Title
Spatial Ecology and Population Dynamics of Tule Elk (Cervus elaphus nannodes) at Point Reyes National Seashore, California

Author
Cobb, McCrea Andrew

Publication Date
2010

Spatial Ecology and Population Dynamics of Tule Elk (*Cervus elaphus nannodes*) at Point Reyes National Seashore, California

by

McCrea Andrew Cobb

A dissertation submitted in partial satisfaction of the

requirements for the degree of

Doctor of Philosophy

in

Environmental Science, Policy and Management

in the

GRADUATE DIVISION

of the

UNIVERSITY OF CALIFORNIA, BERKELEY

Committee in charge:

Professor Reginald H. Barrett, Chair
Professor Justin S. Brashares
Professor Maggi Kelly
Professor Eileen A. Lacey

Spring 2010

Spatial Ecology and Population Dynamics of Tule Elk (*Cervus elaphus nannodes*) at Point Reyes National Seashore, California

by

McCrea Andrew Cobb

Abstract

Spatial Ecology and Population Dynamics of tule elk (*Cervus elaphus nannodes*) at Point Reyes National Seashore, California

by

McCrea Andrew Cobb

Doctor of Philosophy in Environmental Science, Policy and Management

University of California, Berkeley

Professor Reginald H. Barrett, Chair

The tule elk (*Cervus elaphus nannodes*) was reintroduced to Point Reyes National Seashore, California in 1978. After exhibiting irruptive growth for 20 years, elk abundances have fluctuated. Three subpopulations of elk currently inhabit Pt. Reyes: a fenced subpopulation at high density; a free-ranging subpopulation in designated wilderness at low density; and a free-ranging subpopulation on active ranchland at low density. Little is known about the spatial ecology and population dynamics of tule elk. This unusual situation provided an opportunity to quantify and compare factors affecting the home ranges, group sizes, resource selection, small-scale movements and population dynamics of tule elk. I collected biweekly fixes on radio-collared elk cows between 2005 and 2008 to examine herd structures, space use patterns, grouping behavior and survival rates of tule elk. Radio-telemetry data revealed 6 herds of elk at Pt. Reyes (4 at Tomales), which had distinct herd ranges and showed little spatial interaction. Fixed kernel home ranges were some of the smallest for elk in North America (217 ha, SE = 35), and were negatively correlated with elk density. Home range sizes were 300% smaller than previous estimated for elk at Pt. Reyes in 1998. The sizes of elk groups peaked during the winter and mid-summer, and were smallest during the spring parturition and fall rutting periods. Elk with larger home range sizes generally formed smaller groups. Resource selection function (RSF) results indicated that tule elk at Pt. Reyes selected flat, grassland-dominated habitats over hilly, scrub and forest habitats; although resource selection patterns varied among herds. Elk shifted to lower elevations, steeper slopes and more scrub-dominated habitats during the dry season (May – October). Most elk showed an aversion to areas close to roads and trails, but this result was not consistent across all herds. I quantified small-scale movement patterns of tule elk using hourly fixes from GPS-collared elk. Elk exhibited daily cycles in their movement patterns by increased their hourly movements in the morning and evening hours. Elk daily movements were longest during wet spring months and shortest during the dry fall months. Elk slowed when traveling through homogeneous grassland habitat. Windy conditions caused elk to slow, but precipitation had no effect on elk movement. Elk moved faster when closer to roads and trails. Elk in higher density herds moved slower on an hourly scale than lower density herds, but herd density had no affect on daily movement patterns. Using known-fate models applied to radio-telemetry data, I estimated annual cow elk survival was 0.96 (SE = 0.02). I captured and monitored radio-collared elk calves from 2005 to 2007 to estimate calf survival and causes of mortality. Using known-fate models, I estimated annual survival for elk calves was 0.81 (SE = 0.02). The primary cause of death for both cows and calves was starvation, which was often accompanied by copper and selenium deficiencies. Sensitivity and elasticity estimates of elk vital rates revealed that adult cow elk survival contributed the most (30%) to elk annual population change (λ). The D Ranch and Limantour herds were expected irruptive growth and by 2018 increase to 393 and 389 elk, respectively, based on stochastic population projection models. The projected future abundance of elk in the Tomales herds was dependant on the previous year's annual rainfall: models projected increases in elk abundance following years of above-average rainfall but no change in elk abundance following years of below-average rainfall. Future growth of the D Ranch and Limantour elk herds will likely concentrate on adjacent ranchlands, given RSF models results, and will likely result in future conflicts between NPS management, unless proactive actions are taken.

TABLE OF CONTENTS

LIST OF TABLES

Chapter 1

Chapter 2

Chapter 3

Chapter 4

LIST OF FIGURES

Introduction

Chapter 1

Chapter 2

Chapter 3

Chapter 4

ACKNOWLEDGEMENTS

This project would not have been possible without the support of many people. First, I thank my graduate advisor, Reg Barrett, for his help with the initial project design, lending his years of experience and mentoring me throughout this project. I also thank Peter Gogan for guiding towards this project, providing useful advise along the way and giving me the opportunity to add to his original work on tule elk at Point Reyes. I thank Natalie Gates and the National Park Service staff at Point Reyes National Seashore for providing logistical support and beach-front living for my field crew. I thank my dissertation committee for their helpful suggestions that improved the quality of this work: Justin Brashares, Eileen Lacey and Maggi Kelly. I especially thank everyone that got their hands dirty with me in the field. Tracking elk through rain, fog and poison oak would not have been nearly as fun and successful without the following people: Adriana Worley, Anand Varma, Angela Whitney, Ashley Rice, Bryan Voelker, Frank Binney, Jessica Castillo, Johnny Garcia, Juliet Lamb, Kan Dhillon, Katie Andres, Lacey Hughey, Levin Nason, Lisa Sindorf, Luke Macaulay, Matt Strausser, Michelle DesRochers, Michelle LeBeau, Monica Perez-Watkins, Nicole Edmison, Sandra Manzel and Sarah Bassing. Funding for this project was provided by the University of California at Berkeley, the U.S. Geological Survey, the National Park Service and the San Francisco Bay Area Chapter of the Safari Club International. Above all, I thank my wife, Michelle, for her love, support, patience and understanding throughout this adventure. Alaska, here we come!

INTRODUCTION

BACKGROUND

Historically, the North American elk (*Cervus elaphus*) displayed a nearly continuous distribution across the central and northern regions of North America, extending from the Atlantic to the Pacific coasts (O'Gara and Dundas 2002). Following early European exploration and the subsequent introduction of guns and horses, elk were substantially reduced in numbers and range. Currently, elk are patchily distributed in the western United States and Canada, primarily along the Continental Divide and westward, with reintroduced populations in some eastern states and provinces.

Elk are currently composed of three subspecies: Rocky Mountain elk (*C. e. nelsoni*), Roosevelt elk (*C. e. roosevelti*), and tule elk (*C. e. nannodes*). Tule elk, the only subspecies endemic to California, were historically found in large herds throughout much of the San Joaquin and Sacramento valleys (Millias 1915). Market hunting during the Gold Rush period led to a substantial decline in tule elk numbers. By 1895, tule elk were reduced from approximately 500,000 to an estimated two to ten individuals (McCullough et al. 1996). All remaining tule elk were isolated on a private ranch (Miller – Lux Ranch) near Buttonwillow, California. This remnant population was protected by the landowner Henry Miller, allowing the population to increase to 400 elk by 1914 (McCullough 1971). Early relocation efforts were generally unsuccessful, but did establish elk herds at Cache Creek (1922) and Owens Valley, California (1933). In 1971, the California legislator passed the Behr Bill, which limited hunting of tule elk until either the population reached 2000 individuals or no further unoccupied elk habitat could be found (Tule Elk Interagency Task Force 1979). This was followed by efforts by the California Department of Fish and Game to begin relocating tule elk throughout their former range in 1974. Two years later, Congress instructed the Department of the Interior to make land available for the conservation and restoration of tule elk, which facilitated tule elk reintroductions at National Park Service (NPS) units. The current number of tule elk in California is approximately 4,000 animals in 22 herds (Joe Hobbs, CDFG, personal communication) (Figure 1). Herd sizes are generally stable to increasing.

Early records indicate tule elk inhabited the San Francisco Bay area in great numbers, but tule elk were extirpated from the region by 1872 (Millias 1915). Ten tule elk were reintroduced in 1978 to the Tomales Point Elk Reserve (Tomales), a fenced peninsula within Point Reyes National Seashore, California. Following the reintroduction, tule elk initially underwent low population growth (Gogan and Barrett 1987) that was attributed to trace element deficiency (Gogan et al. 1989), disease (Jessup et al. 1981) and inbreeding depression (McCullough et al. 1996). Following the initial period of slow growth, Tomales tule elk numbers exhibited approximately 20 years of exponential growth (Figure 2). By 1998, the population numbered approximately 450 animals (4 elk / ha) (Gates 2000).

The rapid growth of the tule elk population raised concerns over potential negative impacts that a high density elk population at Pt. Reyes may have on other native endangered species (Singer et al. 1998). These concerns resulted in an evaluation of the effectiveness of artificial population control methods within the framework of adaptive management (Parma 1998, Morellet et al. 2007). Between 1997 and 2001, 30 to 50 tule elk cows were contracepted annually with porcine zona pellucida (PZP), which effectively prevented pregnancy for one year (Shideler 2000). In 1998, biologists captured and translocated 45 elk of both sexes to a separate region of Pt. Reyes (Limantour) to temporarily slow growth of the Tomales herd. This established a low-density, free-ranging herd outside the Tomales (Figure 3). Shortly after their release, two to three elk emigrated approximately 10 km west of the Limantour herd and established a third herd (D Ranch) on active cattle ranchlands. Distinct annual surveys for the D Ranch herd began in 2004 (Figure 3).

STUDY AREA

Research was conducted at Pt. Reyes, an NPS unit established in 1962. Pt. Reyes encompasses approximately 28,800 ha on the Point Reyes Peninsula, approximately 65 km northwest of San Francisco in Marin County, California (Figure 4). Elevations range from sea level to 448 m. Adjacent areas include private lands, state lands (Tomales State Park and Samuel P. Taylor State Park) and county lands (Marin Municipal Water District). Elk inhabited three distinct regions within Pt. Reyes: a designated wilderness area within a 1,030 ha fenced peninsula at the northernmost tip of Pt. Reyes (Tomales); a designated wilderness area running along the length of Limantour Beach roughly bordered by Limantour Estero to the north and Coast Camp campground to the south (Limantour); and a region in central Pt. Reyes composed of actively managed and former dairy ranch lands between Lighthouse road and Drake's Beach (D Ranch). At the start of this study (2005), there were an estimated 338 elk at the Tomales, 30 elk at Limantour area and ten elk at D Ranch area.

Climate

The climate at Pt. Reyes is Mediterranean (Gilliam 2002), with most rainfall occurring from October through April (Figure 5). Mean historical annual precipitation is 87 cm (Western Regional Climate Center Historical Data, Point Reyes Lighthouse 1917 - 1943). Annual precipitation during the study period ranged from 50 cm (2007) to 109 cm (2005). Monthly precipitation during the study ranged from no rain in July and August 2006 to 40 cm in December 2005 (Bodega Ocean Observing Node, Bodega Bay Marine Laboratory. Annual temperatures historically range from a low of 7.3^{o}C in January to a high of 16.1^{o}C in September and October (Western Regional Climate Center Historical Data, Point Reyes Lighthouse 1917 - 1943). Average monthly temperatures during the study period ranged from 8.2^{o}C (December 2007) to 13.4^{o}C (September 2007) (Figure 6).

Vegetation

Pt. Reyes is composed of a diverse collection of vegetative communities common to coastal northern California, including coastal prairie, coastal scrub, broadleaved evergreen woodlands, and coniferous forests (Barbour et al. 2007). Coastal prairie habitat at Pt. Reyes is characterized by exotic herbs such as sheep sorrel (*Rumex acetosella*), soft chess (*Bromus hordeaceus*), annual ryegrass (*Lolium multiflorum*), perennial ryegrass (*Lolium. perenne*), brome fescue (*Vulpia bromoides*) and ripgut brome (*Bromus diandrus*), along with the native species like California brome (*Bromus carinatus*), meadow barley (*Hordeum brachyantherum*) and purple needlegrass (*Nassella pulchra*) (Gogan 1986). Common forbs include native perennial cow parsnip (*Heracleum maximum*) and exotic English plantain (*Plantago lanceolata*). The coastal prairie habitat is also includes patchy areas of yellow bush lupine (*Lupinus arboreus*) and coyote bush (*Baccharis pilularis*). Miner's lettuce (*Claytonia perfoliata*) is commonly associated with bush lupine. Coastal scrub habitat is dominated by coyote brush (*Baccharis pilularis*) and buckbrush (*Ceanothus cuneatus*). Broadleaved evergreen woodlands are composed of California bay (*Umbellularia californica*), tanoak (*Lithocarpus densiflorus*) and coast live oak (*Quercus agrifolia*), and coniferous forest is composed of Douglas-fir (*Psuedotsuga menziesii*) and Bishop pine (*Pinus muricata*) overstories. Forest understories are variable, often consisting of coffeeberry (*Rhamnus californica*), huckleberry (*Vaccinium ovatum*), California hazel (*Corylus cornuta*), Swordfern (*Polystichum munitum*), and poison oak (*Toxicodendron diversilobum*).

Habitats within elk ranges varied between Tomales, D Ranch and Limantour (Figure 4). Habitats at Tomales were characterized by a mixture of rolling hills dominated by coastal prairie and valleys dominated by coastal scrub and wetlands. D Ranch was primarily composed of active cattle ranchlands (exotic annual grasses) with patches of coastal scrub along steep hillsides. The elk range at Limantour was dominated by coastal scrub, patches of coastal prairie, coniferous and broadleaved forests and creek bottoms containing wetland habitat.

Fire history

Fire regimes at Pt. Reyes were historically influenced by a long period of Native American settlement. Over 100 Coast Miwok villages are thought to have occupied the Point Reyes peninsula for approximately 10,000 years (Treganza 1961). Native Americans used fire annually to control scrub encroachment and improve grassland seed production (Keeley 2005). Coast Miwoks were mostly extirpated from the area by 1830 (Slayermaker 1983). Six large fires were reported between 1889 and 1945, and a few small fires occurred in the 1950s and 1970 (Sugnet 1985, Brown et al. 1999).

The last large fire at Pt. Reyes occurred on October 3, 1995 (“Vision Fire”) and burned approximately 5,000 ha of coniferous forest on and adjacent to the Limantour elk range. No major fires have occurred since, except small (< 1 ha) prescribed burns at Limantour and D Ranch in 2007.

Wildlife

Pt. Reyes historically supported tule elk at least seasonally (McCullough 1969). Grizzly bears (*Ursus arctos*) were extirpated from the region by the 1860s (Van Atta 1946), mountain lions (*Puma concolor*) were apparently absent from the area from 1930s to the 1970s. Coyotes (*Canis latrans*) were extirpated in the 1940s (Clark 1982), but have been increasingly sighted recently. Carnivores that currently inhabit Pt. Reyes include mountain lions, coyotes and bobcats (*Lynx rufus*). A black bear (*Ursus americanus*) was sighted at Pt. Reyes in 2002, but it has not been observed since. No information exists on the current abundance or distribution of any of these predators at Pt. Reyes or their effect on tule elk. Coyotes can predate neonatal elk (Weldon 1952) and might do so on at Pt. Reyes, however none of the existing predators appear capable of regulating an elk population (Toweill and Thomas 2002).

Other ungulate species at Pt. Reyes included native black-tailed deer (*Odocoileus hemionus*) and two introduced ungulates, fallow deer (*Dama dama*) and axis deer (*Axis axis*). NPS personnel began a fallow and axis deer eradication program during the summer of 2007, which led to axis deer being extirpated from Pt. Reyes and greatly reduced fallow deer numbers by 2008.

Human Activity

Pt. Reyes has one of the highest visitation rates of any NPS unit with approximately two million visitors annually (John Dell'Osso, NPS, personal statement). Foot-accessible camping areas within Pt. Reyes experience heavy usage, including one within the Limantour elk range (Coast Camp). Tomales is the closest area to San Francisco where people can view wild elk. Approximately 400,000 people visit Tomales each year (John Dell'Osso, NPS, personal statement).

RESEARCH GOALS AND OBJECTIVES

The primary goals of this research project were to quantify (by chapter):

1. the herd stability, group behaviors and home sizes of tule elk at Pt. Reyes. Specific objectives included: quantifying the number of elk herds, determining the temporal stability of elk herds, documenting group size and composition dynamics, calculating annual and seasonal elk home range and core area sizes and quantifying the relationship between elk home range and group sizes to herd density.

2. the resource selection patterns of tule elk at Pt. Reyes and determine how these patterns vary among herds of varying densities and with different habitat availability. Specific objectives included: determining the probability of elk occurrence across Pt. Reyes based on their relative selection for habitats (vegetation composition, slope, aspect, relative solar radiation, elevation, distance from the nearest road and distance from the nearest trail), and creating maps of predicted future elk occurrence within Pt. Reyes.

3. the small-scale movement patterns of tule elk at Pt. Reyes. Specific objectives included: quantifying hourly and daily movement patterns of tule elk using GPS collar data, determining the effects that habitat, herd density, human development and weather may have on small-scale elk movements.

4. the population dynamics of tule elk at Pt. Reyes. Specific objectives included: calculating the annual vital rates of tule elk herds (calf survival, adult survival and fecundity), determining how these vital rates vary between herds and years, quantifying the relative contribution of each vital rate to annual rates of change in elk abundance and forecasting future elk abundances by herd.

Irruptive population growth patterns, observed at Pt. Reyes and typified by newly established large ungulate populations that are free of predation pressure, can lead to adverse habitat and population-level effects (Caughley 1970). Best practices for effectively managing ungulate populations in the absence of natural predators and with limited dispersal has been a topic of debate throughout the 20th century (Coughenour and Singer 1996, Singer et al. 1998). The initial rapid increase in elk at Tomales following reintroduction led to concurrent herd range expansions (Howell et al. 2002) and changes in vegetation structure (Johnson and Cushman 2007). The Limantour and D Ranch herds are predicted to show the same range expansion trends that were observed at Tomales because their initial conditions are similar. Understanding the rate and direction of population expansions is important to identify their potential effects on the landscape and other species. Given the close proximity of elk at Pt. Reyes to ranchland and other developments, there is a high likelihood for future human-wildlife conflicts similar to those occurring in other regions (Messmer 2009). Detailed data on herd dynamics, grouping behaviors, resource selection patterns, small-scale movements and population dynamics are critical to forecast future elk abundance and range, and to prepare for any future conflict.

Social living provides benefits (increased predator awareness, predator dilution and increased awareness of local forage resources) and costs (increased conspicuousness for predation and elevated intraspecific competition for resources) (Alexander 1974). Because these competing factors are not static over time, animals would be predicted to attempt to maximize their individual fitness by varying the size and duration of their aggregations over space and time (Wiens et al. 1993). Associations between large herbivores, such as elk, can be classified within a spatial hierarchical framework (Figure 7). The broadest level of the hierarchy is the population, which is defined as all individuals within a given region. Within a population, individuals cluster into smaller subsets, called herds. Within herds, individuals form small-scale spatial associations called groups. The temporal and spatial dynamics of each level of this hierarchy generally increases as you move from population to herd to group levels. Little is known about the spatial ecology and behaviors of the tule elk compared to the other elk subspecies. Having evolved morphological adaptations to mild Mediterranean grasslands of California (McCullough 1971), tule elk may have also developed distinctive behaviors that result in unique herd formations, grouping behaviors and home range sizes.

The stability of herds (the likelihood that individuals within a herd remain together over time) is spatially dynamic, and may be driven by climate and habitat. High herd stability provides increased fitness associated with peer-learning of important forage locations and predation threats (Franklin et al. 1975, Byers 1997), and therefore may be favored. Alternatively, low herd stability may occur when individuals have differential resource needs, which are amplified in unfavorable conditions (Bender and Haufler 1999). Examples of large-scale variations in herd stability occur in elk, and may be driven by large-scale climatic variation (Jenkins and Starkey 1982). It has been proposed that elk experiencing little climate variation show long-term bonds and remain in close proximity for extended periods (Weckerly 1999), but populations experiencing seasonal limitations in forage availability exhibit more fluid herd membership and less herd stability. Support for this hypothesis comes from populations of elk in forested habitats of northern Michigan and Oregon. Comparisons are needed with elk in non-forested habitats, such as coastal California, to further examine test this hypothesis. Understanding herd stability at a local scale also has important applied relevance because the spatial boundaries of herd ranges can be effectively used as management units (Edge et al. 1986, Roloff et al. 2001). If the stability and spatial dynamics of herds are not taken into account, common management techniques such as culling and contraception may be ineffective or have unintended consequences (Millspaugh et al. 2004).

Elk form groups to gain protection from predators and possibility to gain peer knowledge of forage resource locations, but the size and composition of herbivore groups varies over time (Caughley 1964). Fine-scale foraging decisions, predator avoidance and reproductive behaviors can promote grouping behavior in heterogeneous habitats (Fortin et al. 2002). However, as animal densities increase, intraspecific competition for forage may select against large groups and instead promote range expansions and conspecific avoidance. Little is known about the relationship between group sizes and herd densities of large herbivores, but it is reasonable to predict that group sizes within a herd may reach a critical threshold when the benefits of remaining in a large group are outweighed by the costs imposed by intraspecific competition for forage. At this point, animals may decide split into smaller groups relative to herd size. Finally, large herbivores in northern environments also display predictable seasonal shifts in group sizes (Stuart-Smith et al. 1997, Jedrzejewski et al. 2006), but seasonal patterns in grouping behavior in Mediterranean climates are less understood. Understanding the dynamics of grouping behaviors is important because it plays influences animal distributions, especially for populations that are growing and may be expanding into new regions (Van Dyke 2007).

Elk home range sizes can vary widely over time and between populations, thus empirical data are needed to understand the underlying mechanisms driving them. Habitat (Koubek and Hrabe 1996, Winnie et al. 2008) and population density (Henderson et al. 2000, Kilpatrick et al. 2001) have been proposed as drivers of home ranges sizes for large herbivore. At high population densities, I would expect to observe larger home ranges because of elevated intraspecific competition for forage and reduced forage biomass promoting expanded search efforts (Kilpatrick et al. 2001). Even still, population reductions can result in smaller home range sizes (Henderson et al. 2000). Home range sizes estimates for elk at Tomales during the early growth period provide a useful comparison to current home range size estimates, and may provide insight into how the spatial structure of the population has changed with increases in elk abundance. Current elk densities and habitat configurations vary among herds at Pt. Reyes, allowing for a comparison of home range sizes between adjacent herds and an assessment of the importance of density and habitat on home range size.

