

Utah State University

DigitalCommons@USU

---

All Graduate Theses and Dissertations

Graduate Studies

---

5-2007

## Breeding Behavior and Space Use of Male and Female Mule Deer: An Examination of Potential Risk Differences for Chronic Wasting Disease Infection

Leslie R. McFarlane  
*Utah State University*

Follow this and additional works at: <https://digitalcommons.usu.edu/etd>



Part of the [Biology Commons](#)

---

### Recommended Citation

McFarlane, Leslie R., "Breeding Behavior and Space Use of Male and Female Mule Deer: An Examination of Potential Risk Differences for Chronic Wasting Disease Infection" (2007). *All Graduate Theses and Dissertations*. 6619.

<https://digitalcommons.usu.edu/etd/6619>

This Thesis is brought to you for free and open access by the Graduate Studies at DigitalCommons@USU. It has been accepted for inclusion in All Graduate Theses and Dissertations by an authorized administrator of DigitalCommons@USU. For more information, please contact [digitalcommons@usu.edu](mailto:digitalcommons@usu.edu).



BREEDING BEHAVIOR AND SPACE USE OF MALE AND FEMALE  
MULE DEER: AN EXAMINATION OF POTENTIAL RISK  
DIFFERENCES FOR CHRONIC WASTING  
DISEASE INFECTION

by

Leslie R. McFarlane

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

of

MASTER OF SCIENCE

in

Wildlife Biology

Approved:

UTAH STATE UNIVERSITY  
Logan, Utah

2007

## ABSTRACT

Breeding Behavior and Space Use of Male and Female

Mule Deer: An Examination of Potential Risk

Differences for Chronic Wasting

Disease Infection

by

Leslie R. McFarlane, Master of Science

Utah State University, 2007

Major Professor: Dr. Michael L. Wolfe  
Department: Wildland Resources

The dynamics of pathogen and host relationships relative to disease transmission in wildlife populations are important ecological processes to understand, particularly since spatial dynamics of disease can be driven by movement, behavior, and dispersal of animals. Chronic Wasting Disease (CWD) is an example of this important interface, where little is known regarding origin of the disease or routes of transmission. Surveillance data for CWD in free-ranging mule deer indicates that breeding-age male deer have 2-4 times higher prevalence rates than females or younger age males. In an effort to understand differences that might increase risk for exposure to CWD infective agents, I used GPS data to examine breeding behavior and home range sizes of mule deer. GPS radiocollars were placed on adult ( $>2 \frac{1}{2}$  years) males, females, and young ( $<2 \frac{1}{2}$  years) males. Data collected during the breeding season was used to infer visitation

rates of males to females. Cluster analysis was used to separate data into periods of movement (spatio-temporal clusters) and non-movement. Females formed more spatio-temporal clusters and movement paths than males. However, males spent more time moving, had more long-term periods of movement, moved an estimated 1 km/day more than females, and had more tortuous movement paths. Male home ranges for winter, summer, and breeding seasons were also larger than those of females. Overall, data indicates that males may have an increased risk of exposure to CWD relative to females, because of larger movements and greater space use. These male behavioral differences may result in increased encounter rates with CWD infectious material through greater exposure in the environment to sources such as carcasses from infected animals, their excreta, or contaminated soils. Furthermore, during the breeding season increased male sociality, as suggested by increased movement rates and movement path tortuosity, combined with larger space use may further enhance direct contact with infected individuals and increase exposure to excreta sources such as feces and alimentary secretions due to licking and tending behaviors.

(56 Pages)

DEDICATION

To my husband who was always there for me and the rest of my family who have always said shoot for the stars, this is for you!!

Leslie R. McFarlane

## ACKNOWLEDGMENTS

I wish to acknowledge those who helped make this research project possible including the United States Geological Survey (USGS), the Association of Fish and Wildlife Agencies (AFWA), and the Utah Division of Wildlife Resources (UDWR) who provided funding for this project. I would also like to thank Alan Clark and the Utah Division of Wildlife Resources for the chance to do this once in a lifetime project and for the never-ending support. I would also like to thank my committee members Drs. Mike Wolfe, Mary Conner, and Tom Baldwin, for their support and assistance throughout the entire project. Thanks are also given to Mike Ebinger who assisted with analyses of the abundant GPS data.

I also wish to thank various employees from the Utah Division of Wildlife Resources and other volunteers for their support or assistance with trapping, collecting radiocollars, helicopter capture, and data collection including Craig McLaughlin, Heather Bernales, Guy Wallace, Stacey Jones, Bill Bates, Dave Rich, Dana Rock, and Scott McFarlane. I would also like to thank Kevin Duckett from the Colorado Division of Wildlife Resources for his assistance on the capture projects. I also wish to thank Mark Law, Mark Shelton, and the crew from Pathfinder Helicopters for their assistance with deer capture. I could not have completed this project without all of you.

Leslie R. McFarlane

## CONTENTS

	Page
ABSTRACT.....	ii
ACKNOWLEDGEMENTS.....	v
LIST OF TABLES.....	vii
LIST OF FIGURES.....	viii
INTRODUCTION.....	1
STUDY AREA .....	8
METHODS.....	10
Capture Techniques.....	10
Data Collection.....	11
Breeding Season Analysis.....	12
Home Range Size Analysis.....	16
RESULTS.....	18
Animal Capture.....	18
Breeding Behavior Analysis.....	19
Home Range Analysis.....	20
DISCUSSION.....	21
MANAGEMENT IMPLICATIONS.....	26
REFERENCES.....	28
APPENDIX.....	47
Figure 7. Detailed flow chart showing development of logical tests to evaluate the spatial location of a point relative to other points in the recent past and future.....	48

## LIST OF TABLES

Table	Page
1. Analysis of data during the breeding season(1 Nov-15 Dec) for mule deer in the La Sal Mountains, Utah during 2005 and 2006.....	37
2. Analysis of data during the breeding season (1 Nov-15 Dec) for mule deer in the La Sal Mountains, Utah during 2005 and 2006.....	38
3. Home range size for winter, summer, and breeding seasons by sex, age class, and year for mule deer in the La Sal Mountains, Utah during 2005 and 2006. Winter was defined as 15 Dec–15 April, summer was defined as 15 May–15 Oct, and breeding was defined as 1 Nov–15 Dec.....	39
4. Home range differences for winter, summer, and breeding seasons by sex, age class, and year for mule deer in the La Sal Mountains, Utah during 2005 and 2006. Winter was defined as 15 Dec–15 April, summer was defined as 15 May–15 Oct, and breeding was defined as 1 Nov–15 Dec.....	40



## LIST OF FIGURES

Figure	Page
1. Location of the La Sal Mountain study area within Southeastern Utah, showing locations of positive deer, trap site locations in 2005, and helicopter capture locations in 2006.....	41
2. CWD positive mule deer locations in the State of Utah from 2003-2006.....	42
3. Illustration of a spatial cluster algorithm which delineates the non-movement periods and show sequential locations that make up a movement path.....	43
4. Illustration showing short periods of visitation to an area that would not indicate areas of importance because they are visited during different time periods and clusters are not formed.....	44
5. Illustration of how the algorithm assigns locations to one of three classes based on both past and future behavior of the organism.....	45
6. Illustration of how a point may lie outside of a cluster either due to GPS error, animal behavior, or cluster search radius.....	46

## INTRODUCTION

The dynamics of pathogen and host relationships are important ecological processes to understand, particularly when emerging infectious diseases become established among wildlife populations. The spatial dynamics of disease in free-ranging populations may be driven by movements, behavior, and dispersal of animals all of which may act to increase exposure to disease (Gross and Miller 2001, Conner and Miller 2004, Miller and Conner 2005, Farnsworth 2006). Animal behavior is an important aspect of disease dynamics that has not been well documented but may drive transmission in free-ranging wildlife populations. For example, periodic outbreaks of rabies in raccoon (*Procyon lotor*) populations of Ontario, Canada coincide with behavior driven activities such as breeding and denning (Rosatte et al. 2006). Inadequate knowledge relating to aspects of animal behavior and disease transmission may often hinder disease management and control, placing limitations on wildlife managers.

Chronic wasting disease (CWD; Williams and Young 1980), a transmissible spongiform encephalopathy (TSE), is a contagious, slow-acting, degenerative disease that affects members of the cervid family, including white-tailed deer (*Odocoileus virginianus*), mule deer (*Odocoileus hemionus*) (Williams and Young 1980, Miller and Wild 2004), Rocky mountain elk (*Cervus elaphus*) (Williams and Young 1982, Miller et al. 1998, Miller et al. 2000, Williams et al. 2002), and moose (*Alces alces*) (Kreeger et al. 2006, Baeten et al. 2007). CWD has the greatest influence on the central nervous system resulting in weight loss, deterioration of body condition, and eventually death (Williams and Young 1980, 1982, 1992; Spraker et al. 1997, Williams et al. 2002).

Little is known regarding the exact origin of CWD and the manner of transmission, particularly in free-ranging populations, is not fully understood (Spraker et al. 1997, Miller et al. 2000, Williams and Miller 2002, Miller and Williams 2003). Previous research indicates that deer-to-deer, or deer-to-environment routes including saliva, excreta, carcasses (Miller and Williams 2003, Miller et al. 2004), and contaminated soils (Johnson et al. 2007) from infected animals are important for transmission dynamics. These routes may serve to preserve and amplify the CWD agent, particularly when mule deer gather on winter ranges or within matrilineal groups. During seasonal congregations, mule deer could potentially receive more exposure to infectious agents where they may encounter higher densities of infected animals, their carcasses, or their excreta (Williams et al. 2002, Miller and Williams 2003, Conner and Miller 2004, Miller et al. 2004, Miller and Conner 2005, Farnsworth 2006).

Whereas spatial spread of CWD between populations likely transpires through large-scale movements such as seasonal migration or dispersal, spread (transmission) within populations may be due to breeding season exchanges, and cohort interactions among sub-populations (Conner and Miller 2004, Miller and Conner 2005, Farnsworth 2006).

Surveillance data for CWD in some free-ranging mule deer populations has demonstrated differences in prevalence rates that vary by age and sex class (Miller et al. 2004, Miller and Conner 2005), although this discrimination has not been observed in captive cervids (Miller et al. 2000, Williams and Miller 2002). Observed prevalence rates in free-ranging adult male mule deer between the ages of 4-6 years is 2-4 times higher than observed prevalence rates of females or lower age class males between 1-3

years (Miller and Conner 2005). Surveillance in white-tailed deer has also shown similar age and sex variations with males exhibiting a higher overall prevalence than females that increases with age (Gear et al. 2006). Other TSE diseases such as variant Creutzfeldt-Jakob disease (vCJD) and Bovine Spongiform Encephalopathy (BSE) also indicate similar discrepancies in prevalence by age (Heisey and Joly 2004). In deer, it is hypothesized that reproductive behavior is a social interaction that may influence the observed prevalence rate differences in sex and age class (Conner et al. 2000, Gear et al. 2006, Miller and Conner 2005, Farnsworth 2006).

