production oriented paradigm to an ecosystem management paradigm. The artificial feeding of animals is more aligned with a production approach and leads to both ecological and ethical questions about sustainable populations, the potential for domestication and propagation of traits associated with successful feedground use, or release from selection allowing the loss of adaptive characteristics. While winter feeding of elk continues, it is important to continue to examine these populations for evidence of such an effect.

The biological ramifications of winter feeding have been pondered almost since its inception (Craighead 1958). We found evidence for differences in the spatial distribution of parturition sites with differences in winter feeding regime. Parturition sites associated with longer winter feeding periods were more aggregated and closer to winter range when we controlled for other factors. These spatial effects may increase intra- and interspecific contact rates and contribute to brucellosis transmission risk. This effect can be mitigated to some extent by a reduced feeding season either as a deliberate management decision or as an effect of local habitat improvements. To reduce intraspecific transmission among feedground elk during the parturition season, managers could focus on reducing feeding

period on low-elevation feedgrounds and potentially consider moving feedgrounds to lower elevation areas where more management options may be possible. Decreasing length of feeding on lower elevation feedgrounds may be more effective because there would not be as much of a snow or green-up barrier to movement. These animals already have a tendency to move farther from winter range for parturition.

Managing risk of transmission from elk to cattle during the calving season is also important. While feedgrounds may substantially reduce elk-cattle commingling during the peak abortion period, they are also implicated in increased intraspecific transmission and maintaining brucellosis within fed elk populations (Smith 2001, Kreeger 2002). Because feedgrounds subsequently decrease the distance moved by elk prior to calving and increase aggregation on parturition ranges, likelihood of contact between elk or cattle and infective elk parturition sites is further magnified. Specific management activities most likely to be informed by this information are the locations and timing of grazing allotments to allow for spatial and temporal separation of susceptible cattle and parturient elk (Etter and Drew 2006). Large-scale rotational grazing systems in Montana have been successful in creating spatial and temporal separation between elk and cattle during the calving period while maintaining multiple use doctrines and protecting habitat (Aune et al. 2002).

This research does not exist in a void. There is currently a suite of studies looking into various aspects of brucellosis transmission risk and feedground management. Laura Meadows is conducting her thesis research on seroprevalence, culture prevalence, and the effects of test-and-slaughter programs on brucellosis in elk. The Wyoming Game and Fish Department is also actively researching in this area, with current studies on abortion contact rates (Maichak et al. in preparation) and the effectiveness of habitat improvements (Rogerson

et al. in preparation). There are also several planned studies on changes in feeding style and experimentally altering the feeding season. Hopefully, we will soon have a much more complete understanding of brucellosis and the role that elk feedgrounds play in maintaining the disease in this system.

There is certainly no single solution to better managing calving habitat with an eye to winter feeding opportunities. We are able with this research to only address a small portion of the winter feeding dilemma. The issue of how elk feedgrounds affect both overall behavior and behaviors that could contribute to brucellosis transmission risk is an emerging area of study and with every new addition we are able to better manage risks associated with winter feeding. We have shown that there are options while still working within the winter feeding paradigm, but looking forward, it is likely that we will need to look outside of this paradigm for brucellosis management in Wyoming. The ethical dilemma, outside of the science and ecology arena still remains, whether we will attempt to retain as much of the wild character of the landscape as possible and to what degree we will tolerate its subversion. Aldo Leopold once said “The recreational value of a game animal is inverse to the artificiality of its origin and the intensiveness of the management system that produced it.” (Leopold 1931). While feedgrounds are an integral part of the current management regime, it is likely that circumstances will change this in the relatively near future and managers will need to balance the demands of many stakeholders with the tangible and intangible value of elk in one of the last intact ecosystems in the country. In the end “The elk question has always been one of diplomacy” (Sheldon, 1927).

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APPENDIX**CLASSIFICATION OF CALVING RANGES BASED ON
GLOBAL MACROHABITAT MODEL**

Delineating calving ranges is important in informing management decisions relating to this important portion of elk life history. Calving ranges can be delineated directly through observations of birth sites and neonates. With current geographic information system (GIS) technology and habitat selection models, we can also delineate areas with higher probabilities of use for a specific behavior, in this case, calving. We used a macrohabitat resource selection function (RSF) for calving habitat (Barbknecht et al. Chapter 3) to create a raster map of odds ratios of calving probability values. We then used a tree analysis in S-Plus 6.2 (Insightful Corporation, Seattle, WA, USA) to determine RSF values that represented the best cutoff points for moderate and high probability of use for parturition sites. Using these points we then reclassified the map into high, medium, and low probability categories (Figure 1).