Large herbivore population dynamics are strongly influenced by nutritional conditions, which manifest in differential selection of available habitats (Morris 2003). As “selective generalists” (Toweill and Thomas 2002), elk resource selection is dictated by the quality (Langvatn and Hanley 1993) and distribution of available habitat types (Skovlin et al. 2002). The quality of elk habitat is affected by the relative forage value of the underlying vegetation, topography, and potential for predator detection/avoidance. These factors can vary spatiotemporally and are often critical for only short periods (i.e. parturition habitat). Although resource selection patterns have been well documented for Rocky Mountain and Roosevelt elk (Toweill and Thomas 2002), less is known of tule elk resource selection patterns. Tule elk weigh are smaller than other elk subspecies and have unique morphological adaptation to mild Mediterranean grasslands, which may result in different resource selection patterns. At Pt. Reyes, tule elk range over a variety of habitat types and their relative selection of each is unknown. An understanding of tule elk resource selection at Pt. Reyes will aid in their management by identifying current critical habitat and potential future areas of likely population expansion.

Quantifying small-scale movement behaviors of large ungulates is an active area of research (Johnson et al. 2002, Christ et al. 2008, Coulon et al. 2008). The advent of Global Positioning Satellite (GPS) transmitters has allowed researchers to examine animal movements with greater accuracy and at more regular intervals than was previously possible. Generalized spatial movement models [e.g. fractal analyses (Crist et al. 1992), correlated random walks (Kareiva and Shigesada 1983), Levy flights (Viswanathan et al. 1996)] have been developed to quantify movement patterns over space. These models can provide a foundation for analyzing movement process, but they ignore the effects of all underlying abiotic and biotic processes. Little is known about the role that weather, habitat, population density and humans may play in regulating large herbivores’ small-scale movement patterns. A better understanding of the influence that these factors have on the movements of elk at Pt. Reyes will facilitate more accurate predictions of future movement patterns.

Understanding mechanisms regulating a population requires knowing the relative contributions of individual vital rates to annual population variability. Annual vital rate variation can be affected by forage availability or quality (Stewart et al. 2006), climate (Langvatn et al. 1996) or predation (Garrott et al. 2009). These factors can work alone or in combination to drive annual pregnancy (Stewart et al. 2005), calf survival (Singer et al. 1997) and adult survival (Saether 1997). The specific environmental factors regulating tule elk population change at Pt. Reyes are unclear.

LITERATURE CITED

Alexander, R. D. 1974. The evolution of social behavior. Pages 325-383 *in* R. F. Johnston, editor. Annual Review of Ecology and Systematics. Annual Reviews Inc., Palo Alto, CA.

Barbour, M., T. Keeler-Wolf, and A. A. Schoenherr. 2007. Terrestrial vegetation of California. 3rd edition. The University of California Press, Berkeley, CA.

Bender, L. C., and J. B. Haufler. 1999. Social group patterns and associations of nonmigratory elk (*Cervus elaphus*) in Michigan. American Midland Naturalist 142:87-95.

Brown, P. M., M. W. Kaye, and D. Buckley. 1999. Fire history in Douglas-fir and coast redwood forests at Point Reyes National Seashore, California. Northwest Science 73:205-216.

Byers, J. A. 1997. The American pronghorn: social adaptations and the ghosts of predators past. University of Chicago Press, Chicago, IL.

Caughley, G. 1964. Social organization and daily activity of the red kangaroo and the grey kangaroo. Journal of Mammalogy 45:429-436.

_____. 1970. Eruption of ungulate populations, with emphasis on himalayan thar in New Zealand. Ecology 51:53-72.

Christ, A., J. Ver Hoef, and D. L. Zimmerman. 2008. An animal movement model incorporating home range and habitat selection. Environmental and Ecological Statistics 15:27-38.

Clark, K. E. 1982. The mammals of the Point Reyes Peninsula. Unpublished thesis, University of California at Santa Cruz, Santa Cruz, CA.

Coughenour, M. B., and F. J. Singer. 1996. Elk population processes in Yellowstone National Park under the policy of natural regulation. Ecological Applications 6:573-593.

Coulon, A., N. Morellet, M. Goulard, B. Cargnelutti, J. M. Angibault, and A. J. M. Hewison. 2008. Inferring the effects of landscape structure on roe deer (*Capreolus capreolus*) movements using a step selection function. Landscape Ecology 23:603-614.

Crist, T. O., D. S. Guertin, J. A. Wiens, and B. T. Milne. 1992. Animal movements in heterogeneous landscapes - an experiment with eleodes beetles in shortgrass prairie. Functional Ecology 6:536-544.

Edge, W. D., C. L. Marcum, S. L. Olson, and J. F. Lehmkuhl. 1986. Nonmigratory cow elk herd ranges as management units. Journal of Wildlife Management 50:660-663.

Fortin, D., J. M. Fryxell, and R. Pilote. 2002. The temporal scale of foraging decisions in bison. Ecology 83:970-982.

Franklin, W. L., A. S. Mossman, and M. Dole. 1975. Social organization and home range of Roosevelt elk. Journal of Mammalogy 56:102-118.

Garrott, R. A., P. J. White, J. J. Rotella, and F. G. R. Watson. 2009. The Madison headwaters elk herd: transitioning from bottom-up regulation to top-down limitation. Pages 489-517 *in* R. A. Garrott, P. J. White, and F. G. R. Watson, editors. The Ecology of Large Mammals in Central Yellowstone: Sixteen Years of Integrated Field Studies. Elsevier Academic Press, Oxford, UK.

Gates, N. B. 2000. Tomales Point elk census report, Fall 2000. National Park Service, unpublished report. Point Reyes National Seashore, California.

Gilliam, H. 2002. Weather of the San Francisco Bay Region. 2nd edition. University of California Press, Berkeley, CA.

Gogan, P. J. P., and R. H. Barrett. 1987. Comparative dynamics of introduced tule elk populations. Journal of Wildlife Management 51:20-27.

Gogan, P. J. P., D. A. Jessup, and M. Akeson. 1989. Copper deficiency in tule elk at Point Reyes, California. Journal of Range Management 42:233-238.

Henderson, D. W., R. J. Warren, J. A. Cromwell, and R. J. Hamilton. 2000. Responses of urban deer to a 50% reduction in local herd density. Wildlife Society Bulletin 28:902-910.

Howell, J. A., G. C. Brooks, M. Semenoff-Irving, and C. Greene. 2002. Population dynamics of tule elk at Point Reyes National Seashore, California. Journal of Wildlife Management 66:478-490.

Jedrzejewski, W., H. Spaedtke, J. F. Kamler, B. Jedrzejewska, and U. Stenkewitz. 2006. Group size dynamics of red deer in Bialowieza Primeval Forest, Poland. Journal of Wildlife Management 70:1054-1059.

Jenkins, K. J., and E. E. Starkey. 1982. Social organization of Roosevelt elk in an old-growth forest. Journal of Mammalogy 63:331-334.

Jessup, D. A., B. Abbas, D. Behymer, and P. Gogan. 1981. Para-tuberculosis in tule elk in California. Journal of the American Veterinary Medical Association 179:1252-1254.

Johnson, B. E., and J. H. Cushman. 2007. Influence of a large herbivore reintroduction on plant invasions and community composition in a California grassland. Conservation Biology 21:515-526.

Johnson, C. J., K. L. Parker, D. C. Heard, and M. P. Gillingham. 2002. Movement parameters of ungulates and scale-specific responses to the environment. Journal of Animal Ecology 71:225-235.

Kareiva, P. M., and N. Shigesada. 1983. Analyzing insect movement as a correlated random walk. Oecologia 56:234-238.

Keeley, J. E. 2005. Fire history of the San Francisco East Bay region and implications for landscape patterns. International Journal of Wildland Fire 14:285-296.

Kilpatrick, H. J., S. M. Spohr, and K. K. Lima. 2001. Effects of population reduction on home ranges of female white-tailed deer at high densities. Canadian Journal of Zoology 79:949-954.

Koubek, P., and V. Hrabe. 1996. Home range dynamics in the red deer (*Cervus elaphus*) in a mountain forest in central Europe. Folia Zoologica 45:219-222.

Langvatn, R., S. D. Albon, T. Burkey, and T. H. Clutton-Brock. 1996. Climate, plant phenology and variation in age of first reproduction in a temperate herbivore. Journal of Animal Ecology 65:653-670.

Langvatn, R., and T. A. Hanley. 1993. Feeding-patch choice by red deer in relation to foraging efficiency - an experiment. Oecologia 95:164-170.

McCullough, D. R. 1971. The tule elk: its history, behavior, and ecology. University of California Press, Berkeley, CA.

McCullough, D. R., J. K. Fischer, and J. D. Ballou. 1996. From bottleneck to metapopulation: Recovery of the tule elk in California. Pages 375-403 *in* D. R. McCullough, editor. Metapopulations and wildlife conservation. Island Press, Washington D.C.

Messmer, T. A. 2009. Human-wildlife conflicts: emerging challenges and opportunities. Human-Wildlife Conflicts 3:10-17.

Millias, J. G. 1915. Wapiti. Pages 234-403 *in* D. Caruthers, P. B. Van der Byl, R. L. Kennion, J. G. Millias, H. F. Wallace, and F. G. Barclay, editors. The gun at home and abroad: big game of Asia and North America. The London and Counties Press Assoc., London.

Millspaugh, J. J., G. C. Brundige, R. A. Gitzen, and K. J. Raedeke. 2004. Herd organization of cow elk in Custer State Park, South Dakota. Wildlife Society Bulletin 32:506-514.

Morellet, N., J. M. Gaillard, A. J. M. Hewison, P. Ballon, Y. Boscardin, P. Duncan, F. Klein, and D. Maillard. 2007. Indicators of ecological change: new tools for managing populations of large herbivores. Journal of Applied Ecology 44:634-643.

Morris, D. W. 2003. Toward an ecological synthesis: a case for habitat selection. Oecologia 136:1-13.

O'Gara, B. W., and R. G. Dundas. 2002. Distribution: past and present. Pages 67-119 *in* D. E. Toweill, and J. W. Thomas, editors. North American elk: ecology and management. Smithsonian Institution Press, Washington.

Parma, A. M. 1998. What can adaptive management do for our fish, forests, food, and biodiversity? Integrative Biology 1:16-26.

Roloff, G. J., J. J. Millspaugh, R. A. Gitzen, and G. C. Brundige. 2001. Validation tests of a spatially explicit habitat effectiveness model for Rocky Mountain elk. Journal of Wildlife Management 65:899-914.

Saether, B. E. 1997. Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. Trends in Ecology and Evolution 12:143-149.

Shideler, S. E. 2000. Monitoring reproduction and contraception in free ranging wildlife: tule elk (Cervus elaphus nannodes) at Point Reyes National Seashore. Proceedings - Rocky Mountain Research Station, USDA Forest Service:137-142.

Singer, F. J., A. Harting, K. K. Symonds, and M. B. Coughenour. 1997. Density dependence, compensation, and environmental effects on elk calf mortality in Yellowstone National Park. Journal of Wildlife Management 61:12-25.

Singer, F. J., D. M. Swift, M. B. Coughenour, and J. D. Varley. 1998. Thunder on the Yellowstone revisited: an assessment of management of native ungulates by natural regulation, 1968-1993. Wildlife Society Bulletin 26:375-390.

Skovlin, J. M., P. Zager, and B. K. Johnson. 2002. Elk habitat selection and evaluation. *in* D. E. Toweill, and D. L. Thomas, editors. North American Elk: ecology and management. Smithsonian Institution Press, Washington, D.C.

Slayermaker, C. 1983. Ethnological study of Coast Miwoks. University of California, Davis, Davis, CA.

Stewart, K. M., R. T. Bowyer, B. L. Dick, B. K. Johnson, and J. G. Kie. 2005. Density-dependent effects on physical condition and reproduction in North American elk: an experimental test. Oecologia 143:85.

Stewart, K. M., R. T. Bowyer, R. W. Ruess, B. L. Dick, and J. G. Kie. 2006. Herbivore optimization by North American elk: consequences for theory and management. Wildlife Monographs 167:1-24.

Stuart-Smith, A. K., C. J. A. Bradshaw, S. Boutin, D. M. Hebert, and A. B. Rippin. 1997. Woodland caribou relative to landscape patterns in northeastern Alberta. Journal of Wildlife Management 61:622-633.

Sugnet, P. 1985. Fire history and postfire stand dynamics of Inverness bishop pine populations. Unpublished thesis, University of California, Berkeley, CA.

Toweill, D. E., and J. W. Thomas. 2002. North American elk: ecology and management. Smithsonian Institution Press, Washington.

Treganza, R. 1961. The Indian story of Point Reyes, unpublished report. National Park Service. Point Reyes National Seashore, CA.

Tule-Elk-Interagency-Task-Force. 1979. A management plan for the conservation of tule elk. Bureau of Land Management. Sacramento, CA.

Van Atta, C. E. 1946. Notes on the former presence of grizzly and black bears in Marin County, California. California Fish and Game 32:27-29.

Van Dyke, F. 2007. Colonization of non-traditional range in dispersing elk (*Cervus elaphus nelsoni*) populations. Canadian Field Naturalist 121:133-141.

Viswanathan, G. M., V. Afanasyev, S. V. Buldyrev, E. J. Murphy, P. A. Prince, and H. E. Stanley. 1996. Levy flight search patterns of wandering albatrosses. Nature 381:413-415.

Weckerly, F. W. 1999. Social bonding and aggression in female Roosevelt elk. Canadian Journal of Zoology 77:1379-1384.

Weldon, B. R. 1952. Some observations on coyote predation in Yellowstone National Park. Journal of Mammalogy 33:470-476.

Wiens, J. A., N. C. Stenseth, B. Vanhorne, and R. A. Ims. 1993. Ecological mechanisms and landscape ecology. Oikos 66:369-380.

Winnie, J. A., P. Cross, and W. Getz. 2008. Habitat quality and heterogeneity influence distribution and behavior in African buffalo (*Syncerus caffer*). Ecology 89:1457-1468.

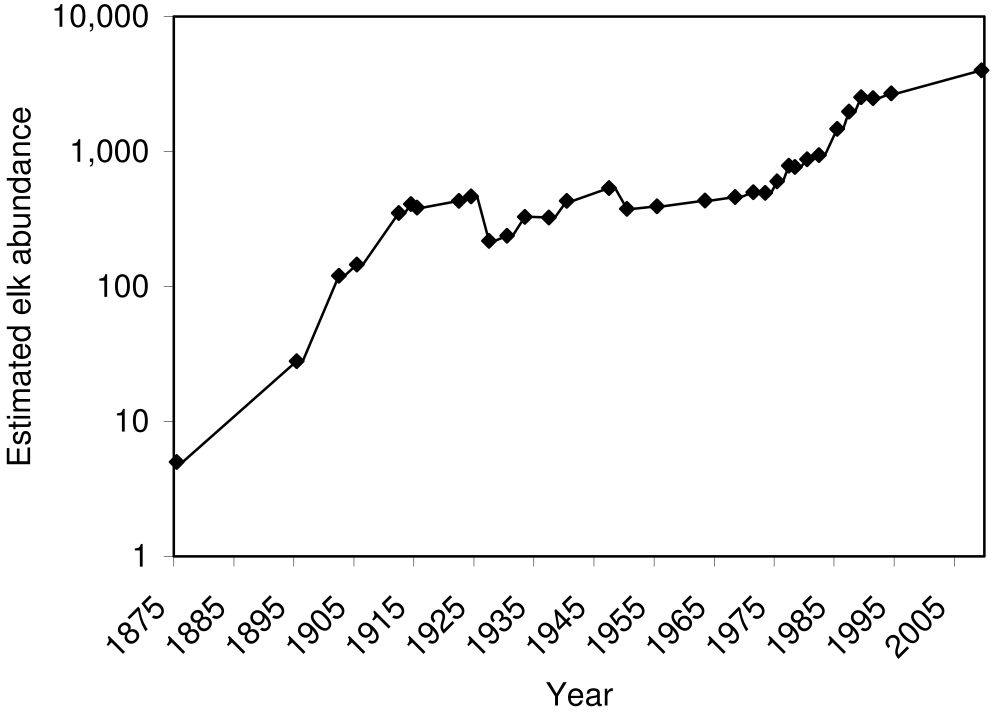

Figure 1. Estimated tule elk abundance in California, 1875 to 2009, plotted on a log-scale. The solid line depicts the two-year moving average of population estimates. Data are extrapolated values from herd counts compiled by D. McCullough (McCullough et al. 1996).

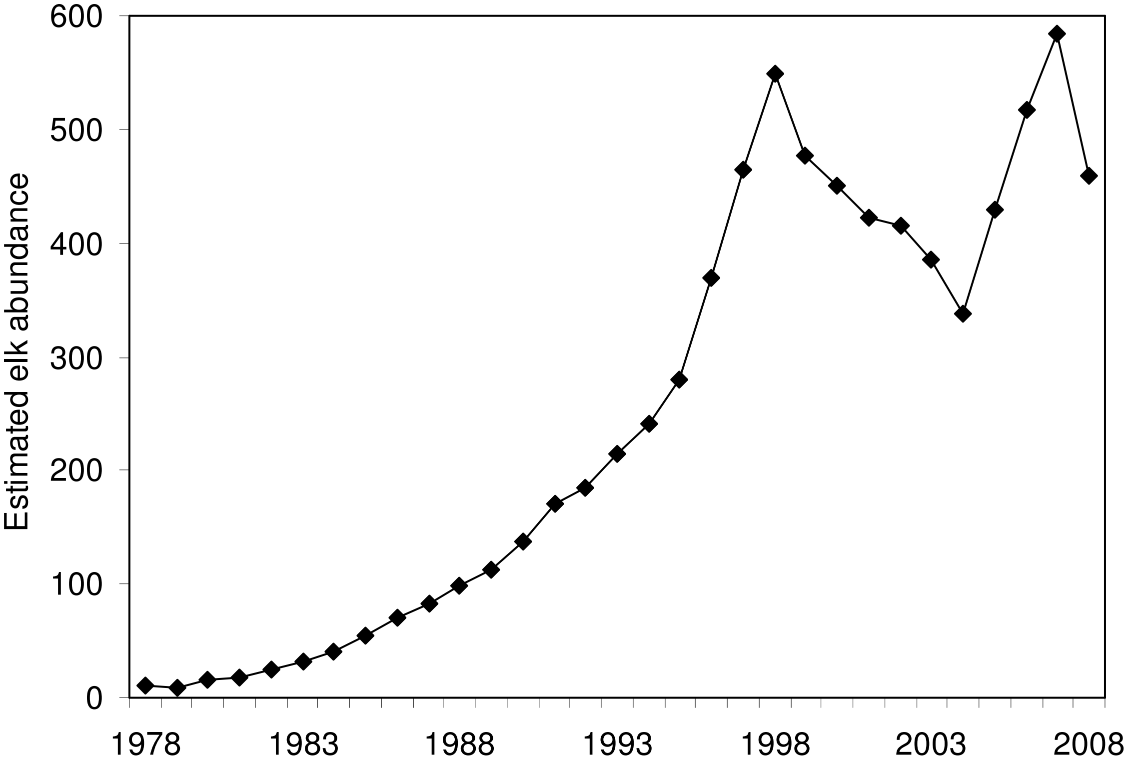

Figure 2. Estimated annual abundance of tule elk at the Tomales Point Elk Reserve, Point Reyes National Seashore, California, 1978 – 2008.

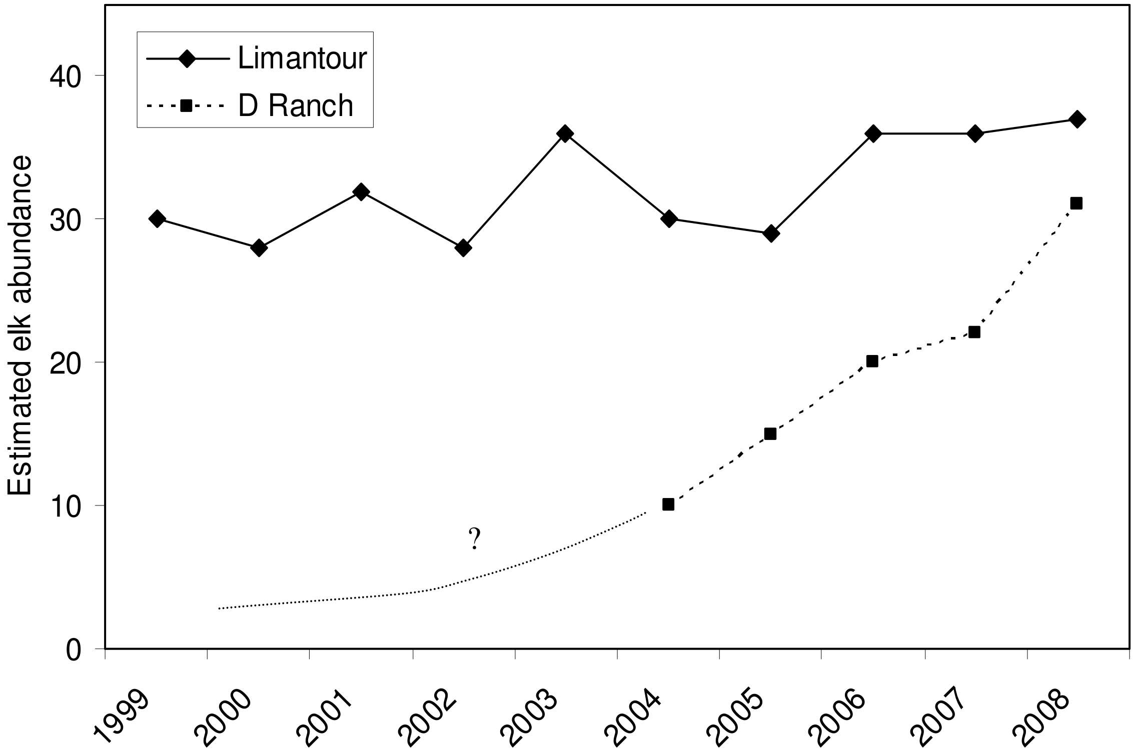

Figure 3. Estimated annual abundance of tule elk at the Limantour and D Ranch herds of Point Reyes National Seashore, California, 1999 – 2008. Values are taken from annual elk surveys conducted by the National Park Service. The dotted line for is an estimate of elk abundance at D Ranch because elk count data are not available before 2004.