During the breeding season, mule deer practice serial polygyny, with the females being polyestrous, a system that obligates the male to form a tending bond to the female (Kucera 1978, Geist 1981). In polygynous mule deer, the female attracts the male, possibly by increasing her activity during the breeding season (Releya and Demarais 1994). The male will then tend the female until she enters estrous, or he is displaced by another male, and then the displaced male will search out another female (Kucera 1978, Geist 1981, Releya and Demarais 1994). Observations of behavior during the breeding season have shown that males will roam large areas searching for receptive females and that rutting males of all ages participate (De Vos et al. 1967, Kucera 1978, Geist 1981, Releya and Demarais 1994, Nicholson et al. 1997). Interactions among males also increase during the breeding season, as males try to disrupt the tending bond to steal the female and challenge each other for the breeding right (DeVos et al. 1967, Kucera 1978, Geist 1981, Koutnik 1981, Nicholson et al. 1997).

The male determines the breeding receptivity of a female by testing previously voided urine (DeVos et al. 1967, Kucera 1978, Geist 1981) or by stimulating the female

to urinate through intense licking and nuzzling of the vulva and perineal area (DeVos et al. 1967, Kucera 1978). During the breeding season, this pre-copulatory act of licking performed by males may be quite extensive (Kucera 1978, Geist 1981). Transmission of CWD may occur through contact with excreta such as feces (Williams and Miller 2002, Miller and Williams 2003, Miller et al. 2004, Miller and Conner 2005) and alimentary tract secretions (Wolfe et al. 2007), which males may contact while testing females for receptiveness. Therefore, it is hypothesized that breeding age adult males that broaden their movements and test females for receptivity may be exposed to the CWD agent more than younger age class males. Additionally, through this behavior an infected female may expose multiple males throughout the breeding season (Miller and Conner 2005, Conner et al. 2007).

Distribution of CWD on the La Sal Mountains appears to be heterogeneous (Figure 1), similar to distributions of CWD observed in Colorado, with CWD occurring in patches across the landscape most likely influenced by spatial, temporal, and demographic dynamics (Conner and Miller 2004, Farnsworth 2005, Miller and Conner 2005). Hence, descriptions of movement, migration routes, and an account of detailed interactions between mule deer and their use of landscape (Farnsworth 2005, Miller and Conner 2005, Conner et al. 2007) on the La Sal Mountains may lead to an increased understanding of CWD spatial dynamics.

Landscape use is defined through knowledge of home range sizes and dispersal movements, and may direct effective management options particularly where disease is involved. Mule deer interactions and movements are known to be quite complex and not all populations behave in similar manners. Previous home range estimations and

observations of mule deer populations have revealed that individuals can be highly mobile and may migrate great distances between seasonal ranges (Garrott et al. 1987, D'Eon and Serrouya 2005), while others are essentially non-migratory (Eberhardt et al. 1984). Descriptions of some populations have reported a mixture of both migratory and non-migratory mule deer (Kufeld et al. 1989, Brown 1992, Nicholson et al. 1997, Conner and Miller 2004). Furthermore, complicated patterns of movement may also involve migration of mule deer from one seasonal range to another while traversing through seasonal ranges occupied by other populations (Gruell and Papez 1963, Nicholson et al. 1997).

Previous home range analyses of several mule deer populations have shown that groups of deer show seasonal site fidelity (Robinette 1966, Garrott et al. 1987, Kufeld 1989, Brown 1992, Nicholson et al. 1997, Conner and Miller 2004) and groups tend not to coalesce with other groups (Geist 1981, Conner and Miller 2004). Groups tend to be matrilineal with a dominant matriarch, who will often allow young related females to stay within the group, but will behave antagonistically toward young males chasing them from home ranges. This often results in dispersal of young males, usually 12-30 months of age, causing them to establish a new individual home range (Robinette 1966, Geist 1981). Adult males are reported to have larger home range sizes than females, sometimes as much as 50% (Robinette 1966) and yearling males are thought to have home ranges larger than females (Dasmann and Taber 1956). These intricate dynamics are likely important for understanding CWD distribution among mule deer in the La Sal Mountains.

As discussed, male behavior during the breeding season may increase the probability of exposure to CWD through greater environmental movements and increased

contact with multiple females (Miller and Conner 2005, Conner et al. 2007). In addition, the behavior of males to test females for breeding receptivity by licking and nuzzling the vulva and perineum (DeVos et al. 1967, Kucera 1978) may lead to direct contact with infected excreta, such as feces and alimentary tract secretions (Wolfe et al. 2007) further enhancing the risk for CWD infection. Because, I could not directly observe and count male visitations to females I used GPS location data to infer visitation. I used short-term spatio-temporal clusters to infer when a male is tending a female. Although, these same clusters may also signify feeding or bedding behaviors, I speculated that tending behaviors would be discernable because I expected them to be shorter in duration than clusters found in female data. I anticipated that both sexes would have a baseline rate of non-movement clusters, but I predicted that males would have a higher number when compared to females due to extra “stops” made when visiting or tending females. Based on these observations, I chose to evaluate the following spatio-temporal cluster hypotheses:

- H<sub>1</sub>: Males would have more spatio-temporal clusters than females.
- H<sub>2</sub>: Males would spend less time in spatio-temporal clusters than females as a result of visiting more females, thus spending less time in clusters when compared to females.
- H<sub>3</sub>: Males would have fewer “long-term” spatio-temporal clusters than females.

Additionally, I believed that the searching and tending behavior of males may be represented in GPS data through increased movements as they visited multiple females. Consequently, I expected that males would have more movement paths, would spend a

greater amount of time moving, and would move at greater rates than females during the breeding season. Additionally, if males did move from female to female during the breeding season I expected male movement paths to exhibit more tortuosity than females, which may indicate searching or tending behavior. Based on suggested links between CWD infection, movement, and breeding behaviors, I tested the following hypotheses based on GPS location data collected during the breeding season:

- H<sub>4</sub>: Males would have more movement paths than females.
- H<sub>5</sub>: Males would spend more time moving in movement paths than females.
- H<sub>6</sub>: Males would have more “long-term” movement paths than females.
- H<sub>7</sub>: Males would have greater movement rates than females.
- H<sub>8</sub>: Males movement paths would be more tortuous than female movement paths.

Research has also indicated that movement and space use may likely increase indirect contact with infectious CWD agents in the environment. In accordance, if males have larger home range sizes than females, they are more likely to come in contact with areas of infectious CWD material in the environment. I expected exposure to be the most pronounced in winter when mule deer population densities are the highest and when the probability of contact with deposited infective material (e.g., excreta and infected carcasses) is the densest. An increased home range size may also lead to an increased probability of direct contact with an infected deer while moving through multiple smaller home ranges, which may be further amplified by behavior during the breeding season. Based on these possible associations, I tested the following hypotheses about home ranges:



- H<sub>0</sub>: Male winter home range size would be larger than that of females.
- H<sub>10</sub>: Male summer home range size would be larger than that of females.
- H<sub>11</sub>: Male breeding home range size would be larger than that of females.

## STUDY AREA

CWD was detected in Utah in free-ranging mule deer in late 2002 and has been found to occur in 3 distinct geographic areas distant from one another in the northeastern, central, and southeastern parts of the state (L. R. McFarlane, Utah Division of Wildlife Resources, unpublished data; Figure 2). Surveillance data from Utah indicates that CWD is present in <1% of male deer in the central and northeastern areas, while on the La Sal Mountains of southeastern Utah prevalence in male deer is approximately 2% (L. R. McFarlane, Utah Division of Wildlife Resources, unpublished data). I chose the La Sal Mountains for the study area because of the higher CWD prevalence rate in mule deer.

The La Sal Mountains are the second highest mountain range within Utah and straddle the Utah-Colorado border, spanning both Grand and San Juan counties (Figure 1). The range encompasses approximately 221,374 ha and contains 6 peaks that rise above 3,600 m, with elevations ranging from 1,524 to 3,877 m (Pederson and Harper 1978).

Climate is typical for the intermountain west with dry, warm summers and cold, snowy winters. The La Sal Mountains had a mean annual precipitation of 31 cm, with the majority of precipitation occurring during fall rain showers and from winter snow accumulation (WRCC 2005). The mean annual temperature recorded at La Sal, Utah was 7.8° C with monthly means of -4.2° C in January and 20.6° C in July (NRCS 2005).

Winter habitat of mule deer in the La Sal mountain range includes sagebrush-steppe interspersed with pinyon-juniper and ranges in elevation between 1,600 to 2,400 m. Predominant winter range vegetation consists of Wyoming big sagebrush (*Artemisia tridentata wyomingensis*), blackbrush (*Coleogyne ramosissima*), low rabbitbrush (*Chrysothamnus viscidiflorus*) Utah juniper (*Juniperus osteosperma*) and pinyon pine (*Pinus edulis*). Perennial grasses consist of crested wheat (*Agropyron cristatum*), western wheat (*Agropyron smithii*), cheat grass (*Bromus tectorum*), Indian rice grass (*Oryzopsis hymenoides*) and bottlebrush squirreltail (*Sitanion hystrix*) (Davis et al. 1999).

Primary summer habitat occurs at higher elevations of 2,100 to 2,400 m and consists of a mixture of aspen and clumps of oak with open meadows dominated by snowberry (*Symphoricarpos oreophilus*). Predominant browse species include mountain big sagebrush (*Artemesia tridentata vaseyana*), Gambel oak (*Quercus gambelii*), serviceberry (*Amelanchier utahensis*), chokecherry (*Prunus virginiana*), alder leaf mountain mahogany (*Cercocarpus montanus*) and snowberry (Davis et al. 1999). Coniferous species include Englemann spruce (*Picea engelmannii*), white fir (*Abies concolor*), Douglas fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*) (Smith 1983). Perennial grasses and forbs consist of Thurber fescue (*Festuca ovina*), Kentucky bluegrass (*Poa pratensis*), lupine (*Lupinus argenteus*), peavine (*Lathyrus lanszwertii*), dandelion (*Taraxacum officinale*), and Oregon fleabane (*Aster spp.*) (Smith 1983, Davis et al. 1999).

Principal land use consists of livestock grazing and some activities relating to mining, oil, and gas drilling. Historically, leases for 6,100 cattle and horses and 21,000 domestic sheep were allotted for grazing on the mountain range as early as 1907.

Currently, sheep grazing is limited to private lands on the range and cattle are permitted to graze U.S. Forest Service lands. Recreation and tourism are common activities in this area, but occur mostly on lower desert areas in National Parks and along the Colorado River. Some farming and agriculture occurs on limited private land areas (Davis et al. 1999).

## METHODS

### Capture Techniques

Throughout the study captures were made and conducted using a variety of capture techniques including Clover traps (Clover 1956), drop nets (Peterson et al. 2003), chemical immobilization (Jessup et al. 1983, Kilpatrick 1997, Caulkett et al. 2000), and helicopter netgunning (White and Bartmann 1994). Trap site locations were limited to areas that were accessible during the time of year and to places that wintering elk were not likely to interfere with trapping activities. Capture techniques were approved based on the Institutional Animal Care and Use Committee (IACUC) guidelines for Utah State University (USU; Permit #1187) and the Utah Division of Wildlife Resources (UDWR).

During the first year of the study (2005) I classified captured males either as young (1 ½-years-old) or adult (>2 ½-years-old) based on tooth replacement and wear (Robinette et al. 1957) and all animals were captured and handled using Clover and drop net trapping. The second year of the study (2006) a commercial helicopter capture company performed the capture work, so I verified sex and age class of collared deer from photographs taken by the helicopter capture crew.