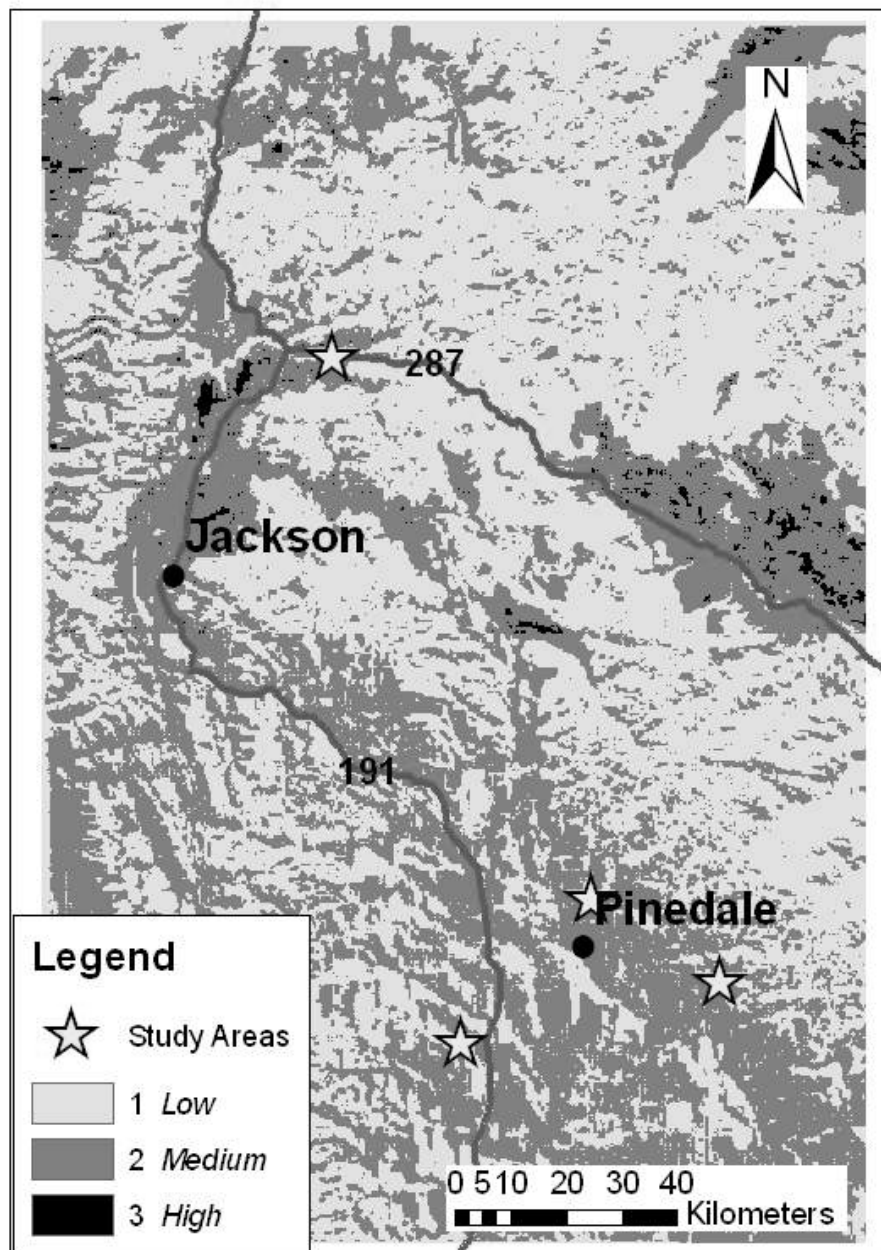


Figure 1. Elk calving range designations for northwestern Wyoming.

The RSF values we used to group categories were 0.42 for moderate probability of use and 0.82 for high probability of use. This map identifies 43% of the available area as at least moderate probability calving range. This speaks to some extent to the general habitat selection of elk at this scale and their ability to be more selective at finer scales (Barbknecht et al. Chapter 3). The overall classification success for elk used to generate the RSF was 62%. The classification success varied with location (Table 1).

Table 1. Calving range delineation classification success (%) for parturition sites by study area.

	2006	2007	Total
Bench Corral	47.8	50.0	48.0
Buffalo Valley	61.5	61.5	61.5
Scab Creek	80.0	60.7	65.8
Soda Lake	68.2	64.7	66.7

We did not have perfect classification success, but this methodology represents a minimum input way to delineate parturition habitat over a large geographical area. We suggest that this range not be used as an endpoint, but as a tool in addition to observation based delineations to inform management decisions.