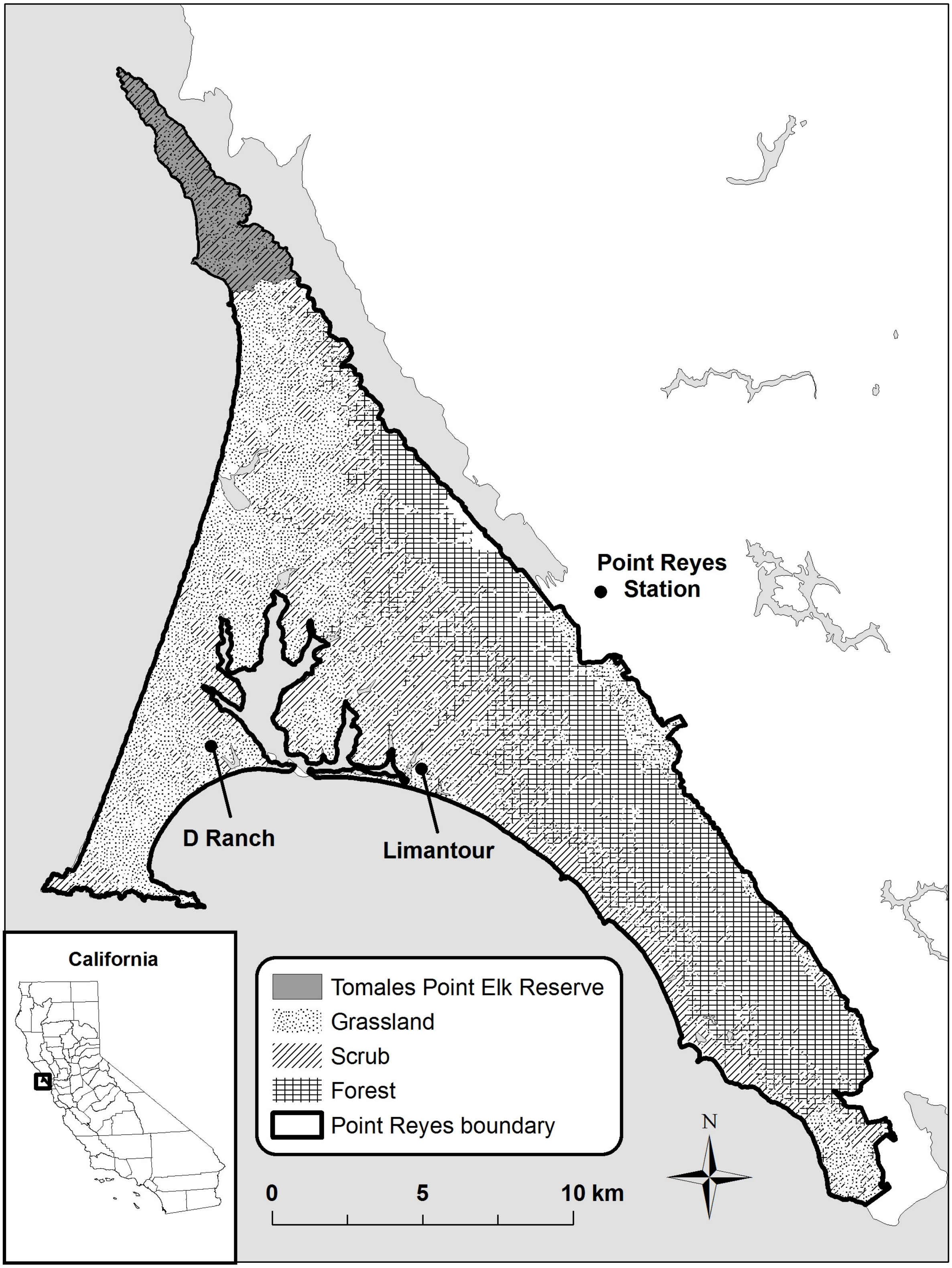

Figure 4. Map of Point Reyes National Seashore, California, and surrounding lands. My study area included lands within the boundary of Pt. Reyes, shown outlined. Tule elk inhabited the Tomales Point Elk Reserve (shaded), and the D Ranch and Limantour regions.

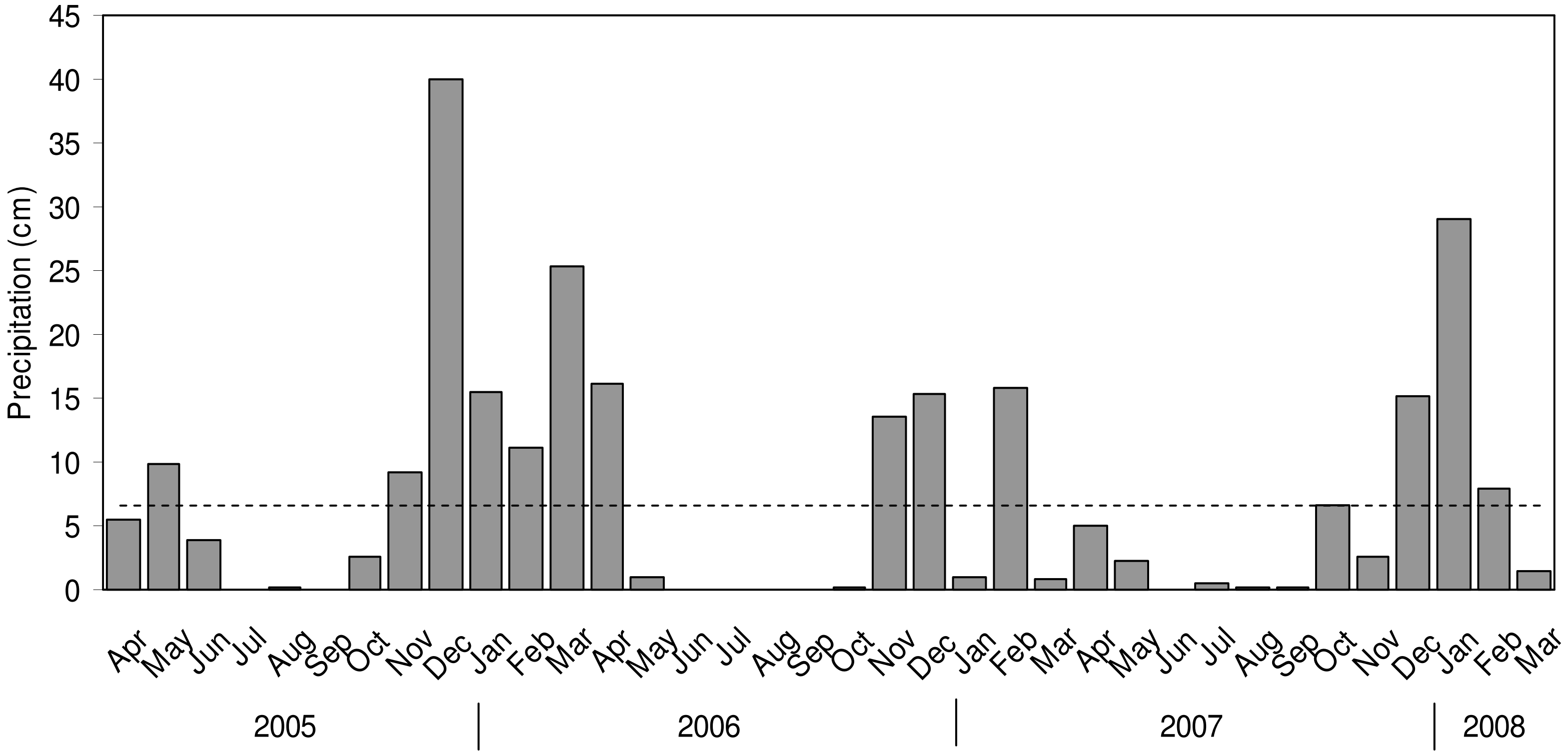

Figure 5. Monthly precipitation (cm) during the study period at Bodega Bay Marine Laboratory, California, approximately 7 km northwest of Tomales Point Elk Reserve, Point Reyes National Seashore, California from1 April, 2005 to 31 March, 2008. The dashed line indicates the average monthly precipitation during this period (7 cm).

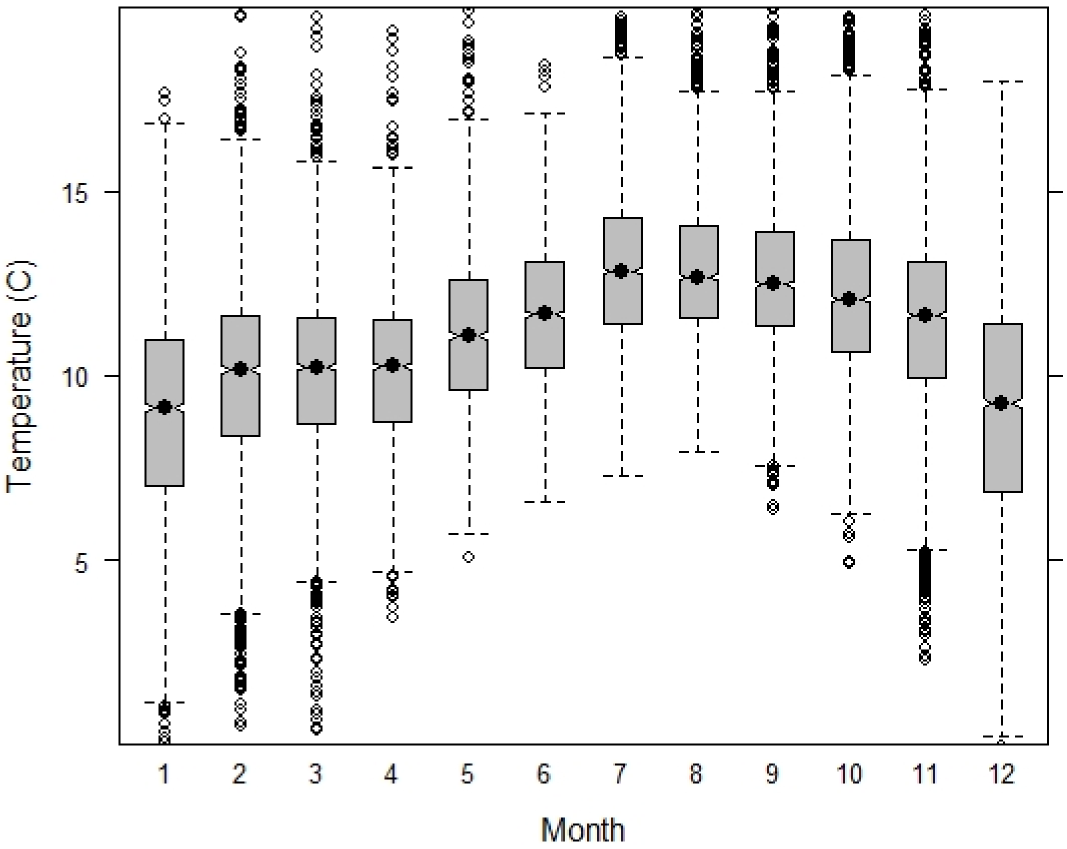

Figure 6. Boxplot of hourly temperatures by month recorded at the Bodega Bay Marine Laboratory, California, approximately 7 km northwest of Tomales Point Elk Reserve, Point Reyes National Seashore, California, 2005 – 2008. Notches represent 95% confidence intervals around the median.

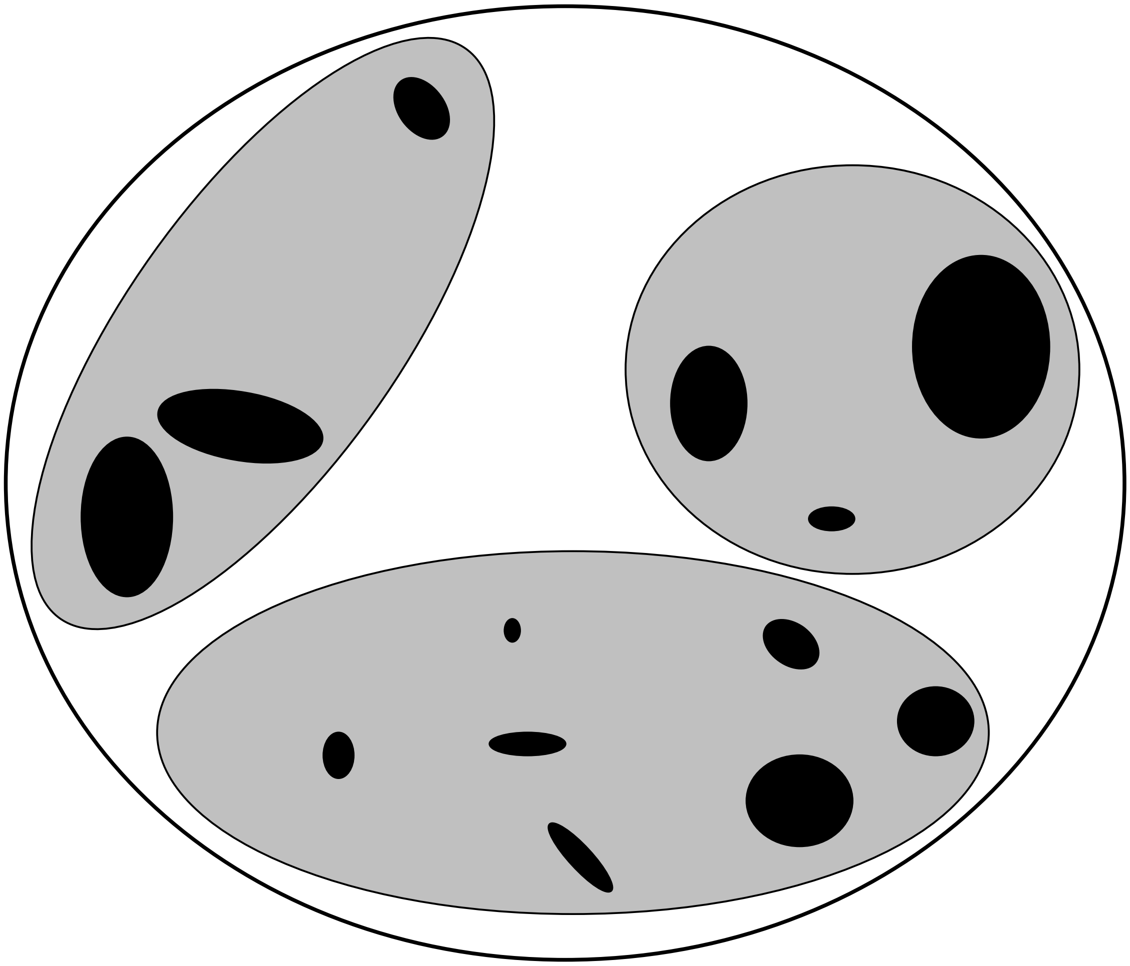

Figure 7. Visual representation of the spatial hierarchy of an imaginary social large herbivore population. The largest circle represents the population, the largest and most temporally stable unit. The gray polygons represent herds within the population. The black polygons represent groups within herds, which are the most spatially and temporally dynamic units.

CHAPTER 1

HERD STABILITY, GROUPING BEHAVIOR AND HOME RANGE SIZES OF TULE ELK AT POINT REYES NATIONAL SEASHORE

INTRODUCTION

Social living provides benefits (increased predator awareness, predator dilution and increased awareness of local forage resources) and costs (increased conspicuousness for predation and elevated intraspecific competition for resources) (Alexander 1974). Because these competing factors are not static over time, animals attempt to maximize their individual fitness by varying the size and duration of their aggregations over space and time (Wiens et al. 1993). Populations of social large herbivores, such as elk (*Cervus elaphus*), tend to form hierarchical aggregations, which impact their distributions and population dynamics. Elk cluster into smaller subsets within populations called herds; and within herds, elk form dynamic, small-scale spatial associations called groups (Toweill and Thomas 2002). The temporal and spatial dynamics of associations between individual elk generally increases from the herd level to the group level (Coulson et al. 1997). Little is known about the spatial ecology and behaviors of the tule elk (*C. e. nannodes*) compared to other elk subspecies. Having evolved morphological adaptations to mild Mediterranean grasslands of California (McCullough 1971), tule elk may have also developed distinctive behaviors that result in unique herd formations, grouping behaviors and home range sizes.

The likelihood of individual large herbivores within a herd to remain together over time, termed herd stability, varies among populations (Van Dyke et al. 1998, Bender and Haufler 1999). High herd stability provides increased fitness associated with peer-learning of important forage locations and predation threats (Franklin et al. 1975, Byers 1997), and therefore may be favored. Alternatively, low herd stability may occur when individuals have differential resource needs, which are amplified in unfavorable conditions (Bender and Haufler 1999). Examples of large-scale variations in herd stability occur in elk, and may be driven by large-scale climatic variation (Jenkins and Starkey 1982). It has been proposed that elk experiencing little climate variation show long-term bonds and remain in close proximity for extended periods (Weckerly 1999), but populations experiencing seasonal limitations in forage availability exhibit more fluid herd membership and less herd stability. Support for this hypothesis comes from populations of elk in forested habitats of northern Michigan and Oregon (Bender and Haufler 1996, Weckerly 1999). Comparisons are needed with elk in non-forested habitats, such as coastal California, to further examine test this hypothesis. Understanding herd stability at a local scale also has important applied relevance because the spatial boundaries of herd ranges can be effectively used as management units (Edge et al. 1986, Roloff et al. 2001). If the stability and spatial dynamics of herds are not taken into account, common management techniques such as culling and contraception may be ineffective or have unintended consequences (Millspaugh et al. 2004).

Large herbivore group sizes within herds are highly temporally dynamic. Fine-scale foraging decisions, predator avoidance and reproductive behaviors can promote grouping behavior in heterogeneous habitats (Fortin et al. 2002). However, as animal densities increase, intraspecific competition for forage may select against large groups and instead promote range expansions and conspecific avoidance. Little is known about the relationship between group sizes and herd densities of large herbivores, but it is reasonable to predict that group sizes within a herd may reach a critical threshold when the benefits of remaining in a large group are outweighed by the costs imposed by intraspecific competition for forage. At this point, animals may decide split into smaller groups relative to herd size. Finally, large herbivores in northern environments also display predictable seasonal shifts in group sizes (Stuart-Smith et al. 1997, Jedrzejewski et al. 2006), but seasonal patterns in grouping behavior in Mediterranean climates are less understood. Understanding the dynamics of grouping behaviors is important because it influences animal distributions, especially for populations that are growing and may be expanding into new regions (Van Dyke 2007).

An animal's home range has traditionally been described as the "area traversed by an individual in its normal activities of food gathering, mating, and caring for young" (Burt 1943). Since a home range is a spatial representation of an animal's resource needs, the factors that influence home range sizes also affect population dynamics, and have applied ecological importance. Within a population, elk home range sizes may be affected by numerous factors, including: habitat quality, time of year and population density (Nugent 1994, Koubek and Hrabe 1996, Henderson et al. 2000, Kilpatrick et al. 2001, Ryan 2006, Winnie et al. 2008). The quality and distribution of habitat is a fundamental driver of the spatial distributions of animals, and play a large role in determining the home range sizes of cervids (Anderson et al. 2005). Elk home ranges in northern seasonal environments often expand during the winter and contract during the summer, reflecting shifts in forage availability and distribution (Kamler et al. 2008). It is not known whether these seasonal changes in home range size also exist for tule elk in a Mediterranean climate, where changes in seasonal forage availability are less pronounced. Finally, ecological theory predicts that herbivores at higher population density should display larger home ranges due to increased forage competition (Damuth 1981), but to date, there have been few opportunities to test this relationship on wild ungulates.

To test these hypotheses, I examined the herd structures, grouping behaviors and home range sizes of 3 distinct subpopulations of tule elk at Point Reyes National Seashore (Pt. Reyes): a high-density, fenced subpopulation within the Tomales Point Elk Reserve (Tomales); a low-density, free-ranging subpopulation inhabiting a wilderness area (Limantour); and a low-density, free ranging subpopulation found on actively managed ranchland (D Ranch). The goals of this chapter were to quantify: 1) the number, spatial distribution and stability of elk herds at Pt. Reyes; 2) how elk home ranges and group sizes vary temporally and among herds at Pt. Reyes; and 3) the relationship between elk home range sizes, group sizes and density. Given the mild climate at Pt. Reyes, I predicted that herd membership would be stable and herd ranges would show little overlap with neighboring elk herd ranges. I predicted that group sizes would decline during the calving and rutting seasons and increase during the summer period. I expected that group sizes would be larger in herds with higher elk density. I expected that home ranges would be larger in herds with higher elk densities due to expanding their searching ranges for quality forage. Finally, I predicted that elk forming larger groups would have larger home ranges than those found in smaller groups, due to the need to increase their searching areas for forage because of higher levels of intraspecific competition.

METHODS

Radio Telemetry

Radio-marking is currently the most effective method of monitoring individual animals in a free-ranging situation to determine population parameters (Millspaugh and Marzluff 2001, Mech and Barber 2002). Between 2005 and 2007, 42 tule elk cows were immobilized at Pt. Reyes using helicopter net-gunning (Table 1). We captured an even proportion of elk from 3 regions (D Ranch, Limantour and Tomales). Captured elk were hobbled, blindfolded and fitted with uniquely numbered ear tags (Nasco, Modesto, CA 95352) and a mortality-sensing VHF radio telemetry collar (Telonics Inc., Mesa, AZ 85204). Each collar had a unique combination of color bands which allowed field researchers to visually identify individual elk. Following the initial capture using helicopters, 10 additional cows were chemically-immobilized by ground darting with a mixture of ketamine and medetomidine, and reversed with atipamezole (Arnemo et al. 1994). These elk were also fitted with mortality-sensing VHF radio telemetry collars and ear tags.

Instrumented elk were located on foot and on horseback approximately 2-times per week for 3 consecutive years. Visual locations were attempted on all animals throughout the study period unless there was a mechanical failure in the radio collar, or the animal was confirmed dead. An elk "group" was defined as elk within 50 m of each other sharing similar activity patterns (Clutton-Brock et al. 1982). The locations of elk groups containing radio-collared elk ("fix") were hand-recorded on 7.5 minute U.S. Geological Survey Digital Raster Graphics (DRG) (http://topomaps.usgs.gov/drg/). Paper-mapped fixes were manually digitized and stored in a Geographic Information System (GIS) (ArcGIS 9.2, ESRI, Redlands, CA 92373). For each fix, I attempted to count the number of elk in the group (group size), and classify the elk group by age and sex (cow, bull, yearling male or calf) using physical characteristics (Smith and McDonald 2002).

Herd Characteristics

To determine the number of herds at Pt. Reyes, I quantified the proportion of time that radio-collared elk were quantified at the same fix using a coefficient of association (Cole 1949). The formula for coefficients of associations between pairs of radio-collared elk was:

$$\frac{(2 * S * T_1)}{T_1 + T_2},$$

where S is the number of fixes shared by a pair of radio-collared elk and T_x is the total number of fixes for elk x. Radio-collared elk with large coefficients of association (> 0.3) were considered members of the same herd, and their fixes were combined for herd range size analyses (White and Garrott 1990).

I quantified 90% fixed kernel herd range sizes using fixes from all radio-collared elk in each herd in ArcView 3.2 (Hooge and Eichenlaub 2002). Smoothing parameters were calculated using the least-squared cross-validation (LSCV) method (Sain et al. 1994).