For this study, mule deer were captured when they were concentrated on key winter ranges between 1,600-2,100 m in elevation during the winters of 2005 and 2006

(Figure 1). Both males and females were fitted with GPS 4400S<sup>TM</sup> radiocollars (Lotek Engineering, Newmarket, Ontario, Canada) that were programmable using two-way radio communications. This capability allowed me to alter point collection schedules as needed. Radiocollar battery life was limited to approximately 1 year, so the collars were also equipped with remote release mechanisms programmed to deploy in 48-52 weeks. This allowed me to recover and refurbish radiocollars in order to reapply them to a new group of mule deer the following year. I provided extra space on male radiocollars to allow for swelling of the neck during the breeding season.

#### Data Collection

For all data analyses, I defined winter, summer, and breeding seasons as well as migration periods. For consistency, I defined “winter” from 15 December – 15 April, “summer” 15 May – 15 October and “breeding” from 1 November – 15 December. The dates between 15 April – 15 May and 15 October – 1 November were considered migration periods as the data indicated that deer were moving between ranges.

Point collection schedules were kept the same for the 2 years of the study. Actual migration dates were unknown at the time of study design, so I purposefully made the periods that location data were collected longer than the seasons defined above to ensure that I would capture actual migration periods. As a result from 1 January to 15 March a location was taken every 12 hours, then to capture spring migration and movements the number of locations was increased to a point collected every 6 hours for the period of 16 March – 30 June. Beginning 1 July – 14 October, I changed the schedule to collect a point every 12 hours, because all animals were believed to be on summer ranges and movements were thought to decrease. During the breeding season, I changed the fix

schedule to collect a point every 30 minutes in order to capture fine scale data beginning 15 October until the collars dropped off and were recovered usually by mid-January the following year.

I recovered collected data from the retrieved radiocollars using a Lotek Handheld Command Unit<sup>TM</sup> (HCU) and Lotek software<sup>TM</sup> (Lotek Engineering, Newmarket, Ontario, Canada). In addition to GPS data collection, radiocollared deer were located using aerial telemetry every 8 weeks between 0800-1500 hours using a Cessna 185 fixed-wing aircraft with a two-element Very High Frequency (VHF) Yagi antenna mounted to each strut of the airplane. For each deer that was relocated Universal Transverse Mercator (UTM) coordinates were recorded using a Long Range Navigation (LORAN) GPS system to monitor radiocollars, animal locations, and mortality signals. Occasionally, I downloaded data remotely from the collars using the Lotek HCU, a VHF receiver, two VHF antennas, and one Ultra High Frequency (UHF) antenna mounted to the strut of the airplane to check that collars were functioning correctly.

#### Breeding Season Analysis

After downloading data from the Lotek collars I used ArcGIS to project the geographic coordinates (latitude/longitude) to the UTM projection. For all analyses, I used ESRI ArcGIS 9.1 and Statistical Analysis Software v9.1 (SAS; SAS Institute Inc. 2002-2005) to prepare the data.

My hypotheses required that I examine location data and the formation of spatio-temporal clusters to infer visitation rates of males to females during the breeding season. These behaviors were buried within high resolution temporal and spatial GPS data. Therefore, I had to determine how to organize this data into meaningful structures for

interpretation. This is a common problem facing wildlife researchers studying location data using either VHF radio telemetry or finer-scale GPS data (Schwager et al. 2007). One structure useful to understanding animal space-use is the separation of movement data into periods of “movement” and “non-movement.” Partitioning data in this manner allows both types of behavioral bouts (i.e. movement and non-movement) to be used as the analytical unit for subsequent analyses.

This methodological approach uses cluster analysis as the principal tool for assigning GPS locations to one of the two structural states (i.e. movement or non-movement). Generally speaking, a spatial cluster algorithm delineates the non-movement periods, while sequential locations between two clusters in time are considered members of the same movement path (Figure 3). Although, space-time clustering algorithms can clearly delineate clusters, and thus movement paths, they can also mask interesting and important information. For example, CWD transmission in mule deer is possible at areas of congregation, such as mineral licks or food sources. If visitations to these areas are short in duration (i.e. too few locations to form a cluster), but numerous over longer periods of time (i.e. seasonal), traditional space-time clusters may fail to identify this important underlying pattern (Figure 4).

I used a more conservative methodology that circumvents the problem of repeated short visitations over long time periods. The concept was designed for short interval GPS data (e.g. 5 minute location intervals) but is easily modified to fit almost any GPS schedule (M. R. Ebinger, unpublished data). It is a two-step process which begins with a purely spatial clustering of GPS locations. These a-temporal clusters are referred to as “global clusters.” After this clustering is complete the dataset is processed sequentially

from the first location to the last for each individual. A set of logical if/then statements are used to assign GPS locations to either spatio-temporal clusters, designated as “local clusters,” or alternatively to individual movements paths (Appendix, Figure 7). The details of this process are outlined below.

*Step 1: Purely Spatial Cluster Analysis (Global Clusters).* - I selected a clustering algorithm based on nonparametric density estimation. Although this family of clustering algorithms have less power to detect clusters (compared to their parametric counterparts), they excel at the detection of non-spherical clusters and clusters with unequal variances. I used PROC MODECLUS in SAS, with a search radius ( $r$ ) of 20m to delineate clusters and define groups of locations representing non-movement. I tried several different radii through a visual trial and error process and ultimately selected this radius. The radius selected is dependent on 1) the interval between locations, and 2) the type of organism being tracked. Visual inspection of the dataset is sufficient to evaluate the performance of a particular search radius (M. R. Ebinger, unpublished data).

*Step 2: Assignment of local clusters and movement paths.* - I used SAS to partition out local clusters from the set of global clusters created in the purely spatial cluster analysis (Step 1). I developed a set of logical tests to evaluate the spatial location of a point relative to other points in the recent past and future (see Appendix, Figure 7 for a detailed flowchart). Based on the recent movement behavior of the organism in time (both past and future), the algorithm will assign the location to one of three classes; a) a new local cluster, b) a member of an existing local cluster, or c) not a member of a local cluster (i.e. part of a movement path) (Figure 5). Taken together, the group of “if/then” statements at first appears overly complex (see Appendix, Figure 7). However, they are

necessary to prevent spurious clusters and movement paths from developing in the dataset. For example, often a point that is temporally located in the middle of a cluster will lie just outside of this cluster spatially (Figure 6). The outside location may be due to GPS error, an artifact of the global clustering search radius (e.g., the chosen radius is too small), or simply the animal's behavior itself (e.g., brief, short-distance foray). By allowing this single location outside the cluster to split the cluster into 2 distinct clusters, will create a spurious local cluster (and movement path). My algorithm (Appendix, Figure 7) sought to prevent, or at least minimize, these spurious classifications based on observed distances and patterns created by the data. I used the same rules to analyze both sex and age classes. Once the location points are classified into a cluster based on the radius the remaining points between clusters form the movement paths. Movement paths begin and end when the animal moves from a cluster and arrives at the next cluster.

*Step #3: Calculation of the straightness index.* - For each unique movement path I calculated a straightness index (Benhamou 2004), which provides a value of the relative tortuosity of a movement path. The index ( $D/L$ ) is calculated as the ratio between the distance between the starting and ending locations of a movement path ( $D$ ) and the actual distance of the path ( $L$ ). A  $D/L$  index of 1 indicates that the animal moved in a perfectly straight line, while deviations toward zero indicate a more tortuous path.

I then used an analysis of variance (ANOVA) model with a repeated measures structure (PROC MIXED; Littell et al. 1996; SAS v9.1; SAS Institute Inc. 2002-2005) to test the hypotheses that cluster formation, movements, and movement path tortuosity would be greater for males during the breeding season than for females. The model construction strategy for analyzing the reproductive behavior was to:



- 1). Construct a global model that included age and sex as a fixed effect, time as a categorical variable, and deer modeled as a random component;
- 2). Fit 4 variance structures to the global model and use Aikake's Information Criterion (AICc) model selection to choose the best structure. The 4 variance structures I evaluated were:
  - a) Variance between deer in their mean behavior rates was allowed to differ by sex and age class;
  - b) Variance within deer (via the repeated measurements) was allowed to differ by sex and age class;
  - c) Both forms of variance were heterogeneous between groups (a and b above); and
  - d) Both forms of variance were homogeneous between groups.
- 3). For the global model with the best variance structure, fit 3 covariance structures to model covariance of the repeated measurements for each response variable and use AICc model selection to choose best structure. The covariance structures I evaluated were appropriate for unequal time intervals and missing data (Littell et al. 1996): variance components (no covariance between measurements, but accounts for repeated measurement and random effects), compound symmetry, and spatial power, which is an autoregressive covariance structure generalized for unequal time intervals.

### Home Range Size Analysis

The several methods that currently exist for estimating home range sizes basically comprise two conceptual approaches. One group features contouring methods such as

least squares cross validation (LSCV) and kernel density estimators (KDE). While, other methods such as the minimum convex polygon (MCP) use centers of activity to place the smallest polygon possible, including outlying points, to build the shape of the home range. Choosing one method over another can be difficult, but ultimately it may depend on the amount and type of data collected and the questions asked (Kenward et al. 2001). Girard et al. (2002) suggest that if the purpose of the study is home range comparisons between groups (i.e. sex and age classes) that the selection of the exact estimator is not as crucial as using comparable sampling efforts for each group.

For comparison of home range size between groups Girard et al. (2002) found that adequate comparisons of home range size could be made using the MCP method if collection fixes are taken between 1-3 times a day and the minimum number of individuals followed is 20. When using other methods for home range estimations such as KDE or nearest-neighbor cluster analysis, the requisite number of individuals needed for within group comparisons doubled. Additionally, when using GPS data for home range analyses, clustering and KDE produced high variability when compared to MCP, particularly if the sample size was small (Girard et al. 2001). Furthermore, LSCV and KDE, home range sizes tended to over-estimate if the data set is large and animals return to chosen areas repeatedly (Hemson et al. 2005).

Based on these findings, I selected the MCP method and home ranges were calculated using the program HRE<sup>TM</sup> (Rodgers and Carr 1998) in ESRI ArcGIS 9.1. Home range sizes were estimated using 100, 95, 90 and 85% of the fixes and were examined visually to determine which best represented the data without adding large tracts of unused space. I chose to use 90% of the fixes because it removed the outliers,

which represented either occasional forays or GPS error, thus eliminating large areas of unused space from my analyses.

The largest source for GPS error comes from inaccurate location acquisition or unsuccessful location attempts (Frair et al. 2004, Hebblewhite et al. 2006) that may result from topography, animal behavior, satellite location, time of day, season, or time between fixes (Hebblewhite et al. 2006). Location inaccuracy may not be much of a concern because errors in location accuracy are reported to be  $\leq 31\text{m}$  95% of the time (Frair et al. 2004). However, missing location data can greatly affect studies that evaluate habitat or resource selection with missing locations causing bias in selection or avoidance estimations (Frair et al. 2004). A fine scale examination of resource selection was not part of this study, therefore I did not believe that GPS error would effect the analysis of cluster or movement data. However, I did chose to correct missing location data by using SAS to examine both the past and future location and replace the missing value mid-point between these two locations. Since my analyses involved examination of cluster and movement paths, replacement of missing values was not considered an issue because past and future locations were used to determine the location of the missing point. Hence, if the missing value was part of a movement path or a cluster the placement of the missing value mid-point between the two known values would constitute a continuation of either a movement path or a cluster.