Home Range and Core Area Sizes

Small sample sizes tend to overestimate kernel home range sizes (Seaman et al. 1999), so I needed to determine the minimum number of fixes needed to accurately estimate home range sizes. I randomly subsampled fix data for each radio-collared elk from the total number of fixes recorded down to 5 fixes, at intervals of 5 fixes. For each subsample, I created 50% and 90% fixed kernel home ranges in ArcView 3.2 (Hooge and Eichenlaub 2002). Smoothing parameters were calculated using the least-squared cross-validation (LSCV) method (Sain et al. 1994). I performed 10 iterations for each elk, and then plotted the resulting means and standard errors of home range sizes against the number of fixes used to create the home range. I expected home ranges sizes to asymptote if a sufficient number of fixes had been reached. If an asymptote was reached, I considered the number of fixes to be sufficient for home range analysis. I then created annual 90% fixed kernel home ranges and 50% fixed kernel core areas for radio-collared elk with sufficient numbers of fixes (Hooge and Eichenlaub 2002). To determine how elk home range sizes varied annually, I compared annual home range and core area sizes among study years (1 April – 31 March) using KW χ^2 tests and t-tests.

Group Sizes

To examine how elk group sizes of elk may vary over time at Pt. Reyes, I compared average annual and seasonal group sizes within herds using Kruskal-Wallis chi square (KW χ^2) tests. I defined seasons as quarterly periods each year (season one = January – March, season two = April – June, season three = July – September and season four = October – December). I also tested for differences in group sizes between herds using KW χ^2 tests and for differences in group sizes between pairs of herds using t-tests (S-Plus, Insightful Software, Palo Alto, CA 94304). I log-transformed group size data prior to analysis to achieve normal distributions (Zar 1998).

Density

I defined elk density as the number of elk / ha of grassland habitat. To quantify elk density by herd, I needed to estimate elk abundance in each herd. To determine this, I summed the daily group counts within herds to get daily herd counts, and selected the largest daily herd count for each month. I then averaged the monthly-high herd counts by study year get estimates of annual herd sizes. I determined the amount of grassland habitat within annual herd ranges (quantified above) by clipping annual herd ranges to a GIS vegetation layer jointly produced by the National Park Service and US Geological Survey (Schirokauer et al. 2003). The layer was created by interpreting 1:24,000 color aerial photographs taken in 1994, and utilized a hierarchical classification system. For the purposes of this study, I selected the "life form" classification level because of the ecological relevance of this classification to elk and because of the ability to extrapolate results to other classifications and regions. The life form classification had an overall thematic accuracy of 84% (Schirokauer et al. 2003). I divided annual herd size estimates by the grassland availability to determine elk density for each herd.

Group Size, Home Range Size and Herd Density Relationship

I used linear regression analyses to independently quantify the relationship between average annual group sizes and herd density, annual home range sizes and herd density, and annual group sizes and annual home range sizes. Data were log-transformed prior to analysis (Zar 1998).

RESULTS

Radio-collared elk were located on a 3.68-day mean interval (Table 1, min = 1, max = 19, SE = 0.02) over a period of 1,095 days (April 1, 2005 – March 31, 2008). With spatial outliers removed, 42 elk were located 9,953 times for a total of 36,005 individual elk days. Each elk was located an average of 237 times (min = 37, max = 315, SE = 14.29). Ten (23.3%) radio-collared elk died during the study. I monitored each radio-collared elk for an average period of 857 days (min = 142, max = 1091, SE = 52.07).

A total of 3,749 elk groups were counted. I was able to classify the compositions of 3,336 (89%) groups by age and sex. I was able to quantify the sizes, but not compositions, of 374 (10%) groups. This was mainly due to increment weather conditions (fog and rain). A small number of groups (39, 1%) could not be counted or classified. Fixes occurred between 7:40h and 19:00h Pacific Standard Time.

Herd Characteristics

I identified 6 elk herds at Pt. Reyes, based on coefficients of association. Four herds were found at the Tomales range (North, Plateau, White Gulch and South), 1 herd at the D Ranch range and 1 herd at the Limantour range (Table 2, 3 and 4). Radio-collared elk showed strong spatial cohesion with fellow herd members (mean coefficient of association = 0.53, SE = 0.01) and very weak associations with elk outside their herd (mean coefficient of association = 0.01, SE < 0.01).

Elk herd range sizes averaged 283 ha (SE = 63.69) (Table 5). Annual herd range sizes varied from 85 ha (White Gulch herd, 2007 – 2008) to 987 ha (Limantour herd, 2006 – 2007). Herd ranges showed very little spatial overlap within the 90% kernel boundary and no overlap within the 50% kernel boundary, further indicating that there were very little inter-herd associations among elk (Figure 1).

I estimated the total elk population size of elk at Pt. Reyes was 424 in 2005, 503 in 2006, and 534 in 2007. The largest average herd size was White Gulch ($\bar{x}$ = 145 elk) and the smallest was D Ranch ($\bar{x}$ = 18 elk).

Elk densities averaged 1.31 elk / ha of grassland habitat (SE = 0.27), and varied among herds (KW χ^2 = 21.77, p-value < 0.001) (Table 6). Elk density was lowest at the D Ranch herd (0.09 elk / ha grassland habitat) and highest at the North herd (4.21 elk / ha grassland habitat) (Figure 2).

Group Size and Classifications

The average elk group size was 30 (min = 1, max = 155, SE = 5.43), but group sizes were not normally distributed (Figure 3). Group sizes varied among herds (F = 223.71, p < 0.001). Herds at Tomales formed larger groups than the Limantour and D Ranch herds (Figure 4). The Limantour herd formed the smallest groups ($\bar{x}$ = 11, SE = .058, t = 32.35, p < 0.001) and the North herd formed the largest groups ($\bar{x}$ = 44, SE = 2.64, t = 7.38, p < 0.001).

Average group sizes varied among study years in most herds (Table 7). Overall average annual group sizes declined slightly from 31 (SE_{05-06} = 0.99 and SE_{06-07} = 0.91) in 2005 – 2006 and 2006 – 2007, to 28 (SE = 0.38) in 2007 – 2008, but the difference was not statistically significant. Average group sizes at the D Ranch herd varied annually from 12 (SE = 0.38) in 2005 – 2006 to 16 (SE = 0.42) in 2006 – 2007, and 15 (SE = 0.50) in 2007 – 2008 (KW χ^2 = 62.94, p < 0. 001). Average group sizes at the Limantour herd showed no significant annual variation (KW $\chi^2 = 3.21$, $p = 0.20$). Most herds at Tomales had average group sizes that declined annually, except White Gulch, where group sizes increased between 2005 – 2006 and 2006 – 2007 (36 to 41 elk), and then declined in 2007 – 2008 to 35 elk.

Elk group sizes varied by month (Figure 5) and season (Table 8). Elk group sizes peaked during the winter (December – February) and to a lesser extent during the summer (June and July). Elk group sizes were smallest during the calving season (April – May) and rutting season (August – October). Seasonal variation in group sizes occurred in all herds, but was most pronounced in the smaller D Ranch and Limantour populations (Figures 6 – 11). Temporal variations in elk group sizes was primarily due to changes in cow elk membership, and less due to changes in bull, yearling and calf memberships.

Home Range and Core Area Sizes

Bootstrap tests showed home range sizes reached an asymptote at approximately 50 fixes. One elk with less than 50 fixes was excluded from home range analyses (ID = 578).

The average 90% kernel home range size was 218 ha (min = 55.13, max = 872.84, SE = 34.58, Table 9), and the average 50% core area was 36 ha (min = 4.73, max = 141.53, SE = 4.91). Mean home range sizes expanded from 2005 – 2006 (193 ha, SE = 26.46) to 2006 – 2007 (248 ha, SE = 48.62), and then contracted in 2007 – 2008 (195 ha, SE = 35.71). Mean core area sizes increased annually from 34 ha (SE = 3.45) in 2005 – 2006 to 43 ha (SE = 8.49) in 2006 – 2007, and 46 ha (SE = 10.38) in 2007 – 2008.

Elk home range and core area sizes varied significantly among herds (Figures 12 and 13, KW $\chi^2_{hr} = 22.67$, $p_{hr} < 0.001$, KW $\chi^2_{core} = 20.71$, $p_{core} < 0.001$). The Limantour herd had the largest annual home ranges ($\bar{x} = 661$ ha, SE = 0.69) and core areas ($\bar{x} = 88$ ha, SE = 0.14). Elk at Limantour and D Ranch had home ranges and core areas that were larger than any home range and core area at Tomales.

Radio-collared elk observed for the entire study period (n = 28) were used to test for annual variations in home range and core area sizes by herd. The D Ranch herd was excluded because of an inadequate sample size (n = 2). I was not able to detect any difference in annual home range size (KW $\chi^2 = 1.79$, $p = 0.409$) or core area size (KW $\chi^2 = 1.79$, $p = 0.409$) among herds at Tomales. Home range sizes at Limantour did not vary annually (KW $\chi^2 = 2.35$, $p = 0.309$), but core area sizes at Limantour approximately doubled annually ($\bar{x}_{05\text{-}06} = 53.21$ ha, $\bar{x}_{06\text{-}07} = 107.66$ ha, $\bar{x}_{07\text{-}08} = 200.86$ ha, KW $\chi^2 = 8.12$, $p = 0.017$).

Group Size, Home Range Size and Herd Density Relationship

Annual home range sizes were negatively correlated with elk density, according to the linear regression model results ($R^2 = 0.82$, $p <0.001$, Figure 14). Although the relationships were not always statistically significant, home range sizes of radio-collared elk were generally smaller during years of lower elk density in all herds, except the North herd (Table 10). Elk in herds with large group sizes had smaller home range sizes, according to the linear regression model results ($R^2 = 0.76$, $p < 0.001$, Figure 15). Within each herd, individual elk also exhibited a similar relationship among study years, but it was not always statistically significant (Table 11). Average annual group sizes of elk were positively correlated with elk densities among herds ($R^2 = 0.91$, $p < 0.001$, Figure 16). Within herds, there was not a consistent correlation between the average annual group sizes of elk and elk density among study years (Table 12).

DISCUSSION

The goals of this research were to quantify the herd structures, grouping behaviors and home range sizes of elk at Pt. Reyes; and to determine the relationship between group sizes, home range sizes and herd densities. I identified 6 distinct herds of elk at Pt. Reyes that showed very little interaction. Elk herd sizes ranged from approximately 18 (D Ranch herd) to 145 elk (North herd), and herd range sizes ranged from 85 ha (White Gulch herd) to 987 ha (Limantour herd). Elk groups were composed on average of 30 elk, although group sizes varied among herds and seasons. Larger groups were generally associated with larger herds, and the rutting and parturition periods. Elk home range sizes (90% fixed kernel) averaged 218 ha (SE = 5.43), and varied by herd. The density of elk within herd ranges at Pt. Reyes averaged 1.31 elk / ha of grassland habitat. Home range sizes were smaller and group sizes were larger in herds with higher densities of elk, which suggests that the spatial distributions and social behaviors of elk at Pt. Reyes were density-dependent. Finally, elk in herds that formed larger group sizes had smaller home ranges.

Herds of elk at Pt. Reyes were more stable than northern elk populations in Michigan, and a similar level of stability to coastal elk populations in Oregon (Bender and Haufler 1999, Weckerly 1999). Adjacent elk herds from the high density Tomales region interacted very little, despite the absence of any physical barriers. High herd stability may have developed to increase elk survival and fitness through peer learning of important foraging areas (Edge et al. 1985, Edge et al. 1986) and reduced predation risk (Franklin and Lieb 1979, Shoesmith 1979). A highly seasonal climate can be a barrier to developing long-term group memberships in ungulate species by promoting migratory behavior (Franklin and Lieb 1979), but this was not evident at Pt. Reyes. Empirical evidence has suggested that northern hemisphere elk populations experiencing season resource limitations generally do not display long-term herd associations (Knight 1970, Houston 1982, Bender and Haufler 1999) while southern climate elk populations in stable environments with less seasonal resource limitations display long-term bonds (Franklin and Lieb 1979, Clutton-Brock et al. 1982, Jenkins and Starkey 1982). The mild Mediterranean climate at Pt. Reyes, which includes relatively short periods of low forage availability, may explain the high herd stability observed in this study. These results support the hypothesis that if climatic conditions are favorable, elk will tend to exhibit long-term herd stability.

Group sizes followed seasonal cycles similar to other elk populations (Franklin and Lieb 1979, Houston 1982). Group sizes peaked during the winter and mid-summer periods, and were smallest during the spring and fall. Seasonal changes in forage availability can lead to group size variations (Moran 1973), and may be responsible for some of the temporal group size changes at Pt. Reyes. Forage availability and quality were lowest during the summer and fall periods (June – November) (Gogan and Barrett 1995), and remaining green forage was unevenly distributed in valley bottoms and patchy riparian area. Spatial heterogeneity of remaining high-quality forage likely promoted clustering and larger group sizes. Temporal patterns in grouping behavior were consistent between Pt. Reyes and more northern elk populations (Bender and Haufler 1999, Jedrzejewski et al. 2006), suggesting that factors additional to climate drive seasonal elk grouping behavior. The reproductive phenology of Pt. Reyes elk was consistent with other populations, and was a likely driver of seasonal grouping behavior. Bulls herded cow elk groups during the fall into more easily defendable harems, leading to reductions in group sizes. Parturition behavior in the spring also reduced group sizes because cow elk usually remained separated from other adult elk for approximately 2 weeks after calving.

The home range sizes of elk at Pt. Reyes were some of the smallest recorded in North America ($\bar{x}$ =217 ha, SE = 35), which is probably due to the site's abundance of grassland habitat and the mild Mediterranean climate. A mild climate, and related high forage availabilities, can reduce home range sizes by restricting search efforts for forage (Fisher and Owens 2000, McLoughlin and Ferguson 2000, Oehler et al. 2003, Celesia et al. 2010). Conversely, elk in northern climates with limited forage availability increase their range to locate quality forage, and thereby display larger home ranges. Migratory elk in Yellowstone National Park had kernel home ranges averaging 13,468 ha (SE = 1,868), over 60-times larger than Pt. Reyes (Anderson et al. 2005). Non-migratory, northern climate elk populations also generally have much larger home ranges, such as in Wisconsin ($\bar{x}$ = 2,134 ha, SE = 1,736) and Alberta, Canada ($\bar{x}$ = 5296 ha, SE = 2869) (Anderson et al. 2005). Climate-related home range size variations are also evident in red deer (*Cervus elaphus*). Red deer in the Mediterranean climates of Italy (Lovari et al. 2007) and Spain (Carranza et al. 1991) showed much smaller home ranges (130 ha and 250 ha, respectively) than those in the temperate climate of Scotland (Catt and Staines 1987) (406 - 2,400 ha). It could be argued that elk in the Tomales region of Pt. Reyes were confined within a fenced peninsula that constrained movement, and therefore led to smaller home ranges. However, there are 2 reasons that I believe that the fence played only a minor role in determining home range sizes. Firstly, only one herd (South) bordered the fence and it did not have a reduced home range size. Also, elk in the South herd rarely moved near the fence, as evidenced by GPS collar data (Chapter 3), and the home range boundary was over 250 m from the fence.

Elk home range sizes contracted by approximately 300% at Tomales between 1998 and 2008. During this period, elk abundances had declined and then increased by over 50%. Elk showed strong cohesion during the initial period of establishment, and had home range sizes that averaged 359 ha (90% isoline) (Gogan 1986). Twenty years later, average home range sizes at Tomales were similar (344 ha, mean of 90% adaptive kernels) (Howell et al. 2002), but then decreased to only 111 ha in this study. Howell et al. quantified elk home ranges using adaptive kernels, which can overestimate home range sizes (Seaman et al. 1999), versus fixed kernels in the study. However, it is unlikely that this methodological difference singly explains the observed large reductions in home range sizes over time. Along with home range contractions, elk at Tomales began utilizing the previously vacant Plateau herd range. What was termed the "South herd" in 1998, split into 2 separate herds (South and White Gulch), and the North herd range compressed in size in this study. Possible explanations for these changes include habitat modifications, changes in matriarchal leadership and differences in sampling protocol. Elk herbivory at Tomales has lead to increased grass biomass and diversity, and has limited shrub encroachment (Johnson and Cushman 2007), but the spatial configuration of these vegetation changes are unknown. Given the importance of grass habitat for elk forage at Pt. Reyes (Gogan and Barrett 1995, Fallon-McKnight 2006), more abundant grass habitat may have increased range quality at Tomales. This may have allowed for elk to remain in a smaller region and still satisfy their forage needs. Spatial habitat changes may also have led to herd fissioning in the southern portion of Tomales. Changes in matriarchal leadership within elk herds has also been proposed as a possible mechanism for changes in elk ranging behavior (Edge et al. 1986), but it is not known how herd leadership has varied over time at Pt. Reyes. Finally, differences in the temporal scale of data collection may explain some of the differences. Kernel home range estimators are sensitive to sampling intervals and sizes (Seaman et al. 1999). Howell et al. located elk at weekly intervals versus biweekly in this study.

I expected that elk in herds that formed larger groups would have larger home ranges, because of increased forage competition causing expanded searching behavior, but the opposite relationship was observed. There are a number of possible explanations for this unanticipated result. Elk at Tomales formed large groups possibly because they were exposed to inter-herd competition and territorial aggression, while D Ranch and Limantour formed smaller groups because they were not exposed to competition with other herds. Pressure from density-related inter-herd competition might have counteracted range expansions, even for herds with larger groups, leading to smaller home ranges. While population density can regulate home range sizes, a more important factor may be the number of neighbors that individuals encounters per unit time (Schradin et al. 2010). Even visual encounters with neighboring herd members may be a deterrent to range expansion. A second possible explanation is that group sizes might not have been large enough to cause an increase in home range sizes. Density dependent effects on wildlife are complex, nonlinear and may vary at extreme values. It is possible that if group sizes increase in the future, there will be correlated increases in home range sizes.

Elk herds at Pt. Reyes at higher densities generally formed larger group sizes than lower density herds. This result is not surprising, given that higher densities of elk may have encouraged individuals to aggregate because of a greater likelihood of seeing and joining neighboring elk in their herd. I predicted that if elk densities were high enough, intraspecific competition for forage may be strong enough to outweigh the benefits of grouping. By fracturing into smaller groups relative to herd size and seeking out less grazed habitats, elk could reduce competition. This was not observed in this study, despite elk densities exceeding 4 elk / ha of grassland habitat. It is possible that intraspecific competition for forage did not reach levels high enough to discourage elk from clustering.

Elk herds at Pt. Reyes at higher densities generally had smaller home ranges than lower density herds. Animal density has been associated with ungulate home range sizes, but its effect appears mixed. Experimental evidence has suggested that cervid home range sizes are inversely density dependent (Loft et al. 1993, Kjellander et al. 2004), but field studies found positive relationships between home range sizes and density (Henderson et al. 2000, Kilpatrick et al. 2001). Inter-herd variations in ungulate home range sizes has usually been inversely associated with habitat quality and heterogeneity (Winnie et al. 2008). As large herbivore populations reach high densities, availability and homogeneity of high quality forage usually declines (Caughley 1979). At Pt. Reyes, however, high density elk foraging led to increases in high quality forage (Johnson and Cushman 2007), which may explain smaller home range sizes at higher densities. Declines in home range sizes at high densities occur in territorial species (Wolff 1985, Celesia et al. 2010), but non-rutting elk are not considered territorial. However, I observed radio-collared cows from neighboring herds harassed (laid-back ears, cow-kicked and chased) by resident cows on a number of occasions at Tomales. Territorial behaviors, such as sign posting and scent marking by cow elk, have been observed (Franklin et al. 1975, Bowyer and Kitchen 1987) but observations of direct inter-herd cow elk aggression are absent from the literature. I propose that territorial behavior may have regulated the spatial ranging behaviors of elk at Pt. Reyes.

CONCLUSIONS

Unlike elk herds in northern climates, elk herds at Pt. Reyes were highly stable and distinct. These findings are likely due to low annual variations in temperatures, and support the hypothesis that climate variability regulates large herbivore herd stability across large spatial scales. Given the lack of interactions between herds at Pt. Reyes, wildlife managers should thoroughly understand the spatial dynamics of this population before initiating active management (i.e. contraception and removal) that may adversely affect population subsets. Elk at Pt. Reyes showed some of the smallest home range sizes on record. Average home range sizes for elk at the high density Tomales herds were substantially smaller than previously reported; possibly due to increases in high-quality forage, changes in herd leadership or differences between observer methodologies. Like elk in northern seasonal environments, elk in the mild coastal California climate of Pt. Reyes exhibited annual cycles in group sizes. This finding suggests that seasonal grouping behaviors of elk may be driven by their reproductive phenology, and climate-related forage availability. Elk herds at high densities exhibited smaller home ranges, possibly due to inter-herd competition. Group sizes of elk increased at higher herd densities. Finally, elk with large home ranges generally formed small groups, possible due to inter-herd territoriality.

LITERATURE CITED

Alexander, R. D. 1974. The evolution of social behavior. Pages 325-383 *in* R. F. Johnston, editor. Annual Review of Ecology and Systematics. Annual Reviews Inc., Palo Alto, CA.

Anderson, D. P., J. D. Forester, M. G. Turner, J. L. Frair, E. H. Merrill, D. Fortin, J. S. Mao, and M. S. Boyce. 2005. Factors influencing female home range sizes in elk (*Cervus elaphus*) in North American landscapes. Landscape Ecology 20:257.

Arnemo, J. M., T. Negard, and N. E. Soli. 1994. Chemical capture of free-ranging red deer (*Cervus elaphus*) with medetomidine-ketamine. Rangifer 14:123-127.

Bender, L. C., and J. B. Haufler. 1996. Relationships between social group size of elk (*Cervus elaphus*) and habitat cover in Michigan. American Midland Naturalist 135:261-265.

_____. 1999. Social group patterns and associations of nonmigratory elk (*Cervus elaphus*) in Michigan. American Midland Naturalist 142:87-95.

Bowyer, R. T., and D. W. Kitchen. 1987. Significance of scent marking by Roosevelt elk. Journal of Mammalogy 68:418-423.

Burt, W. H. 1943. Territoriality and home range concepts as applied to mammals. Journal of Mammalogy 24:346-352.

Byers, J. A. 1997. The American pronghorn: social adaptations and the ghosts of predators past. University of Chicago Press, Chicago, IL.

Carranza, J., S. J. H. Detrucios, R. Medina, J. Valencia, and J. Delgado. 1991. Space use by red deer in a Mediterranean ecosystem as determined by radio-tracking. Applied Animal Behaviour Science 30:363-371.

Catt, D. C., and B. W. Staines. 1987. Home range and habitat selection by red deer (*Cervus elaphus*) in a sitka spruce plantation as determined by radio-tracking. Journal of Zoology 211:681-693.