## RESULTS

### Animal Capture

Between 5 January - 10 February 2005, I captured and radio-collared 21 mule deer; 17 were captured using Clover traps ( $n = 8$  adult females, 3 adult males, and 6

young males) and 4 using a drop net ( $n = 2$  adult females, 1 adult male, 1 young male). On 30 January and 31 January 2006, I used helicopter netgunning to capture and radio collar 35 mule deer ( $n = 8$  adult females, 14 adult males, 13 young males). Some of the female radiocollars (2) from the previous year were not recovered in time for the helicopter capture and 1 young male collar slipped off shortly after it was deployed. I recovered these collars and later captured 2 adult females and 1 adult male and applied these radio collars using chemical immobilization on 21 June and 22 June 2006.

### Breeding Behavior Analysis

Before the start of the breeding season, some deer were harvested, killed by vehicles or, predators, died from unknown causes, or slipped their collars resulting in a total of 25 deer ( $n = 13$  adult females, 6 adult males, 6 yearling males) used in breeding season analyses (Table 1). The number of locations per animal ranged between 1,388 and 2,158, with an average of 2,190 locations per animal (Table 1).

Because sample sizes were smaller than expected, I began each analysis of breeding season movement behavior by constructing 2 models; one with age and sex categories (i.e., adult female, adult male, and young male) and one with just sex categories (i.e., adult and young males grouped). Using AICc values I found that the sex only model fit better ( $\Delta\text{AICc} > 2$ ) for all comparisons. Consequently, I present all results for breeding behavior by sex. For all repeated measurement analyses (i.e., time spent in cluster, time spent in movement path, movement rate, and movement path tortuosity), the best model included heterogeneity in the variance between and within animals by sex. The best covariance structure was variance components for all analyses.

Analysis of cluster data indicates that females formed 25% more clusters compared to males and this difference was significant ( $P \leq 0.001$ ; Table 2). However, neither the time spent in clusters nor the number of long (>5 hr) clusters differed between sexes (Table 2).

Examination of movement path data demonstrates that females formed 18% more movement paths than males ( $P = 0.003$ ; Table 2). In contrast, the overall time spent in movement paths was 71% greater for males than females ( $P \leq 0.001$ ; Table 2) and the number of long (>5 hours) movement paths was 114% greater for males than females ( $P < 0.001$ ; Table 2). The movement rate per day of males (6.8 km/day) was 17% higher than females (5.9 km/day), but this difference was only marginally significant ( $P = 0.106$ ; Table 2). Lastly, male movement paths were 18% more tortuous than females whose movement paths were shorter and straighter ( $P \leq 0.001$ ; Table 2).

#### Home Range Analysis

The mean number of points (28-339) used to estimate winter home range was 226 (54-339) for females, 211 (55-331) for adult males, and 249 (28-334) for young males. Mean winter home range sizes were 113-132% larger for the adult males than for females ( $P \leq 0.001$  in 2005,  $P = 0.004$  in 2006; Tables 3 and 4). Mean winter range sizes were 111-154% larger for young males than for females ( $P = 0.004$  in 2005,  $P = 0.011$  in 2006; Tables 3 and 4). Winter home range sizes for the male groups did not differ from one another (Table 4).

The mean number of points (176-602) used to estimate summer home range was 426 (267-522) for females, 402 (176-526) for adult males and 382 (212-602) for young males. Mean summer home range sizes were 160% larger for the adult males than for

females in 2006 ( $P = 0.012$ ) and no difference was found in 2005 (Tables 3 and 4). Mean summer range sizes were 111-130% larger for young males than for females ( $P = 0.035$  in 2005,  $P \leq 0.001$  in 2006; Tables 3 and 4). Summer home range sizes for the male groups did not differ from one another (Table 4).

The mean number of points (1,251-1,945) used to estimate breeding home range was 1,889 (1,251-1,945) for females, 1,937 (1,900-1,945) for adult males, and 1,883 (1,726-1,944) for young males. Mean breeding home range sizes were 247-267% larger for the adult males than for females ( $P = 0.025$  in 2005,  $P \leq 0.001$  in 2006; Tables 3 and 4). Mean breeding range sizes were not different for young males than females in 2005, however in 2006 they were 390% larger for young males than for females ( $P \leq 0.001$ ; Tables 3 and 4). Breeding home range sizes for the young male group were not different from the adult male group in 2005, but in 2006 they were 41% larger ( $P = 0.044$ ; Tables 3 and 4).

## DISCUSSION

One of my initial predictions was that during the breeding season male deer would have more spatio-temporal clusters than females. I based this prediction on observations that during the breeding season males wander throughout the breeding season, often staying in an area to tend a receptive female anywhere from one to several days (De Vos et al. 1967, Kucera 1978, Geist 1981, Releya and Demarais 1994, Nicholson et al. 1997). Additionally, females enter estrous several times during the breeding season until bred, but overall the period of receptivity is relatively short (De Vos et al. 1967). Therefore, I believed that tending behavior of males would appear in GPS data as clusters, or periods of non-movement. In particular, more clusters would be

formed by males if a male was tending and traveling between females during the breeding season. However, contrary to my prediction, I found that females formed more clusters than males. Moreover, there were no differences between sexes in the amount of time spent in clusters, or the number of clusters that lasted for periods longer than 5 hours. The fact that no differences were detected could be the result of behavioral activities being embedded within clusters and these activities may be difficult to elucidate. Consequently, with respect to male tending behavior, movements rather than non-movements, may be more informative regarding male tending behavior.

Nicholson et al. (1997) found that males move considerably more during the breeding season and winter months than females. For that reason, this prompted an additional comparison of male and female movements, namely that during the breeding season males would have more movement paths, spend more time moving, have more “long-term” movement paths, move at greater rates, and have more tortuous paths than females. The tortuosity of a path has been used as an indicator of efficiency often describing space use and foraging behaviors. More efficient paths should be straight and direct while wandering animals tend to have more convoluted paths (Benhamou 2004).

Contrary to my predictions, females formed more movement paths than males, but the nature of these movements were different. Males spent more time moving and had greater periods of movement that lasted for longer than 5 hours. Additionally, there was a borderline difference in movement rates detected between the sexes, with males moving an estimated 1 km/day more than females. Other studies have estimated movement rates for mule deer in the intermountain west, but none estimated separate rates for males and females that I could use for comparison with this study (Thomas and

Irby 1990, Sawyer et al. 2005). Additionally, I found that male movement paths were more tortuous than female paths, which is likely indicative of searching and tending behaviors. The longer and more tortuous male movement paths may include tending stops that I have not determined how to delineate.

These results indicate that males and females are moving differently during the breeding season. The greater tortuosity of male paths is an indication of greater wandering and searching, which points toward increased sociality toward females and other male deer. It may be that longer male movement paths include female sampling or tending stops that were not identified by my spatio-temporal clustering rules and algorithms. Regardless, the increased movement rate and greater tortuosity of movement for males may lead to increased exposure to CWD infectious agents through broader indirect contact with environmental sources such as excreta, saliva, and alimentary secretions, as well as increased probability of direct contact with infected individuals. This suggested higher male rate of indirect and direct contact with infectious CWD agent may lead to increased CWD infection rates and hence explain the higher prevalence rates observed in breeding-age mule deer.

Several factors including aspects of landscape, habitat, (Kie et al. 2002) and individual characteristics such as body size and weight are thought to influence home range size. Based on a comparison of home range sizes for several mammal species Harestad and Bunnell (1979) concluded that home range sizes vary by age and sex class. In general, males tend to have larger home ranges than females (Pac et al. 1988, Gompper and Gittleman 1991) and home ranges for sub-adults tend to be larger than home ranges for adults, most likely a consequence of dispersal movement (Harestad and Bunnell



1979). Based on these observations, I predicted that male deer would have larger winter, summer, and breeding home range sizes than female deer.

In general, the predictions regarding home range sizes were met. Male mule deer had larger home range sizes than females for all seasons. Differences in home range sizes were especially dramatic during the breeding season; mean male home range sizes were 247-267% larger than those of females. This difference was slightly less dramatic during the winter season in which mean male home range sizes were 111-154% larger than those of females. Both these differences were significant. Although, the mean male home range size was larger than that of females for the summer as well, the results were mixed, with only one year showing significant difference.

For all seasons, larger home range sizes may result in increased exposure to infectious CWD agent. It seems likely that the largest risk of contacting CWD agent due to larger home range sizes would occur primarily during the breeding season and secondarily during the winter season. During the breeding season, males have an increased probability of direct contact with an infected deer while moving through the home range, which may be further amplified by licking and nuzzling behavior to test for female receptiveness. Further amplification may come from increased indirect contact, through larger environmental contact with infectious CWD material, which may be more concentrated within home ranges, particularly in winter. During the winter months CWD exposure is expected to be more prominent because mule deer are congregated at higher population densities, thus increasing the probability of contact with other deer and dense concentrations of deposited infective material (e.g., feces and infected carcasses).

Overall, male movements were longer and they used more space than females which may increase their risk of exposure to CWD, relative to females. Increased movements and space use could result in an increased encounter rate of infectious agent from other infected animals, their carcasses, excreta, or contaminated soils. Contaminated sources in the environment, such as soil, may remain infective for several years (Johnson et al. 2007); if males through increased movements are exposed to these sources more than females, their probability for exposure to CWD increases. Additionally, increased sociality for males during the breeding season, as suggested by increased movement rates and movement path tortuosity, combined with larger space use further enhances direct contact with infected individuals. Furthermore, increased interactions among males also may lead to greater indirect contact with infectious materials in the environment.

The fact that no difference was noted between the young and adult male classes throughout this study most likely is an artifact of sample design and the time of year deer were collared. For a yearling to truly be a yearling, I would have had to collar males for the young age class as fawns and subsequently followed them through their first year of life. I ran into a technical problem with GPS collars for this age class. The collars would have to be small enough to fit a 6-7 month old fawn, but large enough to allow for growth throughout the subsequent year, in addition to an allowance for neck swelling during the breeding season. This option was not available in GPS radiocollars at this time. Therefore, when deer were radiocollared in December – January of both years young males were actually 1 ½-years-old. Subsequently, young males are followed throughout their 2<sup>nd</sup> year of life and may actually be participating in breeding activities as well as

taking on more mature male behavioral characteristics. Additionally, home range comparisons between male age classes may have been influenced by the fact that male sample sizes for both years, particularly 2005, were small, which resulted in high SE values, resulting in an inability to detect a difference possibly because of lack of power to detect a difference.

#### MANAGEMENT IMPLICATIONS

GPS telemetry is still a relatively new technology for marking and re-sighting wildlife. Traditional methods, such as VHF radio collars, require that researchers manually collect data points during set time intervals. Due to time and logistical constraints, the amount of data collected is often limited compared to GPS radio-collars, which can hold large quantities of data (>4,100 locations/deer/year for my study). This is probably the greatest advantage to GPS telemetry, the ability to collect large amounts of accurate location data, with minimal impact to the organism being studied. To date, GPS radio-collars have been used in a variety of research projects and analyses. Some of these projects have been methodological in nature, such as those focused on determining the accuracy of GPS data and appropriate sampling frequencies (Girard et al. 2002, Mills et al. 2006) or evaluating home range estimators (Girard et al. 2002, Terranova et al. 2005). Several ecological studies have examined movement and migration patterns (D'Eon and Serrouya 2005, Sawyer et al. 2005, Burdett et al. 2007) and habitat use (D'Eon and Serrouya 2005). Outside of movement and habitat use, little research has yet focused on other aspects of behavioral activity. I was unable to find anything in the literature relative to breeding behavior in mule deer or any other species. To my knowledge, this is the only project that uses GPS location data to examine aspects of breeding behavior.

Consequently, methods for examining GPS data are still being developed or are in active research phases. This study is an example of a potential methodological approach to quantify GPS data into structural or behavioral states for analysis, from which to better define animal space-use. Partitioning data in this manner allows types of behavioral bouts (e.g., movement and non-movement) to be used as the analytical unit for subsequent analyses. I hope these methods will be a useful step for broadening the understanding of animal movements and behaviors.

The analysis of non-movement clusters was not as effective as hoped, although I believe that unidentified aspects of behavior exist within patterns of cluster formation. Several new ideas/hypotheses about movement and breeding behavior occurred to me when I was evaluating my a priori hypotheses. For example, the spatial distribution of clusters relative to feeding and bedding sites may differ between males and females resulting from male visitations to estrous females. Additionally, examination of the patterns of movement relative to how males and females move during the breeding season and how to infer visitation rates by males to females still needs development. A better understanding of these factors may yield useful information about the dynamics of CWD, and certainly other diseases, that may be useful for management purposes. Much development of methodology is needed before we can fully exploit GPS location data to examine the behavior of wildlife.

## REFERENCES

- Baeten, L. A., B. E. Powers, J. E. Jewell, T. R. Spraker, and M. W. Miller. 2007. A natural case of chronic wasting disease in a free-ranging moose (*Alces alces shirasi*). *Journal of Wildlife Diseases* 43:309-314.
- Benhamou, S. 2004. How to reliably estimate the tortuosity of an animal's path: straightness, sinuosity, or fractal dimension? *Journal of Theoretical Biology* 229:209-220.
- Brown, C. G., 1992. Movement and migration patterns of mule deer in Southeastern Idaho. *Journal of Wildlife Management* 56:246-253.
- Burdett, C. L., R. A. Moen, G. J. Niemi, and D. L. Mech. 2007. Defining space use and movements of Canada lynx with global positioning system telemetry. *Journal of Mammology* 88:457-467.
- Caulkett, N. A., P. H. Cribb, and J. C. Haigh. 2000. Comparative cardiopulmonary effects of carfentanil-xylazine and medetomidine-ketamine use for immobilization of mule deer and mule deer/white-tailed deer hybrids. *Canadian Journal of Veterinary Research*. 64:64-68.
- Clover, M. R. 1956. Single-gate deer trap. *California Fish and Game* 42:199-201.
- Conner, M. M., C. W. McCarty, and M. W. Miller. 2000. Detection of bias in harvest-based estimates of chronic wasting disease prevalence in mule deer. *Journal of Wildlife Diseases* 36:691-699.
- Conner, M. M., and M. W. Miller. 2004. Movement patterns and spatial epidemiology of a prion disease in mule deer population units. *Ecological Applications* 14:1870-1881.

- Conner, M. M., M. W. Miller, M. R. Ebinger, and K. P. Burnham. 2007. A meta-baci approach for evaluating management intervention on chronic wasting disease in mule deer. *Ecological Applications* 17:140-153.
- Dasmann, R. F., and R. D. Taber. 1956. Behavior of Columbian black-tailed deer with reference to population ecology. *Journal of Mammology* 37:143-164.
- Davis, J. N., M. Farmer, and A. Green. 1999. Utah big game range trend studies 1999 Volume 1. Federal Aid Project-135-R-20, publication number 00-01. Utah Division of Wildlife Resources, Salt Lake City, Utah.
- D'Eon, R. G., and R. Serrouya. 2005. Mule deer seasonal movements and multiscale resource selection using global positioning system radiotelemetry. *Journal of Mammology* 86:736-744.
- DeVos, A., P. Brokx, and V. Geist. 1967. A review of social behavior of the North American Cervids during the reproductive period. *The American Midland Naturalist* 77:390-417.
- Eberhardt, L. E., E. E. Hanson, and L. L. Caldwell. 1984. Movement and activity patterns of mule deer in the sagebrush-steppe region. *Journal of Mammology* 65:404-409.
- Farnsworth, M. L., J. A. Hoeting, N. T. Hobbs, and M. W. Miller. 2006. Linking chronic wasting disease to mule deer movement scales: A hierarchical Bayesian approach. *Ecological Applications* 16:1026-1036.
- Farnsworth, M. L., L. L. Wolfe, N. T. Hobbs, K. P. Burnham, E. S. Williams, D. M. Theobald, M. M. Conner, and M. W. Miller. 2005. Human land influences on

- chronic wasting disease prevalence in mule deer. *Ecological Applications* 15:119-126.
- Frair, J. L., S. E. Nielsen, E. H. Merrill, S. R. Lele, M. S. Boyce, R. H. M. Munro, G. B. Stenhouse, and H. L. Beyer. 2004. Removing GPS collar bias in habitat selection studies. *Journal of Applied Ecology* 41:201-212.
- Garrott, R. A., G. C. White, R. M. Bartmann, L. H. Carpenter, and A. W. Alldredge. 1987. Movements of female mule deer in Northwest Colorado. *Journal of Wildlife Management* 51:634-643.
- Geist, V. 1981. Behavior: Adaptive strategies in mule deer. Pages 157-223 in O. C. Wallmo, ed. *Mule and black-tailed deer of North America*. University of Nebraska Press, Lincoln and London.
- Girard, I., J. P. Ouellet, R. Courtouis, C. Dussault, and L. Breton. 2002. Effects of sampling effort based on GPS telemetry on home-range size estimations. *Journal of Wildlife Management* 66:1290-1300.
- Gompper, M. E., and J. L. Gittleman. 1991. Home range scaling: Intraspecific and comparative trends. *Oecologia* 87:343-348.
- Grear, D. A., M. D. Samuel, J. A. Langenberg, and D. Keane. 2006. Demographic patterns and harvest vulnerability of chronic wasting disease infected white-tailed deer in Wisconsin. *Journal of Wildlife Management* 70:546-553.
- Gross, J. E., and M. W. Miller. 2001. Chronic wasting disease in mule deer: Disease dynamics and control. *Journal of Wildlife Management* 65:205-215.
- Gruell, G. E., and N. J. Papez. 1963. Movements of mule deer in Northeastern Nevada. *Journal of Wildlife Management* 27:414-422.

- Harestad, A. S., and F. L. Bunnell. 1979. Home range and body weight – A reevaluation. *Ecology* 60: 389-402.
- Hebblewhite, M., M. Percy, and E. H. Merrill. 2006. Are all global positioning system collars created equal? Correcting habitat-induced bias using three brands in the the Central Canadian Rockies. *Journal of Wildlife Management* 71:2026-2033.
- Heisey, D. M., and D. O. Joly. 2004. Age and transmissible spongiform encephalopathies. *Emerging Infectious Diseases* 10:1164-1165.
- Hemson, G., P. Johnson, A. South, R. Kenward, R. Ripley, and D. McDonald. 2005. Are kernels the mustard? Data from global positioning system (GPS) collars suggests problems for kernel home-range analyses with least-squares cross-validation. *Journal of Animal Ecology* 74:455-463.
- Jessup, D. A., 1983. Immobilization of mule deer with ketamine and xylazine, and reversal of immobilization with yohimbine. *American Veterinary Medical Association*. 183:1339-1340.
- Johnson, C. J., J. A. Pederson, R. J. Chappell, D. McKenzie, and J. M. Aiken. 2007. Oral transmissibility of prion disease is enhanced by binding to soil particles. *PLOS Pathogens* 3:874-881.
- Kenward, R. E., R. T. Clarke, K. H. Hodder, and S. S. Walls. 2001. Density and linkage estimators of home range: Nearest neighbor clustering defines multinuclear cores. *Ecology* 82:1905-1920.
- Kie, J. G., R. T. Bowyer, M. C. Nicholson, B. B. Boroski, and E. R. Loft. 2002. Landscape heterogeneity at differing scales: Effects on spatial distribution of mule deer. *Ecology* 83:530-544.



- Kilpatrick, H. J., 1997. Darting urban deer: techniques and technology. *Wildlife Society Bulletin*. 25:542-546.
- Koutnik, D. L. 1981. Sex-related differences in the seasonality of agonistic behavior in mule deer. *Journal of Mammology* 62:1-11.
- Kreeger, T. J., D. L. Montgomery, J. E. Jewell, W. Schultz, and E. S. Williams. 2006. Oral transmission of chronic wasting disease in captive Shira's moose. *Journal of Wildlife Diseases* 42:640-645.
- Kucera, T. E. 1978. Social behavior and breeding system of the desert mule deer. *Journal of Mammology* 59:463-476.
- Kufeld, R. C., D. C. Bowden, and D. L. Schrupp. 1989. Distribution and movements of female mule deer in the Rocky Mountain foothills. *Journal of Wildlife Management* 53:871-877.
- Littell, R. C., G. A. Milliken, W. W. Stroup, and R. D. Wolfinger. 1996. SAS system for mixed models. SAS Institute, Cary, North Carolina, USA.
- Miller, M. W. and E. S. Williams. 2003. Horizontal prion transmission in mule deer. *Nature* 425:35-36.
- Miller, M. W., E. S. Williams, C. W. McCarty, T. R. Spraker, T. J. Kreeger, C. T. Larsen, and E. T. Thorne. 2000. Epizootology of chronic wasting disease in free-ranging cervids in Colorado and Wyoming. *Journal of Wildlife Diseases* 36:676-690.
- Miller, M. W., E. S. Williams, N. T. Hobbs, and L. L. Wolfe. 2004. Environmental sources of prion transmission in mule deer. *Emerging Infectious Diseases* 10:1003-1006.

- Miller, M. W., and M. A. Wilde. 2004. Epidemiology of chronic wasting disease in captive white-tailed and mule deer. *Journal of Wildlife Diseases* 40:320-327.
- Miller, M. W., M. A. Wild, and E. S. Williams. 1998. Epidemiology of chronic wasting disease in captive Rocky Mountain elk. *Journal of Wildlife Diseases* 34:532-538.
- Miller, M. W., and M. M. Conner. 2005. Epidemiology of chronic wasting disease in free-ranging mule deer: Spatial, temporal, and demographic influences on observed prevalence patterns. *Journal of Wildlife Diseases* 41:275-290.
- Mills, K. J., B. R. Patterson, and D. L. Murray. 2006. Effects of variable sampling frequencies on GPS transmitter efficiency and estimated wolf home range size and movement distance. *Wildlife Society Bulletin* 34:1463-1469.
- Nicholson, M. C., R. T. Bowyer, and J. G. Kie. 1997. Habitat selection and survival of mule deer: Tradeoffs associated with migration. *Journal of Mammology* 78:483-504.
- NRCS. 2005. Accumulated precipitation – since October 1. Retrieved on March 24, 2005 from Natural Resources Conservation Service website:  
[ftp://ftp.wcc.nrcs.usda.gov/data/snow/snotel/table/history/utah/09103s\\_p.txt](ftp://ftp.wcc.nrcs.usda.gov/data/snow/snotel/table/history/utah/09103s_p.txt)
- Pac, H. I., W. F. Kasworm, L. R. Irby, and R. J. Mackie. 1988. Ecology of mule deer, *Odocoileus hemionus*, along the east front of the Rocky Mountains, Montana. *The Canadian Field Naturalist* 102:227-236.
- Pederson, J. C., and K. T. Harper. 1978. Factors influencing productivity of two mule deer herds in Utah. *Journal of Range Management* 31:105-110.