Caughley, G. 1979. What is this thing called carrying capacity? *in* M. Boyce, and L. D. Haydon-Wing, editors. North American elk: ecology, management and behavior. University of Wyoming Press, Laramie, WY.

Celesia, G. G., A. T. Peterson, J. C. K. Peterhans, and T. P. Gnoske. 2010. Climate and landscape correlates of African lion (*Panthera leo*) demography. African Journal of Ecology 48:58-71.

Clutton-Brock, T., F. Guinness, and S. Albon. 1982. Red Deer: Behavior and Ecology of Two Sexes. Edinburgh University Press, Edinburgh, UK.

Cole, L. C. 1949. The measure of interspecific association. Ecology 30:411-424.

Coulson, T., S. Albon, F. Guinness, J. Pemberton, and T. Clutton-Brock. 1997. Population substructure, local density, and calf winter survival in red deer (*Cervus elaphus*). Ecology 78:852-863.

Damuth, J. 1981. Home range, home range overlap, and species energy use among herbivorous mammals. Biological Journal Of The Linnean Society 15:185-193.

Edge, W. D., C. L. Marcum, and S. L. Olson. 1985. Effects of logging activities on home range fidelity of elk. Journal of Wildlife Management 49:741-744.

Edge, W. D., C. L. Marcum, S. L. Olson, and J. F. Lehmkuhl. 1986. Nonmigratory cow elk herd ranges as management units. Journal of Wildlife Management 50:660-663.

Fallon-McKnight, M. 2006. Native and non-native ungulate diet at Point Reyes National Seashore. Unpublished NPS report.

Fisher, D. O., and I. P. F. Owens. 2000. Female home range size and the evolution of social organization in macropod marsupials. Journal of Animal Ecology 69:1083-1098.

Fortin, D., J. M. Fryxell, and R. Pilote. 2002. The temporal scale of foraging decisions in bison. Ecology 83:970-982.

Franklin, W. L., and J. W. Lieb. 1979. The social organization of a sedentary population of North American elk: a model for understanding other populations. Pages 219-277 *in* M. Boyce, and L. D. Hayden-Wing, editors. North American Elk: Ecology and Management. Stackpole Books, Harrisburg, PA.

Franklin, W. L., A. S. Mossman, and M. Dole. 1975. Social organization and home range of Roosevelt elk. Journal of Mammalogy 56:102-118.

Gogan, P. 1986. Ecology of the tule elk range, Point Reyes National Seashore, California. Ph.D. dissertation, University of California, Berkeley.

Gogan, P. J. P., and R. H. Barrett. 1995. Elk and deer diets in a coastal prairie-scrub mosaic, California. Journal of Range Management 48:327-335.

Henderson, D. W., R. J. Warren, J. A. Cromwell, and R. J. Hamilton. 2000. Responses of urban deer to a 50% reduction in local herd density. Wildlife Society Bulletin 28:902-910.

Hooge, P. N., and B. Eichenlaub. 2002. Animal movement extension for ArcView. USGS, Biological Science Office. Anchorage, AK.

Houston, D. B. 1982. The Northern Yellowstone Elk: Ecology and Management. MacMillian Publishing Company, New York, NY.

Howell, J. A., G. C. Brooks, M. Semenoff-Irving, and C. Greene. 2002. Population dynamics of tule elk at Point Reyes National Seashore, California. Journal of Wildlife Management 66:478-490.

Jedrzejewski, W., H. Spaedtke, J. F. Kamler, B. Jedrzejewska, and U. Stenkewitz. 2006. Group size dynamics of red deer in Bialowieza Primeval Forest, Poland. Journal of Wildlife Management 70:1054-1059.

Jenkins, K. J., and E. E. Starkey. 1982. Social organization of Roosevelt elk in an old-growth forest. Journal of Mammalogy 63:331-334.

Johnson, B. E., and J. H. Cushman. 2007. Influence of a large herbivore reintroduction on plant invasions and community composition in a California grassland. Conservation Biology 21:515-526.

Kamler, J. F., W. Jedrzejewski, and B. Jedrzejewska. 2008. Home ranges of red deer in a European old-growth forest. American Midland Naturalist 159:75-82.

Kilpatrick, H. J., S. M. Spohr, and K. K. Lima. 2001. Effects of population reduction on home ranges of female white-tailed deer at high densities. Canadian Journal of Zoology 79:949-954.

Kjellander, P., A. J. M. Hewison, O. Liberg, J. M. Angibault, E. Bideau, and B. Cargnelutti. 2004. Experimental evidence for density-dependence of home range size in roe deer (*Capreolus capreolus L.*): a comparison of two long-term studies. Oecologia 139:478-485.

Knight, R. R. 1970. The Sun River elk herd. Wildlife Monographs 23:5-66.

Koubek, P., and V. Hrabe. 1996. Home range dynamics in the red deer (*Cervus elaphus*) in a mountain forest in central Europe. Folia Zoologica 45:219-222.

Loft, E. R., J. G. Kie, and J. W. Menke. 1993. Grazing in the Sierra Nevada: home range and space use patterns of mule deer as influenced by cattle. California Fish and Game 79:145-166.

Lovari, S., P. Cuccus, A. Murgia, C. Murgia, F. Soi, and G. Plantamura. 2007. Space use, habitat selection and browsing effects of red deer in Sardinia. Italian Journal of Zoology 74:179-189.

McCullough, D. R. 1971. The tule elk: its history, behavior, and ecology. University of California Press, Berkeley, CA.

McLoughlin, P. D., and S. H. Ferguson. 2000. A hierarchical pattern of limiting factors helps explain variation in home range size. Ecoscience 7:123-130.

Millspaugh, J. J., G. C. Brundige, R. A. Gitzen, and K. J. Raedeke. 2004. Herd organization of cow elk in Custer State Park, South Dakota. Wildlife Society Bulletin 32:506-514.

Moran, R. J. 1973. The Rocky Mountain elk in Michigan. Michigan Department of Natural Resources.

Nugent, G. 1994. Home range size and its development for fallow deer in the Blue Mountains, New Zealand. Acta Theriologica 39:159-175.

Oehler, M. W., R. T. Bowyer, and V. C. Bleich. 2003. Home ranges of female mountain sheep, *Ovis canadensis nelsoni:* effects of precipitation in a desert ecosystem. Mammalia 67:385-401.

Roloff, G. J., J. J. Millspaugh, R. A. Gitzen, and G. C. Brundige. 2001. Validation tests of a spatially explicit habitat effectiveness model for Rocky Mountain elk. Journal of Wildlife Management 65:899-914.

Ryan, S. J. 2006. Spatial ecology of African buffalo and their resources in a savanna ecosystem. Dissertation, University of California, Berkeley.

Sain, S. R., K. A. Baggerly, and D. W. Scott. 1994. Cross-validation of multivariate densities. Journal of the American Statistical Association 89:807-817.

Schirokauer, D., T. Keeler-Wolf, J. Meinke, and P. Van der Leeden. 2003. Plant community mapping and classification project final report. National Park Service Report.

Schradin, C., G. Schmohl, H. G. Rodel, I. Schoepf, S. M. Treffler, J. Brenner, M. Bleeker, M. Schubert, B. Konig, and N. Pillay. 2010. Female home range size is regulated by resource distribution and intraspecific competition: a long-term field study. Animal Behaviour 79:195-203.

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

Shoesmith, M. W. 1979. Seasonal movements and social behavior of elk on Mirror Plateau, Yellowstone National Park. Pages 166-176 *in* M. S. Boyce, and L. D. Hayden-Wing, editors. North American Elk: ecology, behavior, and management. University of Wyoming, Laramie, WY.

Smith, B. L., and T. L. McDonald. 2002. Criteria to improve age classification of antlerless elk. Wildlife Society Bulletin 30:200-207.

Stuart-Smith, A. K., C. J. A. Bradshaw, S. Boutin, D. M. Hebert, and A. B. Rippin. 1997. Woodland caribou relative to landscape patterns in northeastern Alberta. Journal of Wildlife Management 61:622-633.

Toweill, D. E., and J. W. Thomas. 2002. North American elk: ecology and management. Smithsonian Institution Press, Washington.

Van Dyke, F. 2007. Colonization of non-traditional range in dispersing elk (*Cervus elaphus nelsoni*) populations. Canadian Field Naturalist 121:133-141.

Van Dyke, F. G., W. C. Klein, and S. T. Stewart. 1998. Long-term range fidelity in Rocky Mountain elk. Journal of Wildlife Management 62:1020-1035.

Weckerly, F. W. 1999. Social bonding and aggression in female Roosevelt elk. Canadian Journal of Zoology 77:1379-1384.

White, G. C., and R. A. Garrott. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, CA.

Wiens, J. A., N. C. Stenseth, B. Vanhorne, and R. A. Ims. 1993. Ecological mechanisms and landscape ecology. Oikos 66:369-380.

Winnie, J. A., P. Cross, and W. Getz. 2008. Habitat quality and heterogeneity influence distribution and behavior in African buffalo (*Syncerus caffer*). Ecology 89:1457-1468.

Wolff, J. O. 1985. The effects of density, food, and interspecific interference on home range sizes in Peromyscus leucopus and Peromyscus maniculatus Canadian Journal of Zoology 63:2657-2662.

Zar, J. H. 1998. Biostatistical analysis. Volume 4.Prentice Hall, Upper Saddle River, NJ.

Table 1. Summary of radio-collared tule elk data, Point Reyes National Seashore, California, 2005 – 2008.

ID	Herd	Age at capture	Fate	Fixes	Fix Interval, days (SE)	Duration (days)
57	North	13	Died	230	3.78(0.14)	855
227	North	UNK	Survived	299	3.65(0.1)	1087
476	North	5	Survived	78	3.59(0.21)	273
486	North	5	Survived	294	3.74(0.11)	1087
489	North	4	Survived	295	3.74(0.1)	1087
491	North	3	Survived	298	3.7(0.1)	1087
492	North	9	Survived	296	3.72(0.11)	1087
495	North	11	Died	270	3.79(0.12)	1045
584	North	7	Died	109	3.42(0.14)	360
624	North	11	Survived	51	3.5(0.13)	175
478	Plateau	10	Died	199	3.91(0.16)	759
488	Plateau	3	Survived	315	3.52(0.1)	1087
493	Plateau	5	Survived	313	3.54(0.1)	1087
497	Plateau	13	Died	261	3.64(0.13)	933
224	White Gulch	7	Died	297	3.61(0.11)	1049
475	White Gulch	6	Survived	222	3.59(0.12)	780
487	White Gulch	8	Survived	309	3.6(0.1)	1084
490	White Gulch	7	Died	253	3.73(0.13)	916
496	White Gulch	5	Survived	287	3.89(0.12)	1091
499	White Gulch	1	Survived	301	3.73(0.12)	1084
501	White Gulch	UNK	Survived	306	3.65(0.11)	1087
503	White Gulch	5	Died	260	3.58(0.11)	924
506	White Gulch	UNK	Survived	310	3.6(0.1)	1084
578	White Gulch	2	Survived	37	4.05(0.52)	142
623	White Gulch	9	Survived	57	3.49(0.14)	192
474	South	5	Died	201	3.5(0.13)	691
477	South	8	Survived	153	3.53(0.13)	530
480	South	4	Survived	305	3.6(0.1)	1084
498	South	6	Survived	308	3.6(0.1)	1091
500	South	UNK	Survived	306	3.67(0.11)	1091
502	South	5	Survived	311	3.58(0.1)	1091
505	South	8	Survived	309	3.58(0.1)	1091
479	D Ranch	UNK	Survived	307	3.55(0.1)	1087
482	D Ranch	2	Survived	65	3.48(0.21)	223
483	D Ranch	2	Survived	306	3.56(0.1)	1087
13	Limantour	10	Survived	296	3.71(0.11)	1089
35	Limantour	9	Died	173	3.86(0.16)	664
248	Limantour	4	Survived	237	4.47(0.19)	1087
472	Limantour	3	Survived	65	3.54(0.14)	227
484	Limantour	3	Survived	290	3.78(0.11)	1089
485	Limantour	2	Survived	301	3.64(0.1)	1089
8	Limantour	14	Survived	73	3.5(0.19)	252

*recollared

Table 2. Coefficients of association among radio-collared tule elk fixes in the D Ranch herd, Point Reyes National Seashore, CA, 2005 - 2008. High values (> 0.3) indicate shared herd membership.

ID	479	482	483
479	X	0.95	0.94
482	0.95	X	0.91
483	0.94	0.91	X

Table 3. Coefficients of association among radio-collared tule elk fixes in the Limantour herd, Point Reyes National Seashore, CA, 2005 - 2008. "NA" indicates elk pairs that were not collared during the same time period. High values (> 0.3) indicate shared herd membership.

ID	8	13	35	248	472	484	485
8	X	0.55	0.77	0.36	*NA*	0.34	0.67
13	0.55	X	0.46	0.58	0.45	0.62	0.66
35	0.77	0.46	X	0.38	*NA*	0.39	0.54
248	0.36	0.58	0.38	X	0.52	0.70	0.64
472	*NA*	0.45	*NA*	0.52	X	0.54	0.49
484	0.34	0.62	0.39	0.70	0.54	X	0.65
485	0.67	0.66	0.54	0.64	0.49	0.65	X

Table 4. Coefficients of association among radio-collared tule elk fixes at the Tomales Point Elk Reserve, Point Reyes National Seashore, CA, 2005 - 2008. Shared herd membership (bold values) is indicated by high coefficients of association (> 0.3). "*NA*" indicates elk pairs that were not collared during the same time period. "N" = North herd, "P" = Plateau herd, "WG" = White Gulch herd, and "S" = South herd.

ID	Herd	57	227	476	486	489	491	492	495	624	478	488	493	497	584	224	475	487	490	496	499	501	503	506	578	623	474	477	480	498	500	502	505
57	N	**X**	**0.62**	**0.60**	**0.68**	**0.66**	**0.63**	**0.66**	**0.64**	**NA**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
227	N	**0.62**	**X**	**0.60**	**0.60**	**0.64**	**0.65**	**0.62**	**0.59**	**0.55**	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
476	N	**0.60**	**0.60**	**X**	**0.59**	**0.65**	**0.65**	**0.59**	**0.54**	**NA**	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
486	N	**0.68**	**0.60**	**0.59**	**X**	**0.67**	**0.62**	**0.69**	**0.57**	**0.51**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
489	N	**0.66**	**0.64**	**0.65**	**0.67**	**X**	**0.68**	**0.69**	**0.60**	**0.53**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
491	N	**0.63**	**0.65**	**0.65**	**0.62**	**0.68**	**X**	**0.66**	**0.60**	**0.59**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
492	N	**0.66**	**0.62**	**0.59**	**0.69**	**0.69**	**0.66**	**X**	**0.55**	**0.53**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
495	N	**0.64**	**0.59**	**0.54**	**0.57**	**0.60**	**0.60**	**0.55**	**X**	**0.50**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
624	N	**NA**	**0.55**	**NA**	**0.51**	**0.53**	**0.59**	**0.53**	**0.50**	**X**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	NA	0.00	0.00	0.00	0.00	0.00	0.00	0.00
478	P	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**X**	**0.69**	**0.65**	**0.36**	**0.49**	0.03	0.02	0.03	0.01	0.01	0.02	0.02	0.03	0.04	0.03	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00
488	P	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**0.69**	**X**	**0.68**	**0.39**	**0.54**	0.02	0.03	0.03	0.02	0.01	0.01	0.01	0.03	0.03	0.03	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00
493	P	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**0.65**	**0.68**	**X**	**0.47**	**0.52**	0.03	0.03	0.03	0.03	0.03	0.01	0.02	0.03	0.04	0.03	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00
497	P	0.00	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	**0.36**	**0.39**	**0.47**	**X**	**0.30**	0.03	0.03	0.05	0.04	0.05	0.02	0.03	0.06	0.06	0.03	NA	0.00	0.00	0.01	0.01	0.01	0.00	0.00
584	P	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**0.49**	**0.54**	**0.52**	**0.30**	**X**	0.02	0.01	0.00	0.01	0.00	0.00	0.00	0.02	0.02	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00
224	WG	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.02	0.03	0.03	0.02	**X**	**0.48**	**0.49**	**0.49**	**0.53**	**0.42**	**0.50**	**0.56**	**0.49**	**0.65**	**0.47**	0.02	0.05	0.02	0.02	0.01	0.02	0.03
475	WG	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.03	0.03	0.03	0.01	**0.48**	**X**	**0.48**	**0.36**	**0.46**	**0.37**	**0.51**	**0.40**	**0.51**	**0.49**	**0.54**	0.01	0.01	0.02	0.04	0.01	0.03	0.04
487	WG	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.03	0.03	0.05	0.00	**0.49**	**0.48**	**X**	**0.46**	**0.51**	**0.38**	**0.49**	**0.47**	**0.50**	**0.46**	**0.58**	0.02	0.04	0.02	0.03	0.02	0.02	0.04
490	WG	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.02	0.03	0.04	0.01	**0.49**	**0.36**	**0.46**	**X**	**0.46**	**0.34**	**0.46**	**0.47**	**0.55**	**0.35**	**NA**	0.01	0.00	0.02	0.02	0.00	0.00	0.04
496	WG	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.03	0.05	0.00	**0.53**	**0.46**	**0.51**	**0.46**	**X**	**0.43**	**0.45**	**0.42**	**0.60**	**0.51**	**0.54**	0.03	0.01	0.01	0.02	0.00	0.01	0.03
499	WG	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.01	0.01	0.02	0.00	**0.42**	**0.37**	**0.38**	**0.34**	**0.43**	**X**	**0.43**	**0.38**	**0.43**	**0.30**	**0.44**	0.05	0.11	0.07	0.08	0.07	0.07	0.08
501	WG	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.01	0.02	0.03	0.00	**0.50**	**0.51**	**0.49**	**0.46**	**0.45**	**0.43**	**X**	**0.49**	**0.49**	**0.51**	**0.58**	0.04	0.07	0.05	0.05	0.03	0.06	0.08
503	WG	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.03	0.03	0.06	0.02	**0.56**	**0.40**	**0.47**	**0.47**	**0.42**	**0.38**	**0.49**	**X**	**0.47**	**0.62**	**0.13**	0.01	0.03	0.02	0.03	0.00	0.01	0.03
506	WG	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.03	0.04	0.06	0.02	**0.49**	**0.51**	**0.50**	**0.55**	**0.60**	**0.43**	**0.49**	**0.47**	**X**	**0.51**	**0.56**	0.03	0.03	0.02	0.02	0.00	0.01	0.04
578	WG	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.03	0.03	0.03	0.00	**0.65**	**0.49**	**0.46**	**0.35**	**0.51**	**0.30**	**0.51**	**0.62**	**0.51**	**X**	**NA**	0.00	0.00	0.00	0.00	0.00	0.03	0.03
623	WG	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	NA	0.05	0.02	0.05	NA	0.02	**0.47**	**0.54**	**0.58**	**NA**	**0.54**	**0.44**	**0.58**	**0.13**	**0.56**	**NA**	**X**	0.00	0.00	0.00	0.00	0.00	0.00	0.00
474	S	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.01	0.02	0.01	0.03	0.05	0.04	0.01	0.03	0.00	0.00	**X**	**0.50**	**0.46**	**0.43**	**0.47**	**0.40**	**0.44**
477	S	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.01	0.04	0.00	0.01	0.11	0.07	0.03	0.03	0.00	0.00	**0.50**	**X**	**0.64**	**0.60**	**0.53**	**0.58**	**0.58**
480	S	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.02	0.02	0.02	0.02	0.01	0.07	0.05	0.02	0.02	0.00	0.00	**0.46**	**0.64**	**X**	**0.53**	**0.57**	**0.60**	**0.55**
498	S	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.02	0.04	0.03	0.02	0.02	0.08	0.05	0.03	0.02	0.00	0.00	**0.43**	**0.60**	**0.53**	**X**	**0.43**	**0.50**	**0.49**
500	S	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.01	0.01	0.02	0.00	0.00	0.07	0.03	0.00	0.00	0.00	0.00	**0.47**	**0.53**	**0.57**	**0.43**	**X**	**0.56**	**0.50**
502	S	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.03	0.02	0.00	0.01	0.07	0.06	0.01	0.01	0.03	0.00	**0.40**	**0.58**	**0.60**	**0.50**	**0.56**	**X**	**0.55**
505	S	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.04	0.04	0.04	0.03	0.08	0.08	0.03	0.04	0.03	0.00	**0.44**	**0.58**	**0.55**	**0.49**	**0.50**	**0.55**	**X**

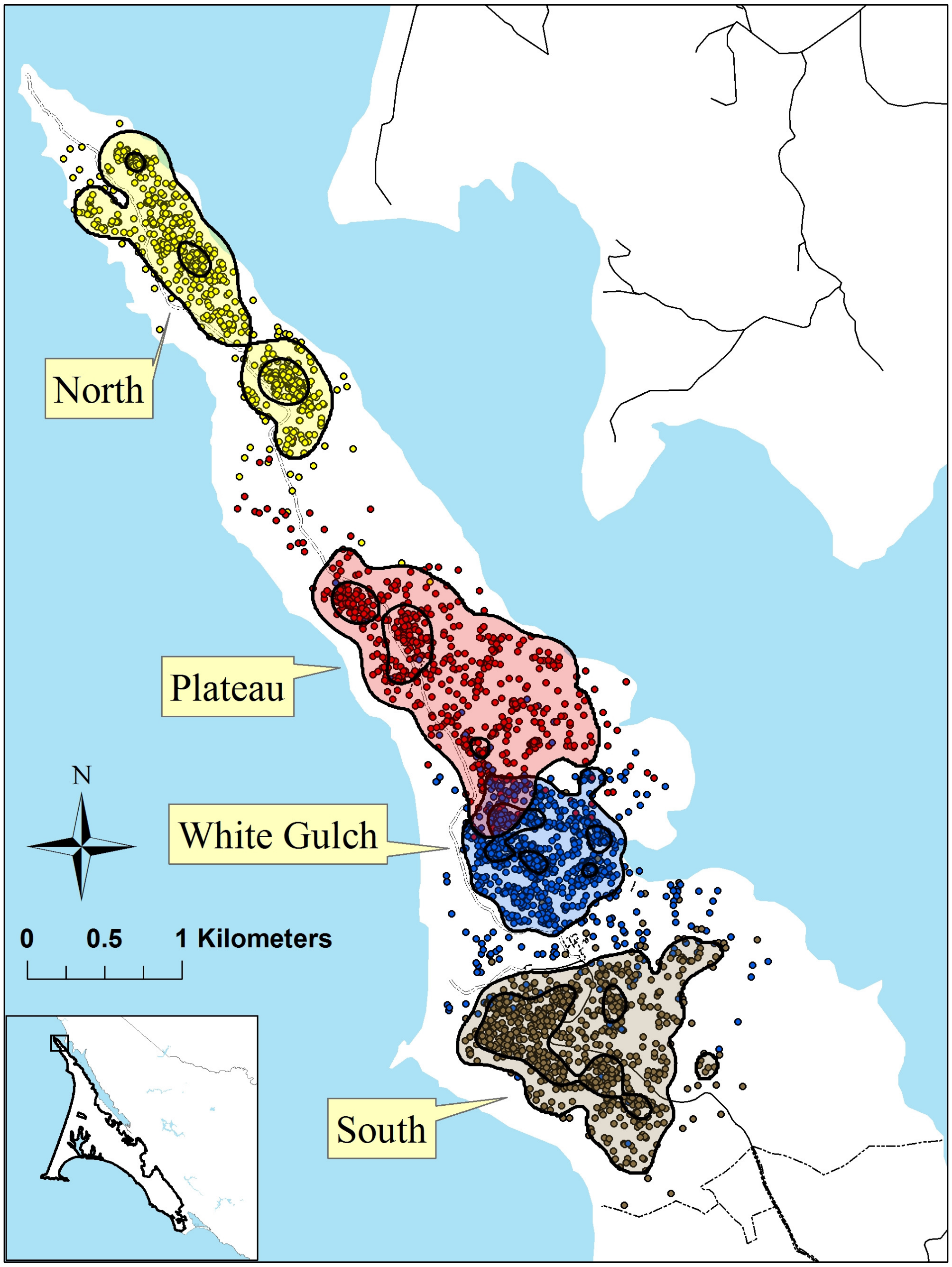

Figure 1. Radio telemetry fixes and herd ranges (50% and 90% fixed kernels) of radio-collared tule elk at the Tomales Point Elk Reserve, Point Reyes National Seashore, California, 2005 – 2008. Fixes were taken on radio-collared elk approximated every three days. Neighboring elk herd ranges showed little spatial overlap.