- Peterson, M. N., R. R. Lopez, P. A. Frank, M. J. Peterson, and N. J. Silvy. 2003. Evaluating capture methods for urban white-tailed deer. *Wildlife Society Bulletin* 31:1176-1187.
- Relyea, R. A., and S. Demarais. 1994. Activity of desert mule deer during the breeding season. *Journal of Mammalogy* 75:940-949.
- Robinette, W. L., 1957. Notes on tooth development and wear for Rocky Mountain mule deer. *Journal of Wildlife Management* 31:312-326. check this cite
- Robinette, W. L., 1966. Mule deer home range and dispersal in Utah. *Journal of Wildlife Management* 30:335-349.
- Rodgers, A. R. & A. P. Carr. 1998. HRE: the home range extension for ArcView. Users Manual. Ontario Ministry of Natural Resources, Thunder Bay, Ontario. 36 pp.
- Rosatte, R., K. Sobey, D. Donovan, L. Bruce, M. Allan, A. Silver, K. Bennett, M. Gibson, H. Simpson, C. Davies, A. Wandeler, and F. Muldoon. 2006. Behavior, movements, and demographics of rabid raccoons in Ontario, Canada: Management implications. *Journal of Wildlife Diseases* 42:589-605.
- SAS Institute Inc., SAS OnlineDoc® 9.1.3, Cary, NC: SAS Institute Inc., 2002-2005.
- Sawyer, H., F. Lindzey, and D. McWhirter. 2005. Mule deer and pronghorn migration in western Wyoming. *Wildlife Society Bulletin* 33:1266-1273.
- Schwager, M., D. Anderson, Z. Butler, and D. Rus. 2007. Robust classification of animal tracking data. *Computers and Electronics in Agriculture* 56:46-59.
- Smith, R. B., 1983. Mule deer reproduction and survival in the La Sal Mountains, Utah. M. S. Thesis, Utah State University, Logan, Utah. 102pp.

- Spraker, T. R., M. W. Miller, E. S. Williams, D. M. Getzy, W. J. Adrian, G. G. Schoonveld, R. A. Spowart, K. I. O'Rourke, J. M. Miller and P. A. Merz. 1997. Spongiform encephalopathy in free-ranging mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*) and Rocky Mountain elk (*Cervus elaphus nelsoni*) in North-central Colorado. *Journal of Wildlife Diseases* 33:1-6.
- Terranova, P., B. C. Wheeler, C. C. Gilbert, and S. A. Suarez. 2005. Day range and home range assessments: A comparison of GPS and grid-based methods. *American Journal of Primatology* 66:193.
- Thomas, T., and L. Irby. 1990. Habitat use and movement patterns by migrating mule deer in Southeastern Idaho. *Northwest Science* 64:19-27.
- White, G. C., and R. M. Bartmann. 1994. Drop net versus helicopter net guns for capturing mule deer fawns. *Wildlife Society Bulletin* 22:248-252.
- Williams, E. S. and M. W. Miller. 2002. Chronic wasting disease in deer and elk in North America. Scientific and Technical Review Office of International Epizootics 21:305-316.
- Williams, E. S., M. W. Miller, T. J. Kreeger, R. H. Kahn, and E. T. Thorne. 2002. Chronic wasting disease of deer and elk: A review with recommendations for management. *Journal of Wildlife Management* 66:551-563.
- Williams, E. S. and S. Young. 1980. Chronic wasting disease of captive mule deer: A spongiform encephalopathy. *Journal of Wildlife Diseases* 16:89-98.
- Williams, E. S., and S. Young. 1982. Spongiform encephalopathy of Rocky Mountain elk. *Journal of Wildlife Diseases* 18:463-471.

- Williams, E. S., and S. Young. 1992. Spongiform encephalopathies in Cervidae. Scientific and Technical Review Office of International Epizootics 11:551-567.
- Wolfe, L. L., T. R. Spraker, L. Gonzalez, M. P. Dagleish, T. M. Sirochman, J. C. Brown, M. Jeffrey, and M. W. Miller. 2007. PrP<sup>CWD</sup> in rectal lymphoid tissue of deer (*Odocoileus* spp). Journal of General Virology 88:2078-2082.
- WRCC. 2005. 1971-2000. Monthly climate summary La Sal, Utah. Retrieved April 20, 2005, from Western Region Web site: <http://www.wrcc.dri.edu/cgi-bin/cliNORM2000tM.pl?utlasa>

Table 1. Analysis of data during the breeding season (1 Nov-15 Dec) for mule deer in the La Sal Mountains, Utah during 2005 and 2006.

GPS ID	Breeding points <i>n</i>	No. of clusters	$\bar{x}$ time spent in clusters (hrs)	No. Clusters longer than 5 hrs	$\bar{x}$ clusters >5hrs	No. Mvmt Paths	$\bar{x}$ km/hr in mvmt path	$\bar{x}$ time spent in mvmt path (hrs)	No. Mvmt paths >5 hrs	$\bar{x}$ mvmt paths >5hrs
AF4862006	2158	226	3.2	21	0.09	200	4.6	2.3	6	0.03
AF4892005	2158	202	3.8	37	0.18	145	5.4	2.7	11	0.08
AF4892006	1388	107	3.3	16	0.15	88	8.8	4.4	26	0.30
AF4902006	2158	235	2.7	7	0.03	183	5.9	2.9	13	0.07
AF4912005	2158	238	2.5	12	0.05	180	6.3	3.2	25	0.14
AF4912006	2158	193	3.4	21	0.11	179	5.6	2.8	11	0.06
AF4922005	2158	230	3.0	20	0.09	196	5.0	2.5	12	0.06
AF4922006	2158	201	3.8	41	0.20	144	5.4	2.7	8	0.06
AF4932005	2158	211	3.1	15	0.07	183	5.7	2.9	14	0.08
AF4932006	2158	236	3.1	20	0.08	178	5.0	2.5	11	0.06
AF4942005	2158	244	2.9	22	0.09	188	4.8	2.4	7	0.04
AF4942006	2158	198	3.0	18	0.09	176	6.5	3.2	19	0.11
AF4952005	2158	200	3.5	25	0.13	160	5.7	2.8	13	0.08
AM3862005	2158	137	3.8	18	0.13	126	9.9	5.0	33	0.26
AM3902005	2158	174	3.0	17	0.10	157	8.1	4.1	30	0.19
AM6912006	2062	155	3.1	17	0.11	132	9.4	4.7	22	0.17
AM6922006	2062	142	2.9	18	0.13	127	10.6	5.3	32	0.25
AM6932006	2062	166	3.2	19	0.11	144	7.9	3.9	25	0.17
AM6942006	2158	176	3.0	12	0.07	148	7.8	3.9	25	0.17
YM3902006	2158	154	2.7	9	0.06	139	10.5	5.2	18	0.13
YM4982006	2158	188	2.7	10	0.05	157	8.3	4.1	32	0.20
YM4992005	2001	157	4.0	36	0.23	128	6.7	3.4	17	0.13
YM5002006	2158	156	2.6	2	0.01	140	10.6	5.3	29	0.21
YM5032005	2085	136	3.5	18	0.13	121	10.3	5.2	27	0.22
YM6972006	2062	154	3.0	11	0.07	140	9.2	4.6	30	0.21

Table 2. Analysis of data during the breeding season (1 Nov-15 Dec) for mule deer in the La Sal Mountains, Utah during 2005 and 2006.

ANALYSIS TYPE	SEX	<i>n</i> of <i>df</i>	MEAN	SE	<i>t</i> or <i>F</i>	<i>P</i>
Number of clusters	Male	13	157.92	4.58	4.73	≤ 0.001
	Female	12	209.31	9.86		
Time spent in clusters *	Male	23	2.63	0.13	0.04	0.836
	Female	23	2.66	0.11		
Number of long clusters (lasting >5 hrs)	Male	13	0.10	0.02	0.22	0.827
	Female	12	0.10	0.01		
Number of movement paths	Male	13	138.25	3.43	3.46	0.003
	Female	12	169.23	8.26		
Time spent in movement paths (hours)*	Male	23	4.04	0.19	49.97	≤ 0.001
	Female	23	2.36	0.14		
Number of long movement paths (lasting >5 hrs)	Male	13	0.19	0.01	-4.54	≤ 0.001
	Female	12	0.09	0.02		
Movement rate*	Male	23	6.83	0.46	2.83	0.106
	Female	23	5.85	0.37		
Movement path tortuosity*	Male	23	0.54	0.01	21.22	≤ 0.001
	Female	23	0.66	0.02		

\*Comparison of these factors was completed using repeated measures and uses *df* and *F* statistics.

Table 3. Home range size for winter, summer, and breeding seasons by sex, age class, and year for mule deer in the La Sal Mountains, Utah during 2005 and 2006. Winter was defined as 15 Dec–15 April, summer was defined as 15 May–15 Oct, and breeding was defined as 1 Nov–15 Dec.

AGESEX	YEAR	WINTER			SUMMER			BREEDING		
		<i>n</i>	Home range size (km <sup>2</sup> )	SE	<i>n</i>	Home range size (km <sup>2</sup> )	SE	<i>n</i>	Home range size (km <sup>2</sup> )	SE
AF	2005	9	5.1	0.7	8	2.8	0.9	7	5.7	2.8
AF	2006	6	5.1	1.6	7	2.3	1.1	6	2.7	0.7
AM	2005	3	11.9	1.3	3	4.5	1.1	2	21.1	5.7
AM	2006	14	10.9	1.2	14	6.4	1.5	4	9.2	0.9
YM	2005	7	13.1	2.5	6	6.0	1.2	2	24.4	12.4
YM	2006	12	10.7	1.4	12	9.7	1.1	4	13.0	1.5



Table 4. Home range differences for winter, summer, and breeding seasons by sex, age class, and year for mule deer in the La Sal Mountains, Utah during 2005 and 2006. Winter was defined as 15 Dec–15 April, summer was defined as 15 May–15 Oct, and breeding was defined as 1 Nov–15 Dec.

AGESEX	YEAR	WINTER					SUMMER					BREEDING				
		df	DIFF	SE	<i>t</i>	<i>P</i>	df	DIFF	SE	<i>t</i>	<i>P</i>	df	DIFF	SE	<i>t</i>	<i>P</i>
AF vs. AM	2005	45	-6.79	1.48	-4.59	≤0.001	44	-1.66	1.43	-1.16	0.251	19	-15.37	6.33	-2.43	0.025
AF vs. AM	2006	45	-5.86	1.93	-3.04	0.004	44	-4.08	1.55	-2.62	0.012	19	-6.57	1.16	-5.65	≤0.001
AF vs. YM	2005	45	-7.92	2.58	-3.07	0.004	44	-3.17	1.45	-2.18	0.035	19	-18.61	12.72	-1.46	0.160
AF vs. YM	2006	45	-5.65	2.12	-2.66	0.011	44	-7.32	0.88	-8.28	≤0.001	19	-10.36	1.64	-6.31	≤0.001
AM vs. YM	2005	45	-1.13	2.78	-0.41	0.687	44	-1.51	1.62	-0.93	0.356	19	-3.23	13.66	-0.24	0.815
AM vs. YM	2006	45	0.22	1.70	0.13	0.900	44	-3.24	1.64	-1.98	0.054	19	-3.79	1.76	-2.16	0.044

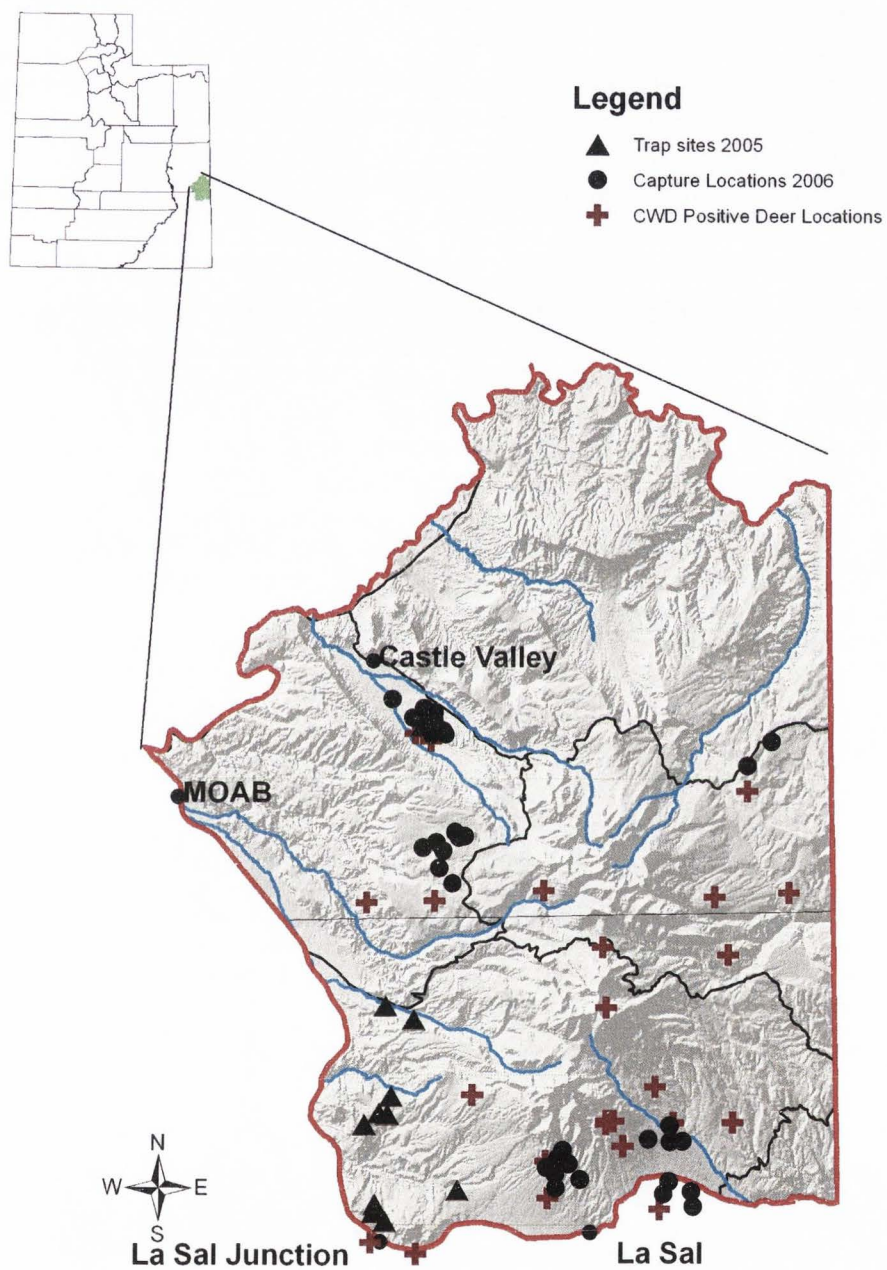


Figure 1. Location of the La Sal Mountain study area within Southeastern Utah, showing locations of positive deer, trap site locations in 2005, and helicopter capture locations in 2006.

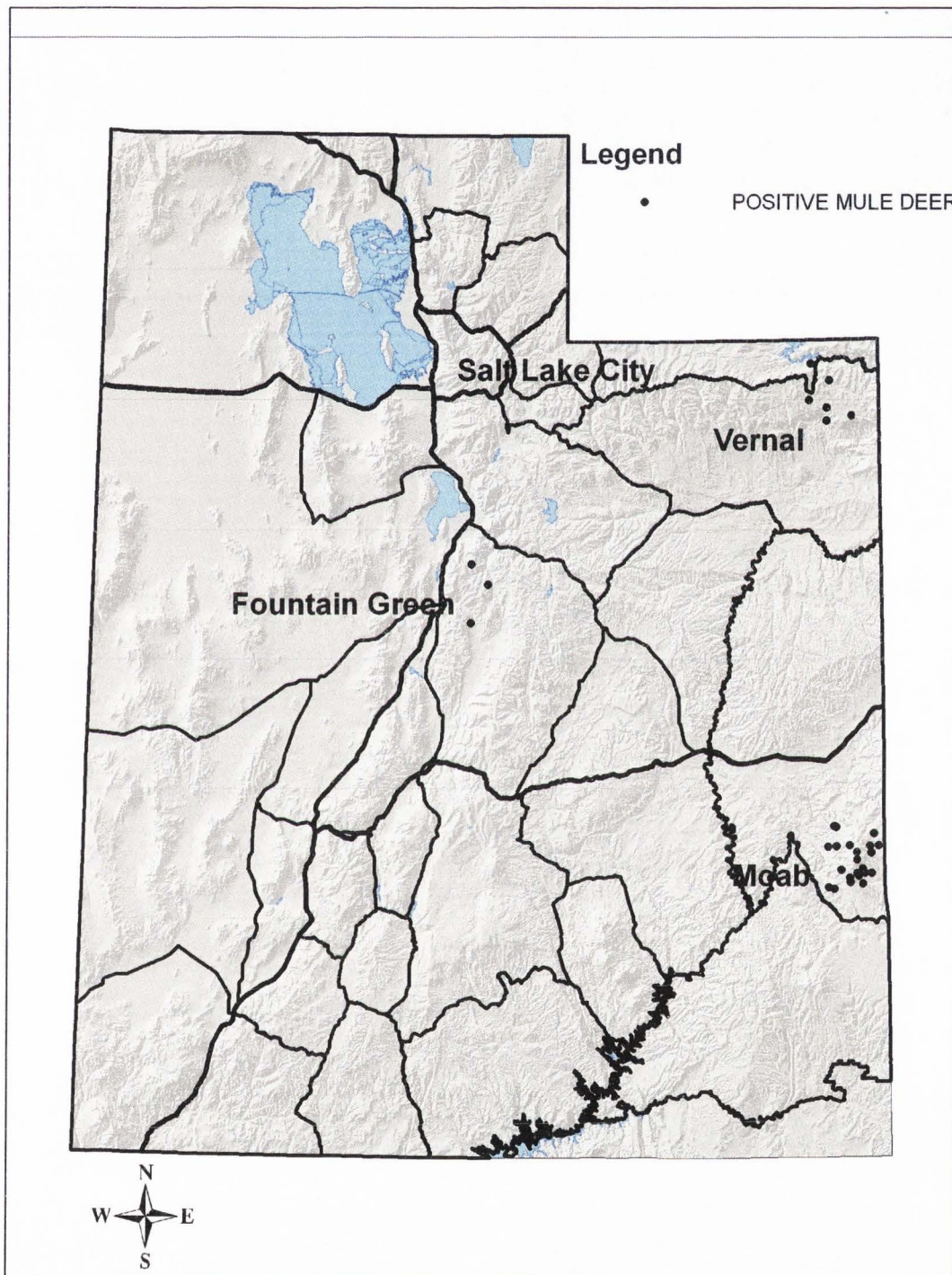


Figure 2. CWD positive mule deer locations in the State of Utah from 2003-2006.

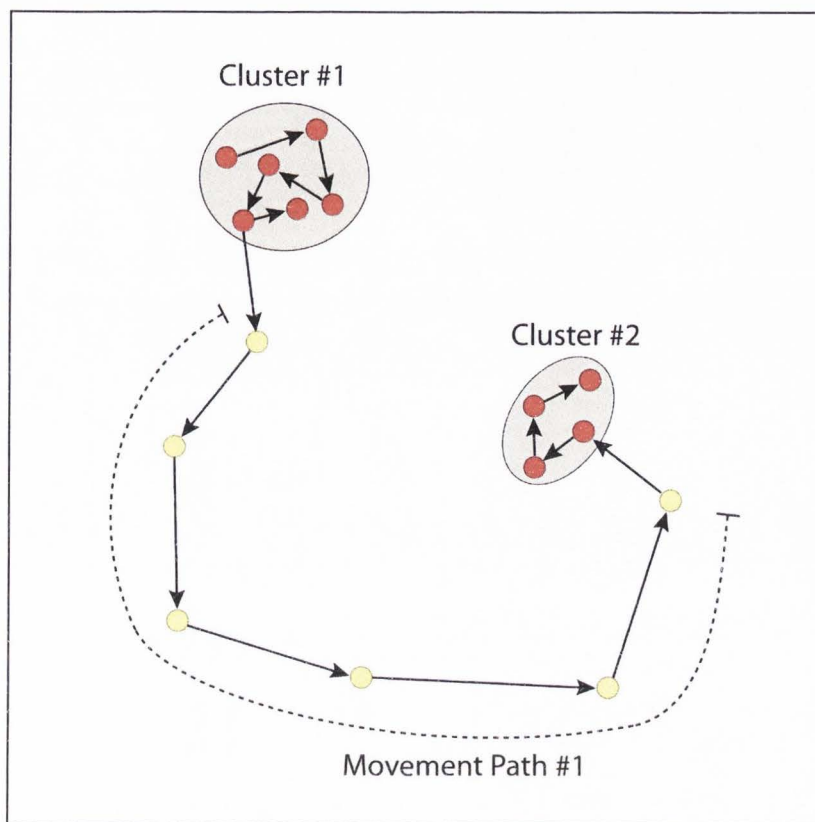


Figure 3. Illustration of a spatial cluster algorithm which delineates the non-movement periods and show sequential locations that make up a movement path.