Table 5. Average annual herd range sizes for tule elk at Point Reyes National Seashore, California, 2005 – 2008.

Herd	Herd range size (ha)	SE
D Ranch	336.23	9.46
Limantour	827.67	97.26
North	119.92	6.93
Plateau	183.65	11.93
South	136.94	5.20
White Gulch	94.27	4.64
Average	283.11	63.59

Table 6. Estimated annual herd size, available grassland (ha), and herd density (elk / ha of grassland habitat) at Point Reyes National Seashore, California, 2005 – 2008. Study years ran from April 1 – March 31.

Herd	Year	Herd size	Grassland area (ha)	Herd density
D Ranch	2005-2005	15	206.75	0.07
	2006-2007	19	219.56	0.09
	2007-2008	20	193.84	0.10
	average	18	206.72	0.09
	SE	2	7.43	0.01
Limantour	2005-2005	25	112.96	0.22
	2006-2007	24	150.05	0.16
	2007-2008	28	160.40	0.18
	average	26	141.14	0.18
	SE	1	14.40	0.02
Plateau	2005-2005	57	82.34	0.70
	2006-2007	68	89.71	0.76
	2007-2008	71	70.93	1.00
	average	65	80.99	0.81
	SE	4	5.46	0.09
South	2005-2005	87	61.71	1.42
	2006-2007	110	56.23	1.96
	2007-2008	122	58.28	2.08
	average	106	58.74	1.81
	SE	10	1.60	0.21
White Gulch	2005-2005	127	59.86	2.13
	2006-2007	156	61.17	2.55
	2007-2008	152	53.49	2.84
	average	145	58.17	2.49
	SE	9	2.37	0.21
North	2005-2005	113	30.23	3.72
	2006-2007	126	28.94	4.35
	2007-2008	142	31.27	4.54
	average	127	30.15	4.21
	SE	8	0.67	0.25

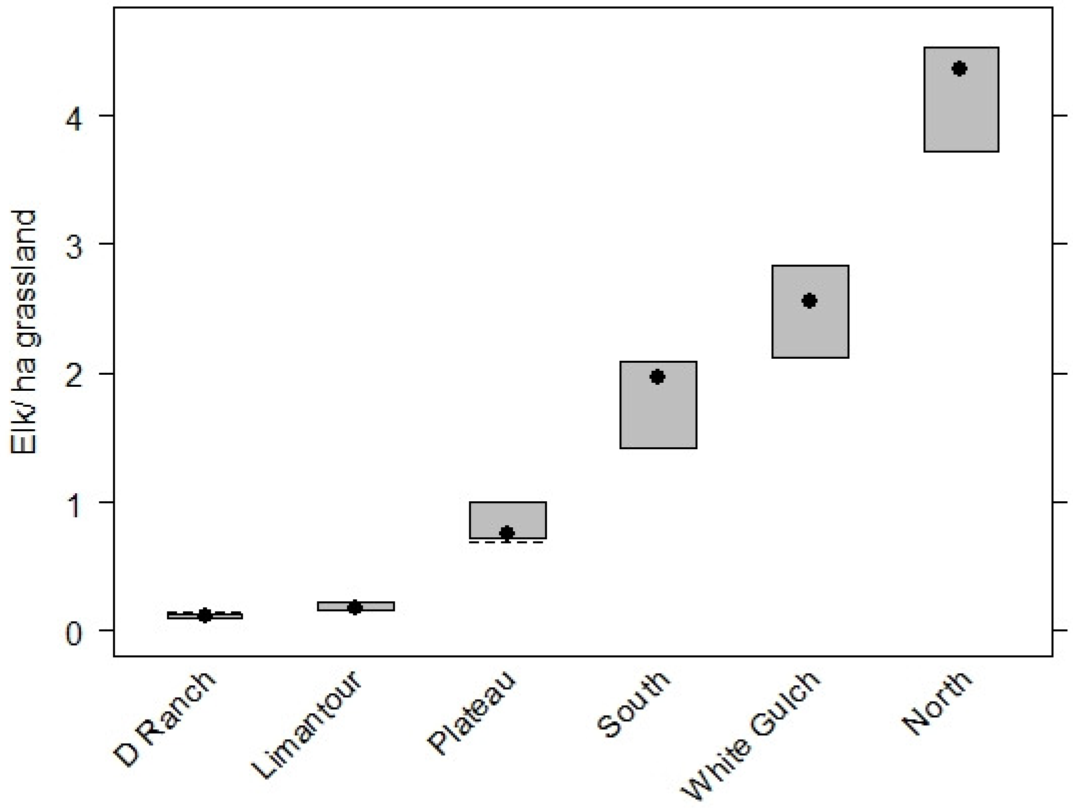

Figure 2. Box plot of annual tule elk density (elk / ha of grassland habitat) by herd, Point Reyes National Seashore, California, 2005 – 2008. Solid points are median values, boxes represent upper and lower quartiles and whiskers extend the smallest observations.

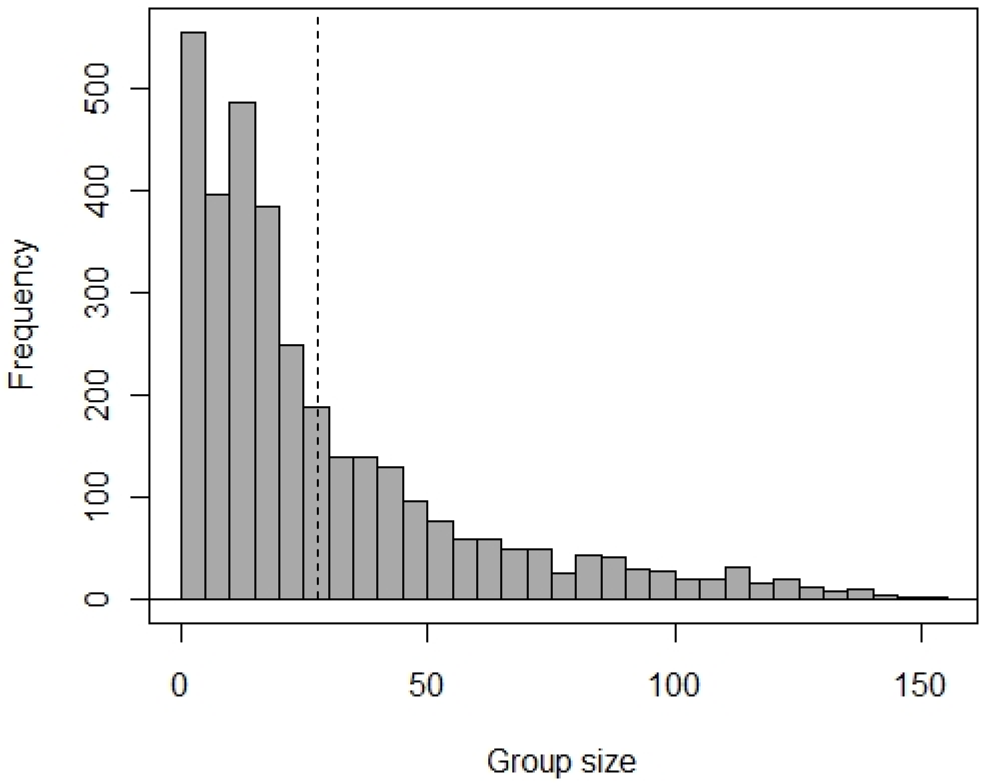

Figure 3. Histogram of tule elk group sizes, Point Reyes National Seashore, California, 2005 – 2008. A "group" was defined as elk within 50 m of each other that shared similar activity patterns (Clutton-Brock et al. 1982). The average group size was 30 elk (dashed line).

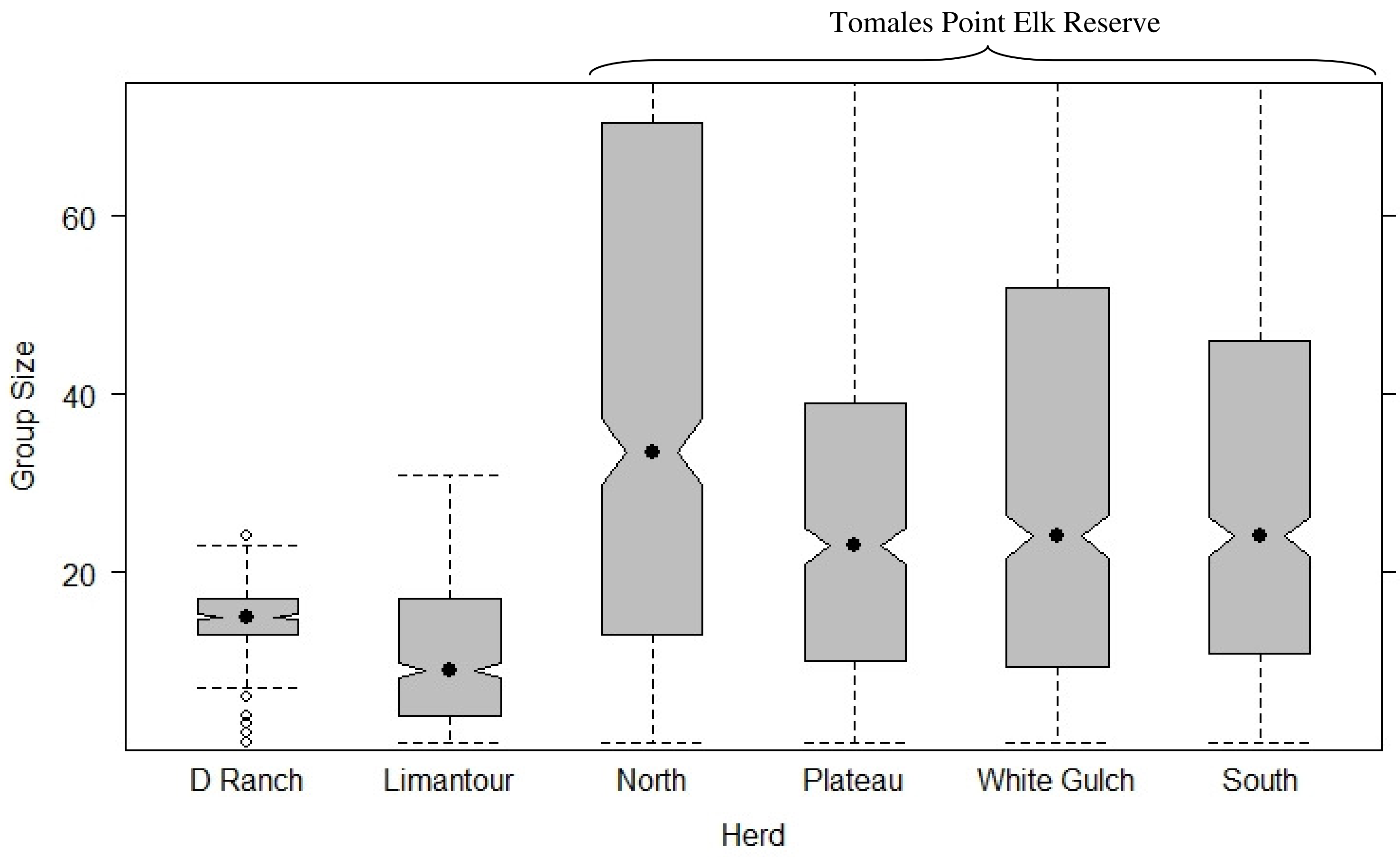

Figure 4. Box plot of tule elk group sizes by herd, Point Reyes National Seashore, California, 2005 – 2008. Solid circles represent medians, notched area represents 95% confidence interval ($\alpha = 0.05$) around the median. Boxes represent first and third quartiles. Open circles are outliers. The North, Plateau, White Gulch and South herds were located at the Tomales Point Elk Reserve.

Table 7. Average group sizes and age/sex classifications of tule elk by herd and study year, Point Reyes National Seashore, California, 2005 – 2008. Study years ran from 1 April – 31 March.

Herd	Study Year	n	Group size	SE	Cows	SE	Bulls	SE	Yearling ♂	SE	Calves	SE	Unknown	SE
D Ranch	2005-2006	105	12	0.38	5	0.14	1	0.07	2	0.11	4	0.19	0	0.02
	2006-2007	100	16	0.42	8	0.17	2	0.16	2	0.08	4	0.17	0	0.02
	2007-2008	109	15	0.50	8	0.23	2	0.17	1	0.16	4	0.16	0	0.07
Limantour	2005-2006	146	11	0.59	7	0.36	0	0.05	1	0.13	3	0.18	0	0.03
	2006-2007	170	10	0.54	7	0.37	0	0.05	0	0.04	3	0.17	0	0.02
	2007-2008	196	12	0.62	8	0.42	0	0.04	1	0.06	3	0.16	0	0.10
Plateau	2005-2006	128	30	1.39	22	0.98	1	0.12	1	0.15	5	0.39	1	0.17
	2006-2007	164	28	1.44	16	0.82	0	0.04	2	0.23	8	0.65	0	0.06
	2007-2008	231	22	1.24	14	0.83	1	0.10	3	0.26	3	0.25	0	0.05
South	2005-2006	134	36	2.26	22	1.35	1	0.19	4	0.36	8	0.72	2	0.34
	2006-2007	226	32	1.78	18	1.04	1	0.11	3	0.21	9	0.72	1	0.11
	2007-2008	273	30	1.61	22	1.16	1	0.14	2	0.18	5	0.35	0	0.11
White Gulch	2005-2006	185	36	2.38	21	1.30	1	0.11	3	0.32	9	0.82	2	0.26
	2006-2007	238	41	2.59	23	1.45	1	0.07	3	0.27	12	0.94	1	0.12
	2007-2008	336	35	2.01	26	1.48	1	0.07	2	0.16	6	0.43	0	0.10
North	2005-2006	138	52	3.19	37	2.20	1	0.17	3	0.30	10	0.93	2	0.31
	2006-2007	200	45	2.45	28	1.54	1	0.13	4	0.35	10	0.82	1	0.15
	2007-2008	255	40	2.27	27	1.53	2	0.25	3	0.26	6	0.51	1	0.15
Combined	2005-2006	836	31	0.99	19	0.64	1	0.05	2	0.12	7	0.29	1	0.10
	2006-2007	1098	31	0.91	18	0.54	1	0.04	3	0.11	8	0.33	0	0.05
	2007-2008	1400	28	0.79	19	0.56	1	0.06	2	0.09	5	0.17	0	0.04
	Combined	3334	30	5.46	19	0.34	1	0.03	2	0.06	6	0.15	1	0.04

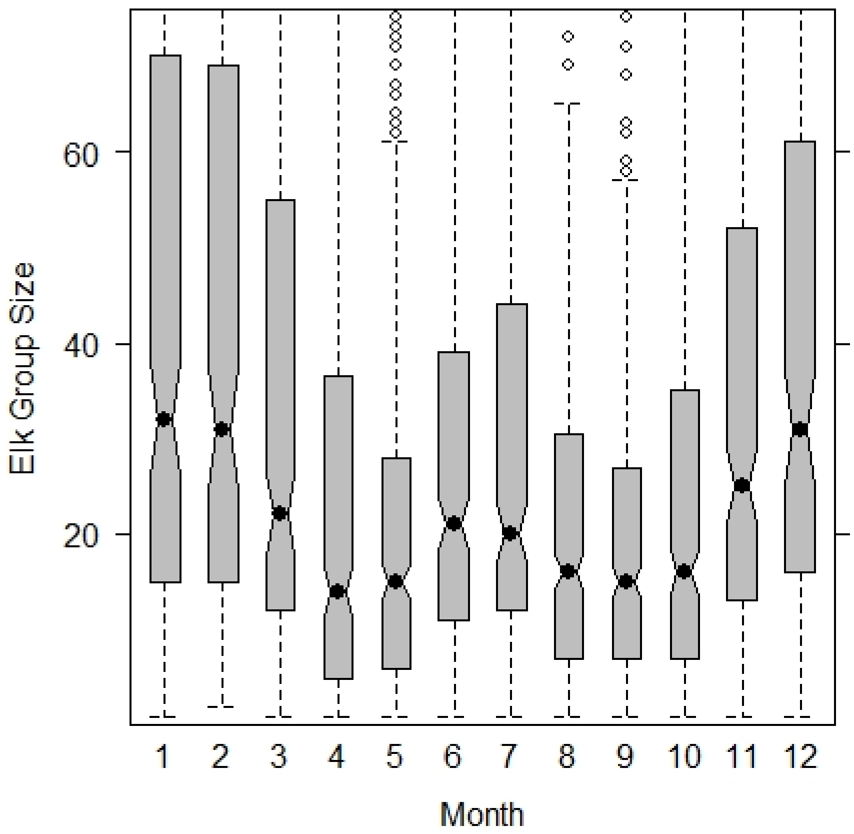

Figure 5. Box plot of tule elk group sizes by month, Point Reyes National Seashore, California, 2005 – 2008. Solid circles represent medians, notched area represents 95% confidence interval (α = 0.05) around the median. Boxes represent first and third quartiles. Open circles are outliers.

Table 8. Average group sizes and age/sex classifications of tule elk by season and herd, Point Reyes National Seashore, California, 2005 – 2008. Seasons were quarter annual, starting in January.

Herd	Season	n	Group size	SE	Cows	SE	Bulls	SE	Yearling (♂)	SE	Calves	SE	Unk	SE
D Ranch	1	75	14	0.31	8	0.20	1	0.12	1	0.10	5	0.12	0	0.03
	2	97	12	0.68	6	0.31	2	0.19	2	0.14	2	0.20	0	0.03
	3	77	16	0.31	8	0.18	2	0.14	2	0.14	5	0.08	0	0.09
	4	65	16	0.38	8	0.17	2	0.19	2	0.16	5	0.05	0	0.02
	All	314	15	0.27	7	0.13	2	0.09	2	0.07	4	0.10	0	0.03
Limantour	1	108	13	0.70	9	0.49	0	0.02	1	0.07	3	0.23	0	0.09
	2	150	10	0.70	6	0.46	0	0.05	1	0.12	2	0.18	0	0.07
	3	144	11	0.62	7	0.41	1	0.05	0	0.07	3	0.17	0	0.09
	4	110	11	0.67	7	0.42	0	0.05	1	0.10	3	0.17	0	0.06
	All	512	11	0.34	7	0.23	0	0.03	1	0.05	3	0.10	0	0.04
Plateau	1	99	37	1.92	24	1.19	1	0.10	3	0.33	10	0.80	0	0.08
	2	157	19	1.21	15	0.92	1	0.09	3	0.30	2	0.27	0	0.06
	3	162	20	1.10	12	0.64	1	0.10	2	0.22	5	0.35	0	0.10
	4	105	33	1.94	20	1.31	1	0.14	3	0.33	8	0.57	1	0.17
	All	523	26	0.80	17	0.52	1	0.05	2	0.14	5	0.27	0	0.05
South	1	120	50	2.84	31	1.80	1	0.15	3	0.29	14	1.03	1	0.25
	2	177	28	1.75	20	1.30	1	0.22	4	0.29	2	0.37	1	0.17
	3	198	24	1.50	15	0.92	1	0.12	2	0.23	5	0.37	0	0.08
	4	138	32	2.24	19	1.38	1	0.10	2	0.24	9	0.78	1	0.30
	All	633	32	1.06	20	0.69	1	0.08	3	0.14	7	0.34	1	0.10
White Gulch	1	112	61	4.32	39	2.82	0	0.07	3	0.30	17	1.54	2	0.37
	2	185	35	2.51	26	1.78	1	0.09	4	0.35	4	0.60	1	0.19
	3	281	26	1.62	16	0.98	1	0.08	2	0.21	6	0.43	0	0.09
	4	181	41	2.85	24	1.72	1	0.10	2	0.20	12	0.94	1	0.16
	All	759	37	1.34	24	0.86	1	0.05	3	0.14	9	0.42	1	0.09
North	1	116	65	3.78	43	2.49	1	0.28	4	0.33	16	1.21	1	0.30
	2	181	36	2.27	27	1.68	1	0.20	4	0.35	3	0.34	1	0.17
	3	174	36	2.30	23	1.53	2	0.22	3	0.34	7	0.50	1	0.15
	4	122	48	3.54	30	2.24	2	0.31	3	0.37	12	1.04	1	0.30
	All	593	44	1.49	30	0.99	1	0.12	4	0.18	8	0.42	1	0.11
	Combined	3334	30	5.46	19	0.34	1	0.03	2	0.06	6	0.15	1	0.04

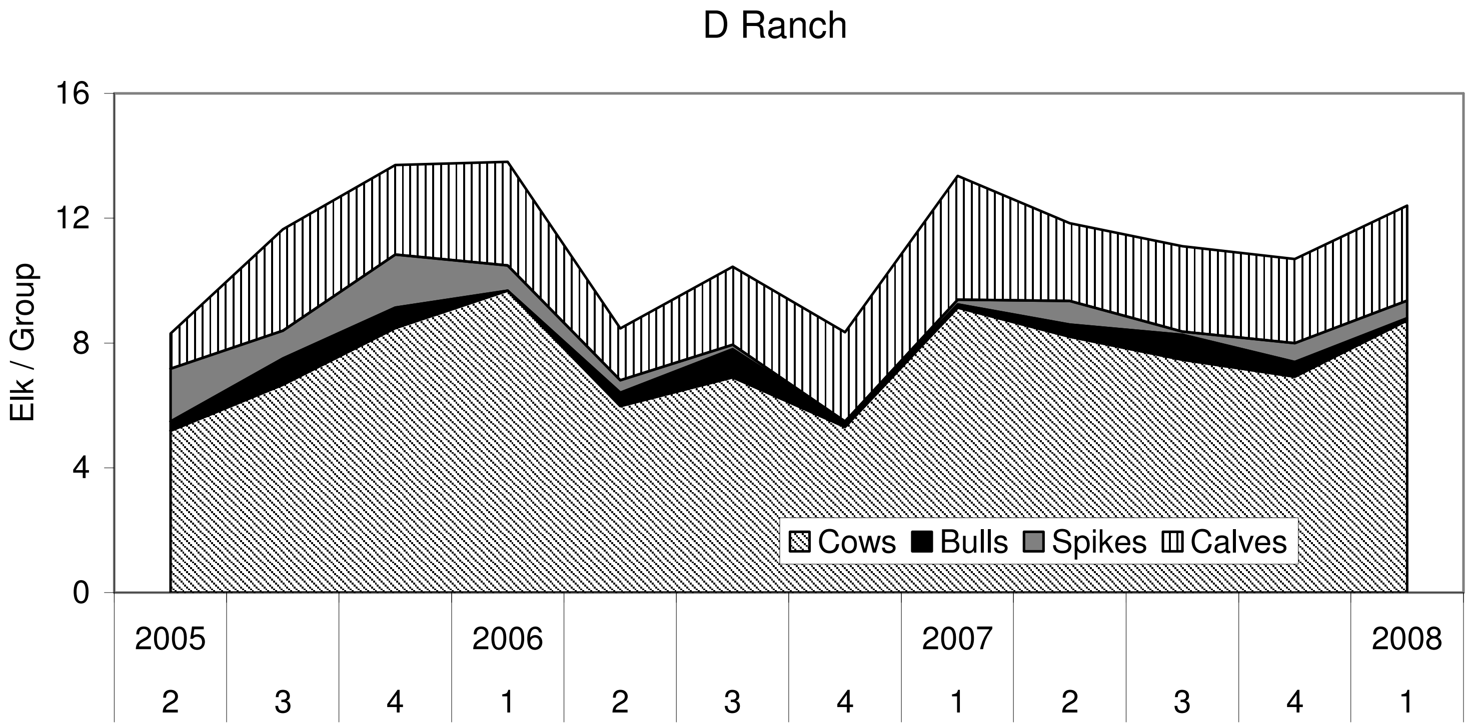

Figure 6. Stacked area graph of average tule elk group classifications by season for the D Ranch herd, April 2005 - March 2008, Point Reyes National Seashore, California. (Season 1 = January-March, 2 = April – June, 3 = July – September, 4 = October – December).

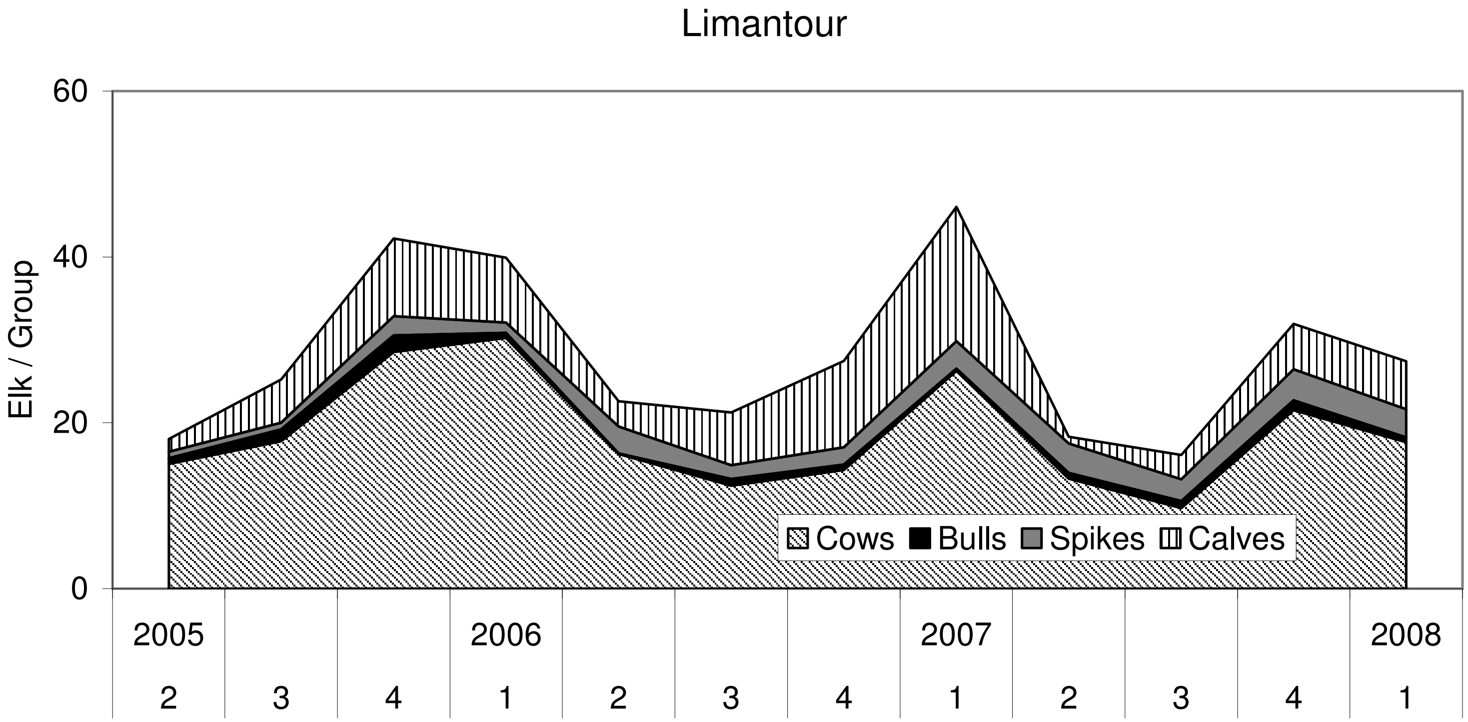

Figure 7. Stacked area graph of average tule elk group classifications by season for the Limantour herd, April 2005 - March 2008, , Point Reyes National Seashore, California. (Season 1 = January-March, 2 = April – June, 3 = July – September, 4 = October – December).

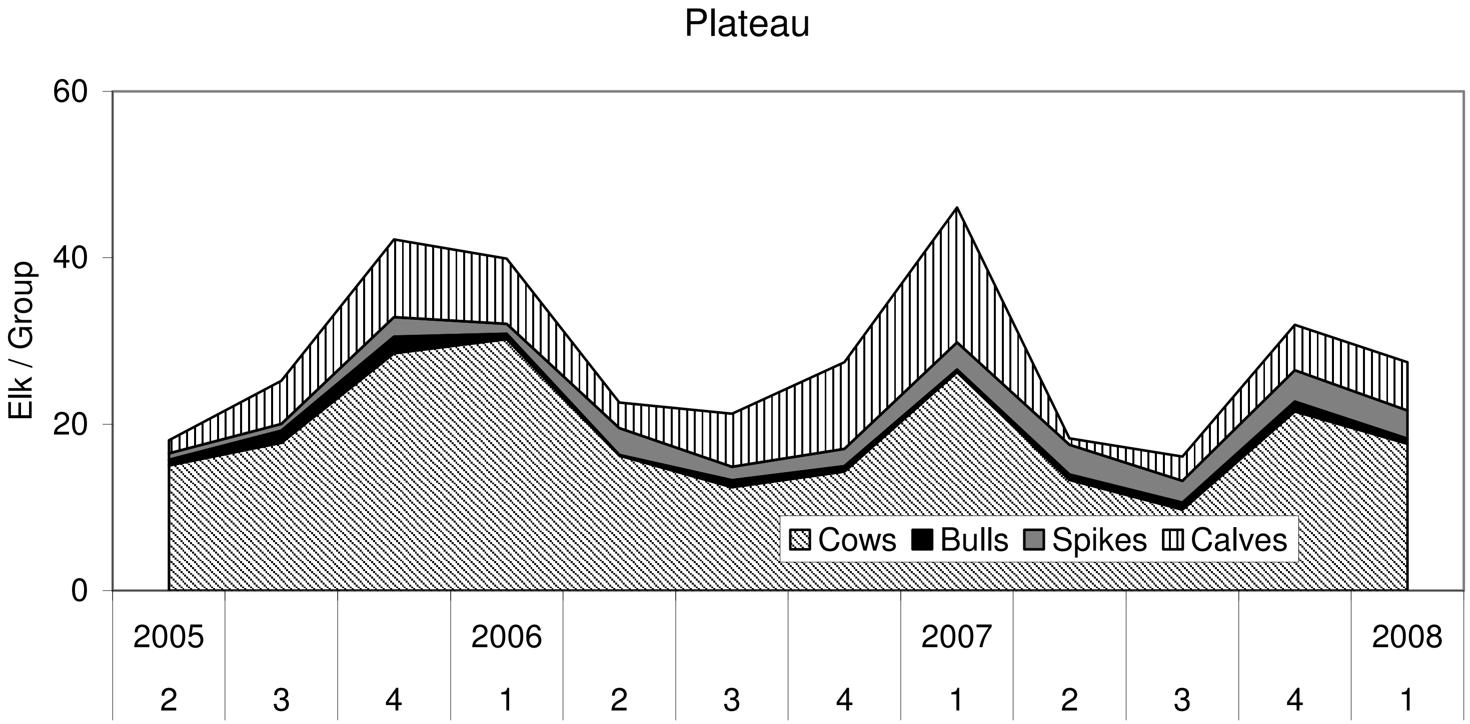

Figure 8. Stacked area graph of average tule elk group classifications by season for the Plateau herd, April 2005 - March 2008, , Point Reyes National Seashore, California. (Season 1 = January-March, 2 = April – June, 3 = July – September, 4 = October – December).

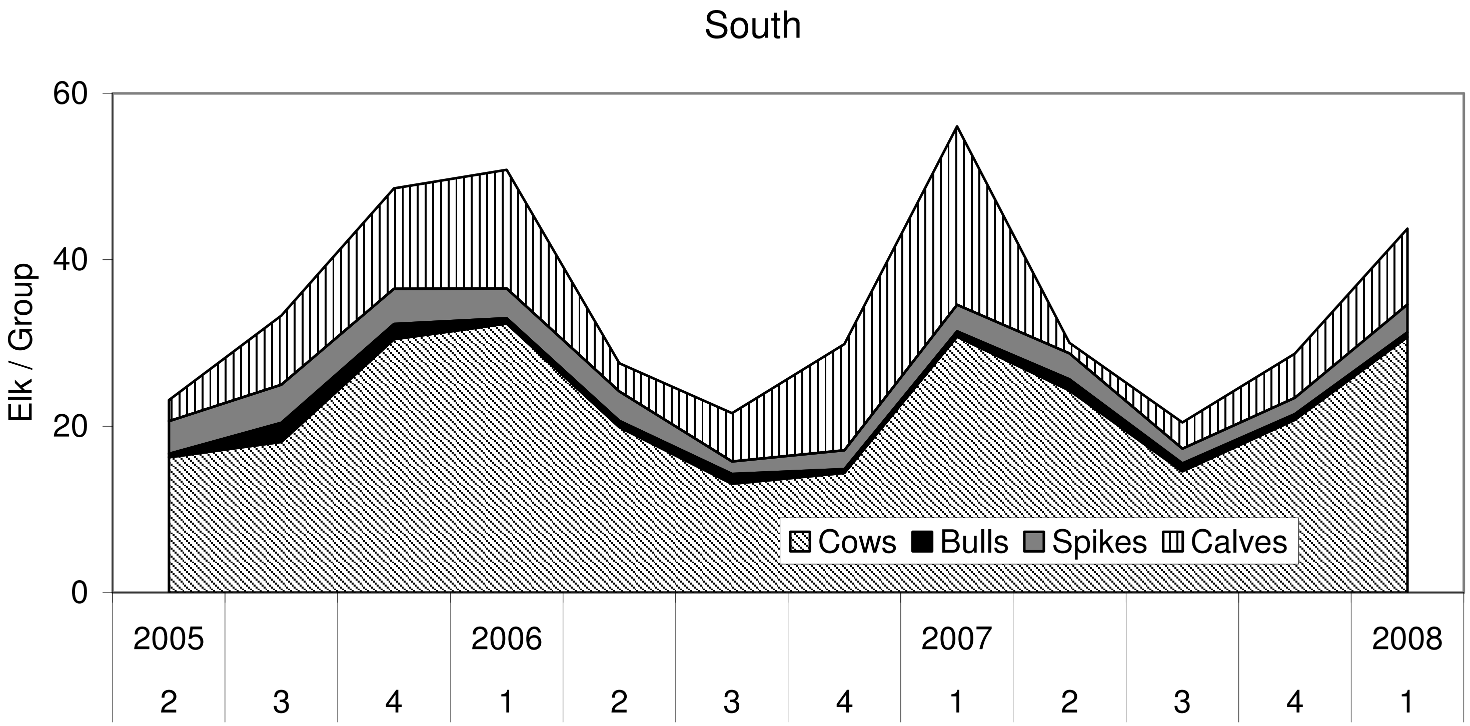

Figure 9. Stacked area graph of average tule elk group classifications by season for the South herd, April 2005 - March 2008, , Point Reyes National Seashore, California. (Season 1 = January-March, 2 = April – June, 3 = July – September, 4 = October – December).

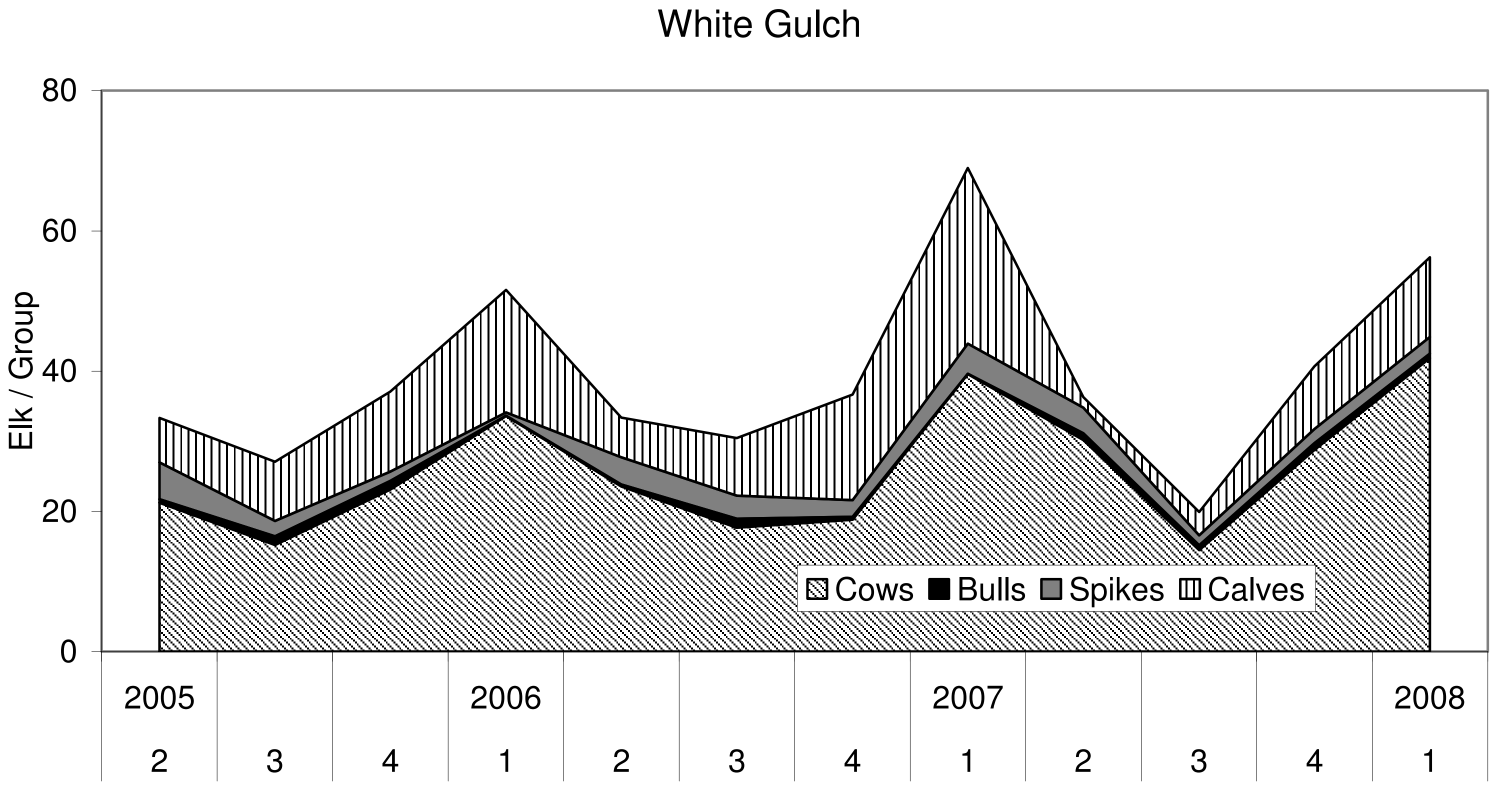

Figure 10. Stacked area graph of average tule elk group classifications by season for the White Gulch herd, April 2005 - March 2008, Point Reyes National Seashore, California. (Season 1 = January-March, 2 = April – June, 3 = July – September, 4 = October – December).

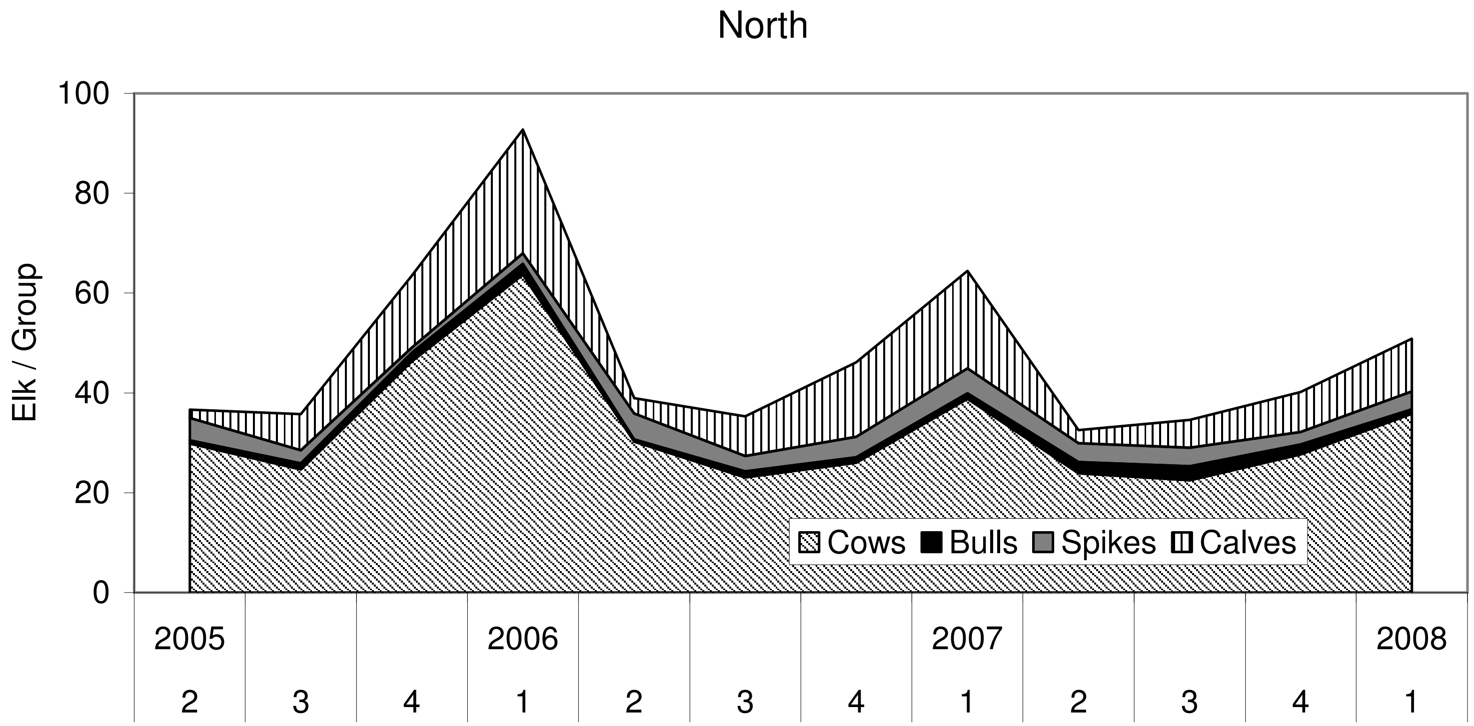

Figure 11. Stacked area graph of average tule elk group classifications by season for the North herd, April 2005 - March 2008, Point Reyes National Seashore, California. (Season 1 = January-March, 2 = April – June, 3 = July – September, 4 = October – December).

Table 9. Home range (90% fixed kernel) and core area (50% fixed kernel) sizes of radio-collared tule elk by study year, Point Reyes National Seashore, California, 2005-2008. Study years ran from 1 April – 31 March. Measurements are in hectares. “*N/A*” indicates elk absent from the study (not collared or not alive during that period) and *n* indicates the number of fixes.