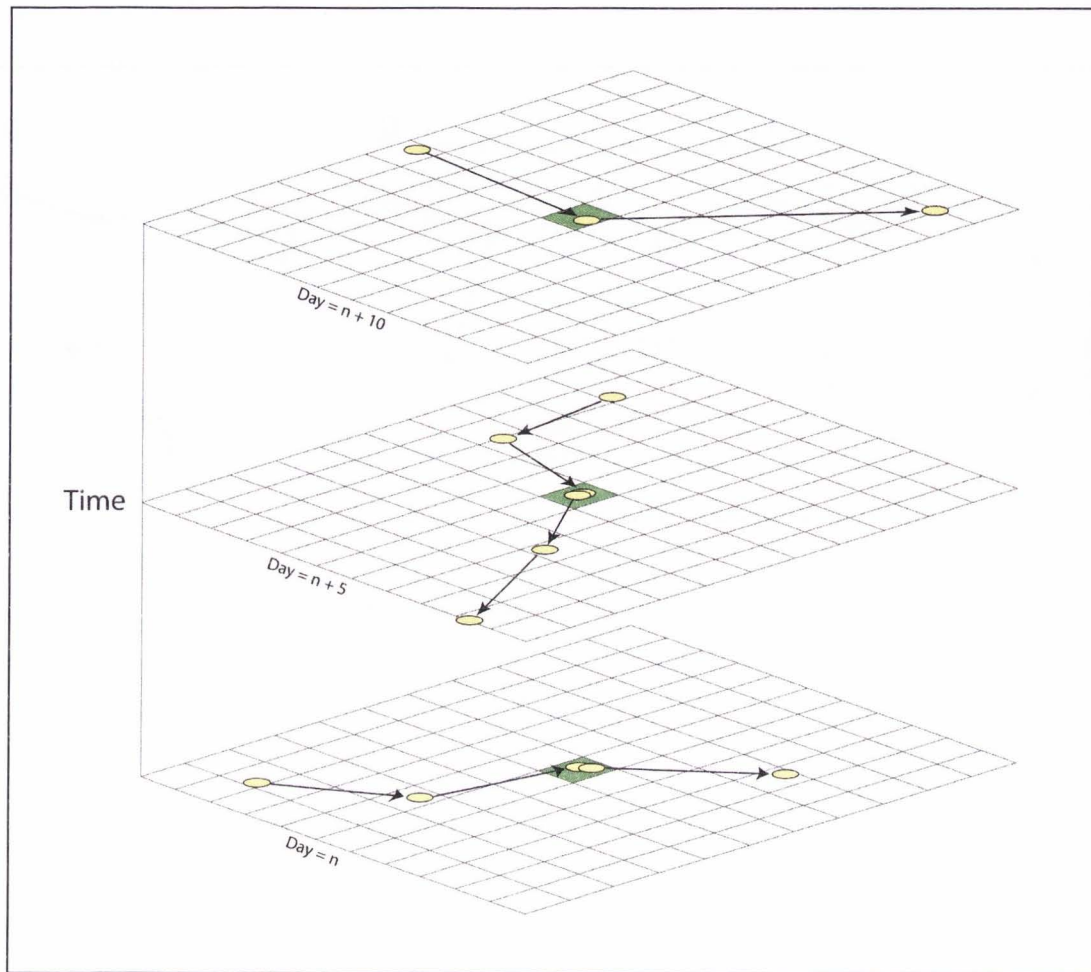


Figure 4. Illustration showing short periods of visitation to an area that would not indicate areas of importance because they are visited during different time periods and clusters are not formed.

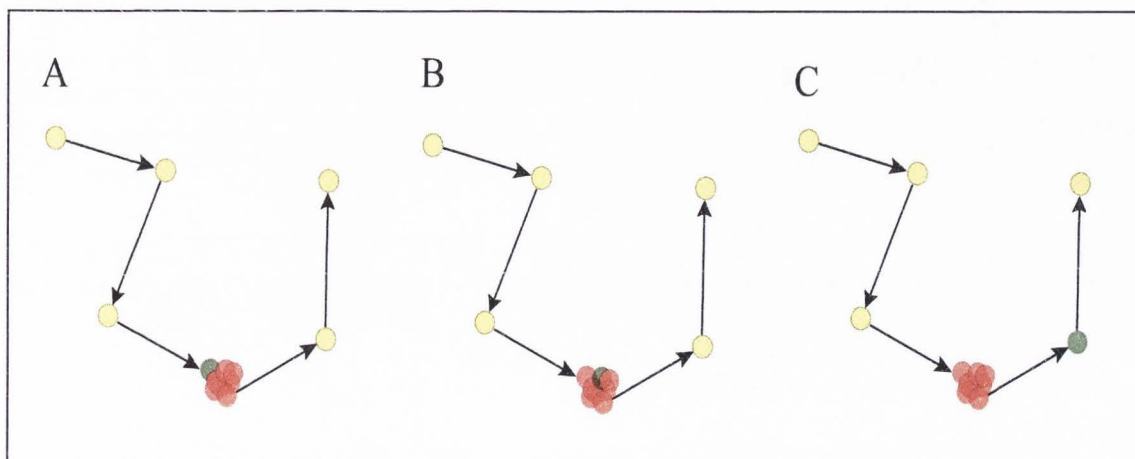


Figure 5. Illustration of how the algorithm assigns locations to one of three classes based on both past and future behavior of the organism.

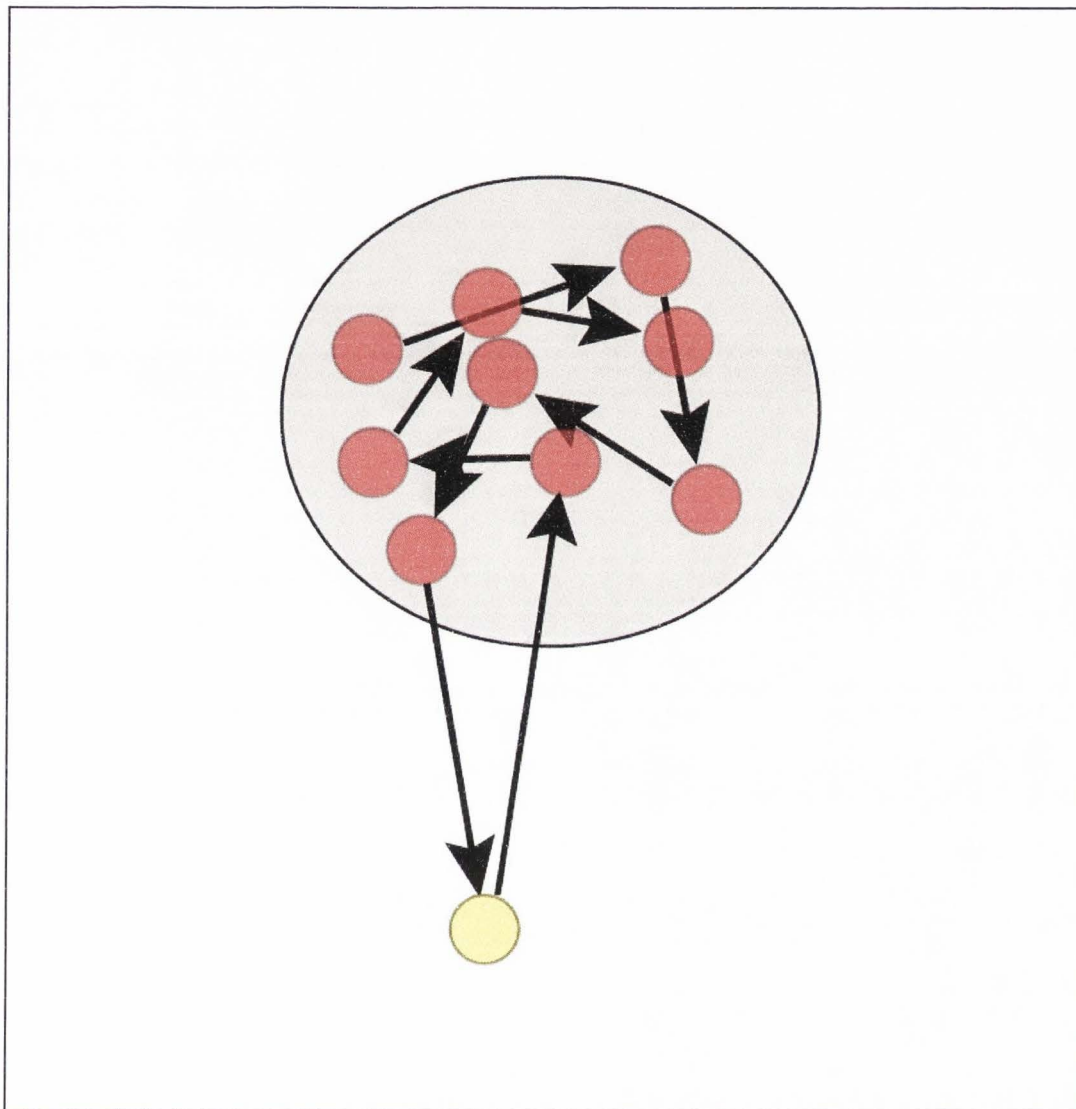


Figure 6. Illustration of how a point may lie outside of a cluster either due to GPS error, animal behavior, or cluster search radius.

APPENDIX



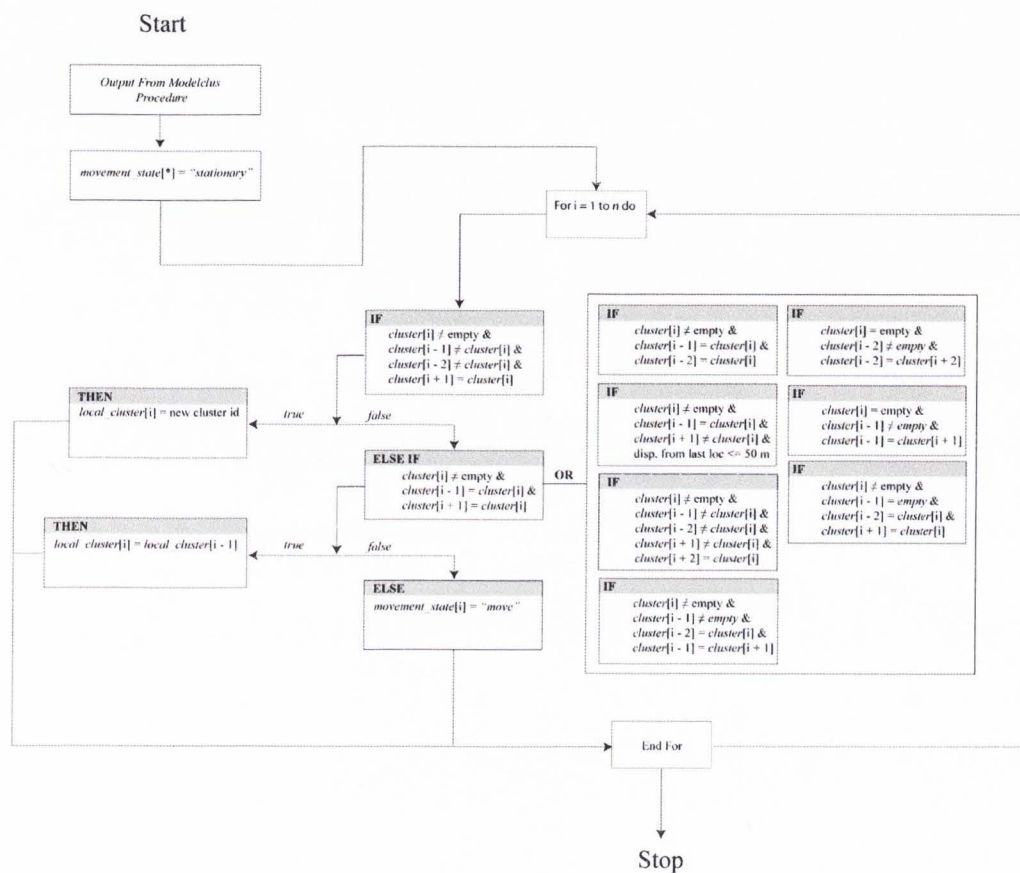


Figure 7. Detailed flow chart showing development of logical tests to evaluate the spatial location of a point relative to other points in the recent past and future.