		2005-2006			2006-2007			2007-2008		
ID	Herd	90%	50%	*n*	90%	50%	*n*	90%	50%	*n*
479	D Ranch	319.97	61.47	98	350.86	52.42	105	292.42	41.12	104
482	D Ranch	355.10	61.12	65	*N/A*	*N/A*	*N/A*	*N/A*	*N/A*	*N/A*
483	D Ranch	332.88	62.60	99	350.45	52.73	105	312.01	50.08	102
13	Limantour	434.27	43.19	92	987.02	129.61	101	822.86	254.48	103
248	Limantour	341.64	44.56	70	389.33	59.65	78	512.74	127.27	89
472	Limantour	*N/A*	*N/A*	*N/A*	*N/A*	*N/A*	*N/A*	491.17	102.71	65
484	Limantour	621.41	50.64	93	535.98	75.10	94	589.64	192.51	103
485	Limantour	514.59	74.47	96	949.22	166.28	103	898.17	229.17	102
8	Limantour	*N/A*	*N/A*	*N/A*	962.15	140.07	63	*N/A*	*N/A*	*N/A*
35	Limantour	491.23	64.72	92	1132.44	245.34	81	*N/A*	*N/A*	*N/A*
57	North	85.57	10.37	90	131.54	20.64	101	*N/A*	*N/A*	*N/A*
227	North	90.09	12.40	93	106.58	22.56	102	97.44	9.34	104
476	North	*N/A*	*N/A*	*N/A*	158.87	24.22	62	*N/A*	*N/A*	*N/A*
486	North	83.95	10.66	90	138.66	13.43	99	140.40	29.90	105
489	North	81.97	11.22	91	111.25	14.70	100	108.22	9.23	104
491	North	82.89	10.78	94	111.38	13.33	100	104.57	16.34	104
492	North	89.37	11.52	90	115.52	13.73	102	128.56	16.30	104
495	North	89.19	12.10	92	99.62	12.88	99	110.59	12.20	79
624	North	*N/A*	*N/A*	*N/A*	*N/A*	*N/A*	*N/A*	121.60	37.08	51
478	Plateau	*N/A*	*N/A*	*N/A*	135.23	28.29	92	119.39	26.64	92
488	Plateau	155.90	30.01	102	156.09	28.19	101	140.59	32.46	112
493	Plateau	162.62	32.02	103	157.69	22.39	102	160.75	37.82	108
497	Plateau	202.96	45.42	102	218.34	69.85	99	122.51	28.83	60
584	Plateau	*N/A*	*N/A*	*N/A*	*N/A*	*N/A*	*N/A*	162.98	39.67	92
474	South	*N/A*	*N/A*	*N/A*	150.42	30.92	104	155.04	38.46	84
477	South	126.64	47.12	101	80.48	13.01	52	*N/A*	*N/A*	*N/A*
480	South	145.50	47.44	93	100.42	24.73	107	97.53	16.48	105
498	South	127.99	30.10	96	110.64	20.91	106	81.67	13.02	106
500	South	115.52	27.74	92	121.95	27.67	106	117.81	27.79	108
502	South	129.59	42.08	98	113.45	28.35	105	87.57	12.13	108
505	South	156.81	61.67	99	113.39	24.48	103	135.45	32.51	107
224	White Gulch	100.34	24.47	101	87.92	14.97	101	69.65	18.97	95
475	White Gulch	*N/A*	*N/A*	*N/A*	99.81	22.13	100	66.04	13.84	105
487	White Gulch	113.64	32.05	100	79.19	15.15	102	59.42	10.14	107
490	White Gulch	82.75	14.93	98	81.96	15.00	99	77.42	18.91	56
496	White Gulch	81.22	20.99	93	82.26	15.15	94	59.33	9.27	100
499	White Gulch	187.48	35.90	84	190.11	42.57	104	94.64	27.55	113
501	White Gulch	94.46	19.74	93	88.32	21.34	100	87.07	15.42	113
503	White Gulch	79.93	10.94	101	44.12	5.29	102	53.81	8.36	57
506	White Gulch	94.85	26.27	102	67.96	11.63	102	67.14	23.92	106

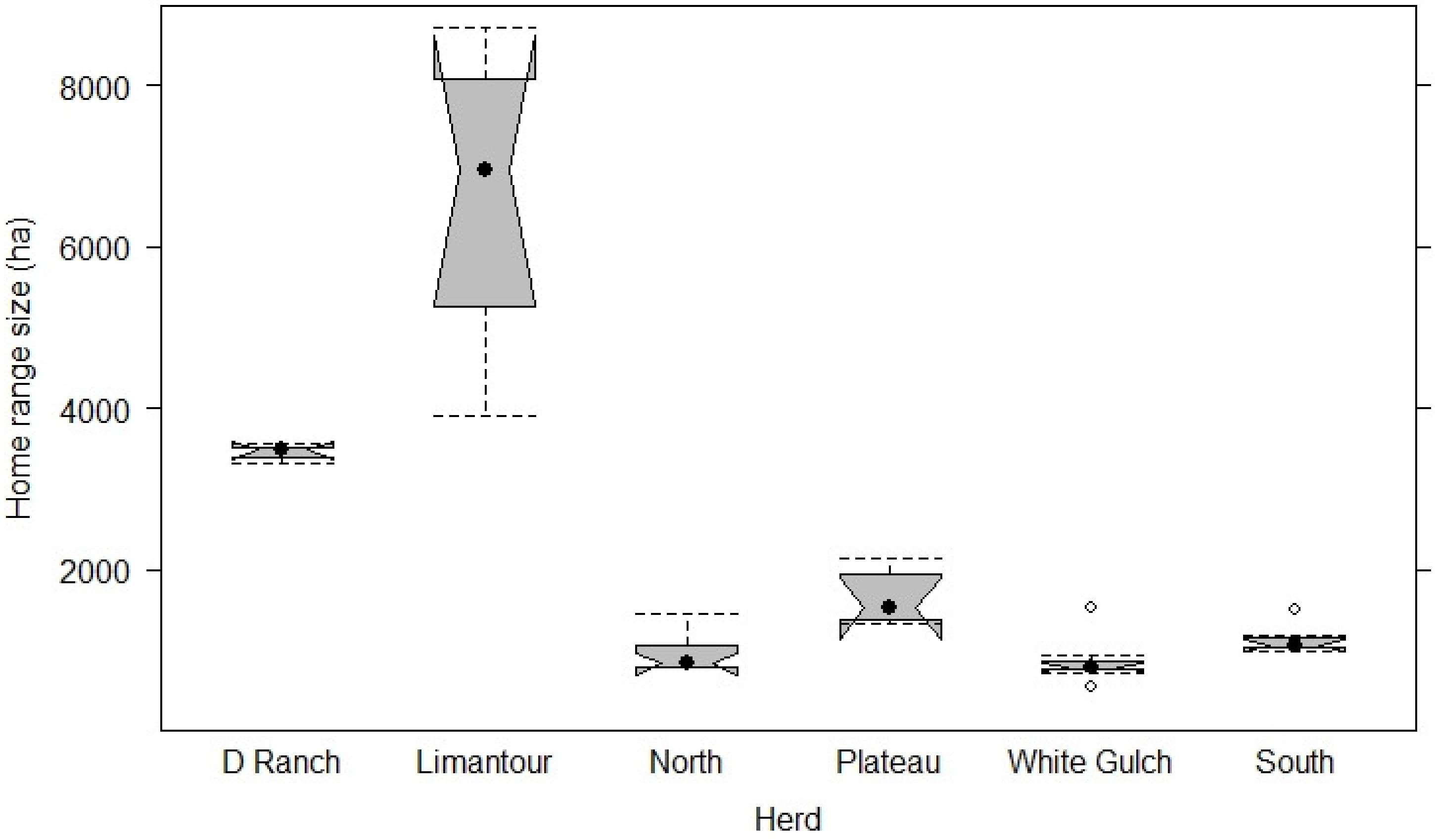

Figure 12. Box plot of home range sizes (90% fixed kernel) of radio-collared tule elk by herd, Point Reyes National Seashore, California, 2005 – 2008. Herds are ordered from left to right by increasing herd density (elk/ ha grassland habitat).

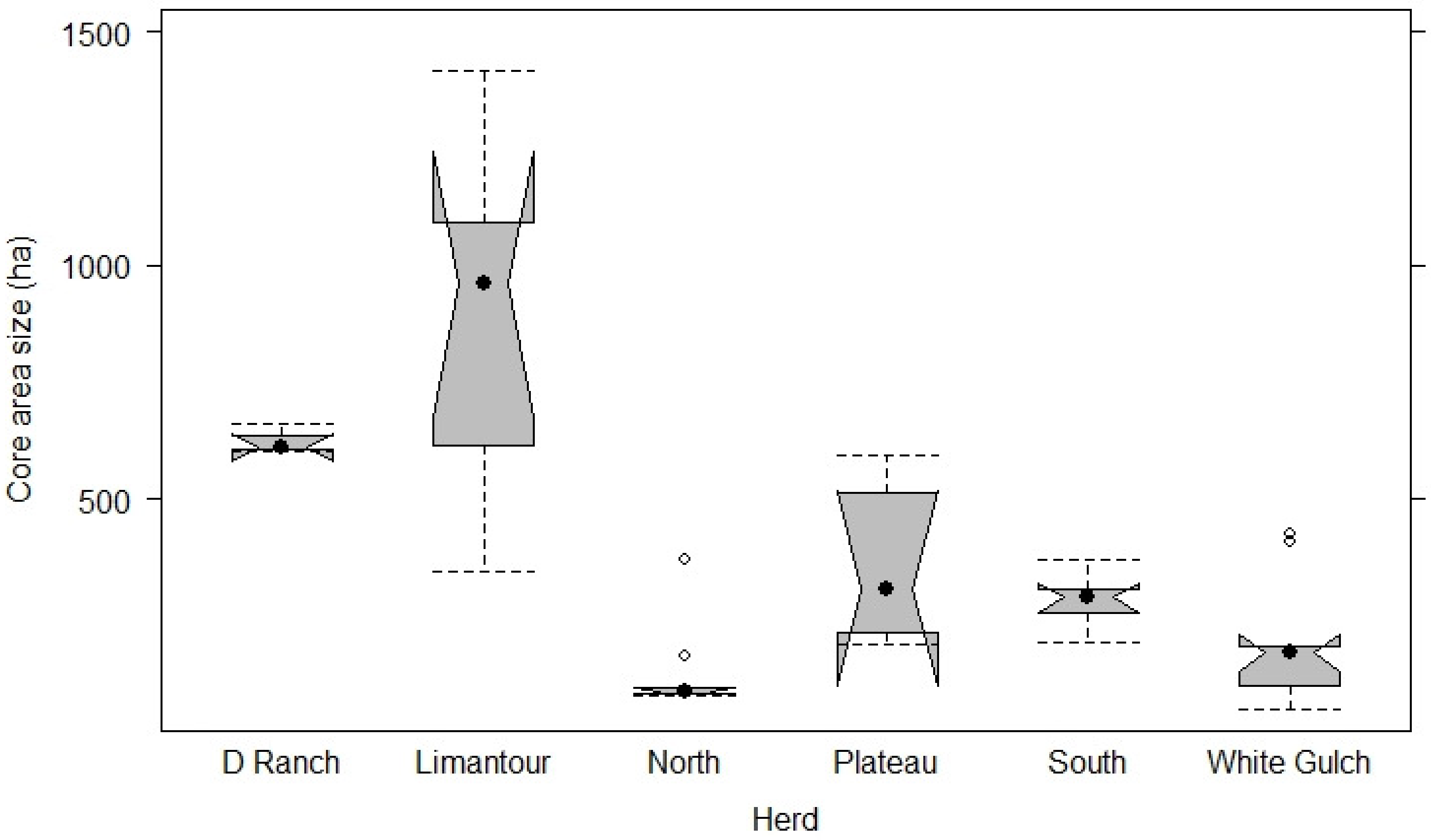

Figure 13. Box plot of core area sizes (50% fixed kernel) of radio-telemetry collared tule elk by herd, Point Reyes National Seashore, California, 2005-2008. Herds are ordered from left to right by increasing herd density (elk/ ha grassland habitat

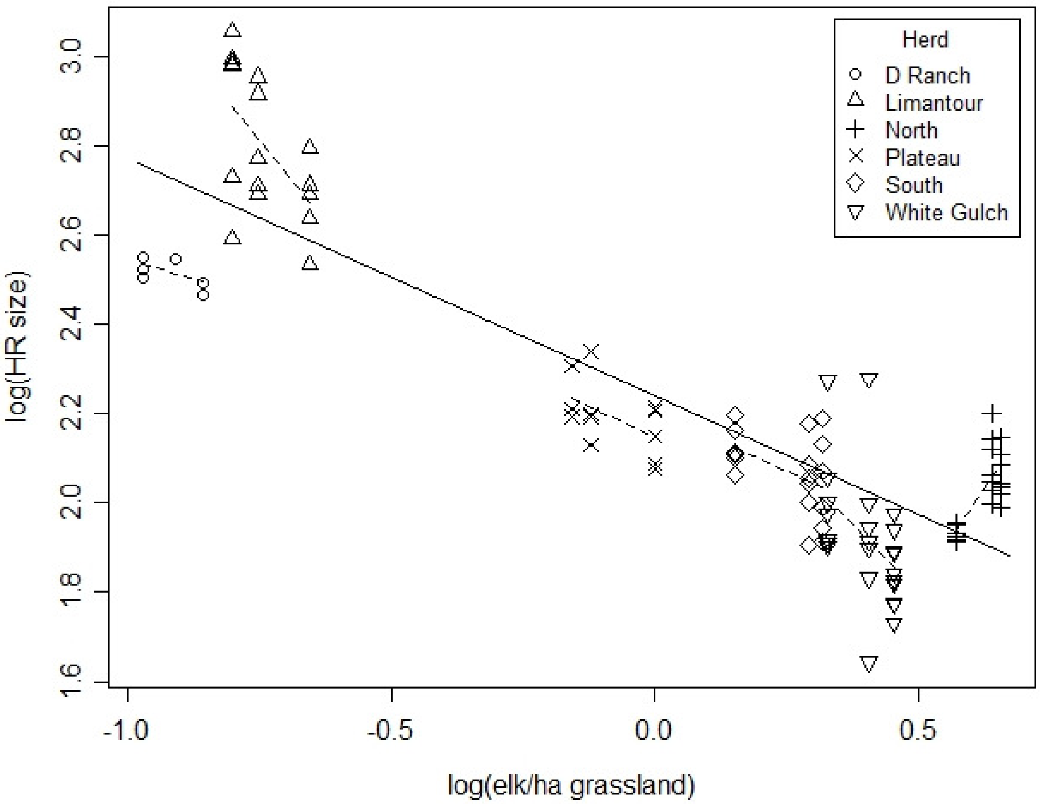

Figure 14. Scatter plot of average annual home range sizes and tule elk density by herd (elk/ ha grassland) for radio-collared tule elk, Point Reyes National Seashore, California, 2005-2008. The solid line is the linear regression for combined herds (n = 103, $R^2 = 0.82$), and dashed lines are linear regressions by herd. Data have been log-transformed.

Table 10. Results of linear regression analyses of annual home range sizes (90% fixed kernel, log-transformed) against annual herd density (elk / ha grassland habitat) by herd and for all herds combined ("Combined") for tule elk at Point Reyes National Seashore, California, 2005 – 2008.

Herd	Slope	*F*	R^2	*p*-value
D Ranch	-0.92	2.29	0.18	0.19
Limantour	-0.23	6.70	0.28	0.02*
North	0.34	26.20	0.55	<0.001**
Plateau	-0.50	4.00	0.21	0.07*
White Gulch	-0.18	6.85	0.18	0.01**
South	-0.37	4.03	0.14	0.60
Combined	-1.42	319.90	0.76	<0.001**

"*" = 0.10 < *p*-value > 0.05, "**" = *p*-value < 0.05

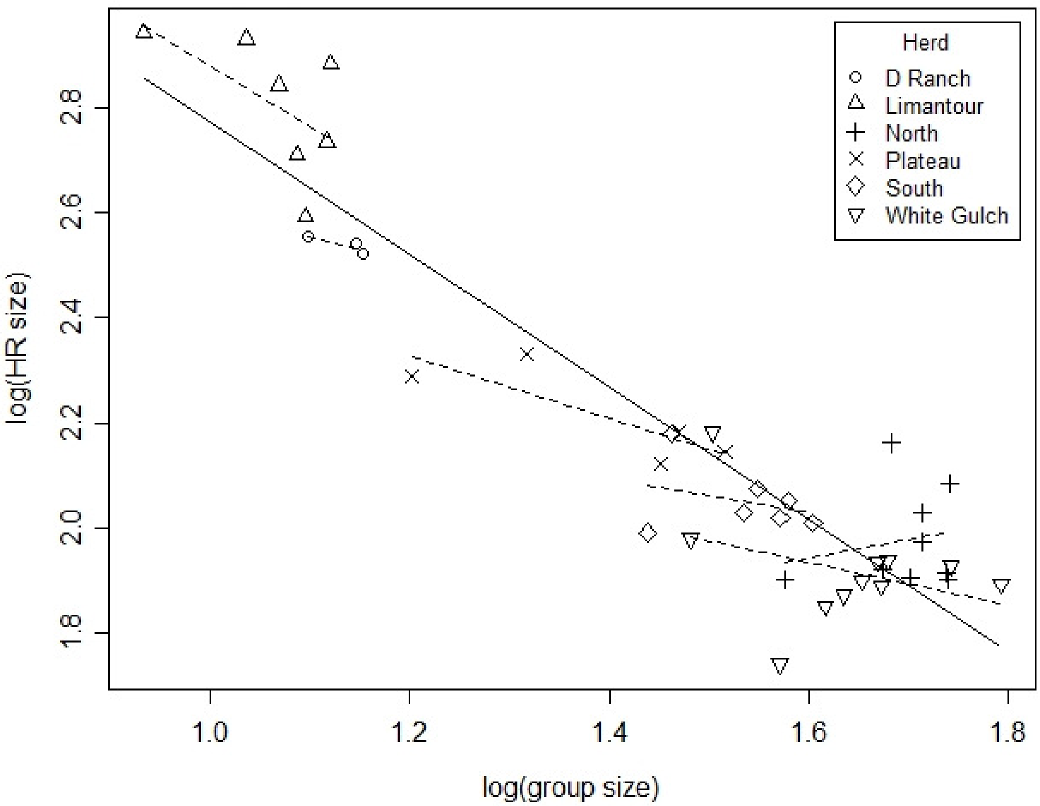

Figure 15. Scatter plot of average group sizes and home range sizes (90% fixed kernel) by herd for radio-collared tule elk, Point Reyes National Seashore, California, 2005 – 2008. The solid line is the linear regression for combined herds (n = 103, $R^2 = 0.76$), and dashed lines are linear regressions by herd. Data have been log-transformed.

Table 11. Results of linear regression analyses of annual home range sizes (90% fixed kernel, log-transformed) against mean annual group sizes (log-transformed) by herd and for all herds combined ("Combined") for tule elk at Point Reyes National Seashore, California, 2005 – 2008.

Herd	Slope	F	R^2	p-value
D Ranch	-0.14	0.50	0.09	0.51
Limantour	-0.60	0.24	0.02	0.64
North	1.24	12.25	0.38	0.002**
Plateau	-0.86	2.31	0.18	0.16
White Gulch	-1.25	3.66	0.12	0.07*
South	-0.63	3.81	0.18	0.07*
Combined	-0.09	376.60	0.79	< 0.001**

"*" = 0.10 < p-value > 0.05, "**" = p-value < 0.05

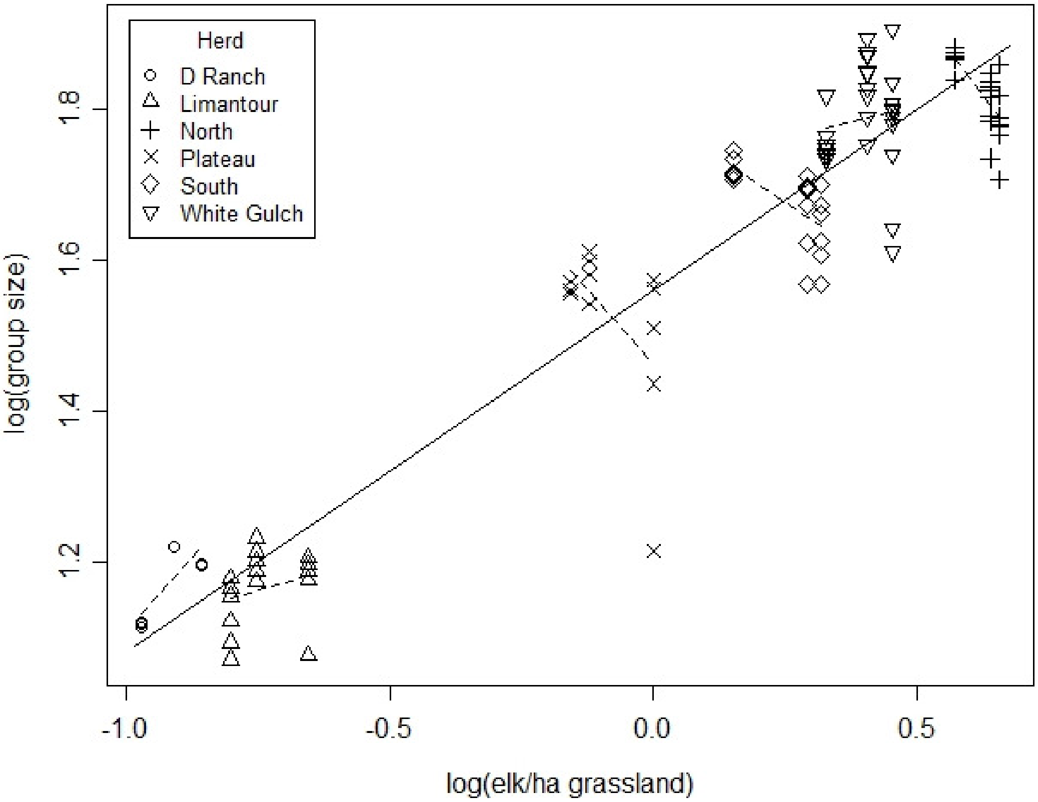

Figure 16. Scatter plot of average annual average annual group sizes and tule elk densities by herd (elk/ ha grassland habitat) for radio-collared tule elk, Point Reyes National Seashore, California, 2005-2008. The solid line is the linear regression for combined herds (n = 103, R^2 = 0.91), and dashed lines are linear regressions by herd. Data have been log-transformed.

Table 12. Results of linear regression analyses of annual herd density (elk / ha grassland habitat) against mean annual group sizes (log-transformed) by herd and for all herds combined ("Combined") for tule elk at Point Reyes National Seashore, California, 2005 – 2008.

Herd	Slope	*F*	R^2	*p*-value
D Ranch	0.83	9.11	0.57	0.03**
Limantour	0.34	1.01	<0.001	0.33
North	-0.55	21.21	0.49	<0.001**
Plateau	-0.35	3.74	0.20	0.08*
White Gulch	0.11	0.51	0.02	0.48
South	-0.90	11.93	0.38	0.003**
Combined	1.92	950.20	0.90	<0.001**

"*" = 0.10 < *p*-value > 0.05,   "**" = *p*-value < 0.05

CHAPTER 2

HABITAT USE AND RESOURCE SELECTION OF TULE ELK AT POINT REYES NATIONAL SEASHORE, CALIFORNIA

INTRODUCTION

Understanding how species utilize their habitats is a fundamental goal of ecology (Morris 2003) and essential to effective management (Gordon et al. 2004, Brook 2009). Our current knowledge of elk (*Cervus elaphus*) resource selection and subsequent management guidelines is based on the results of studies of the Rocky Mountain (*C. e. nelsoni*) and Roosevelt elk (*C. e. roosevelti*) subspecies (Toweill and Thomas 2002). Little information is available on elk habitat use and resource selection in Mediterranean climates such as coastal California. No information exists on resource selection patterns of tule elk (*C. e. nannodes*), a smaller subspecies with unique physiological adaptations that may result in distinctive resource selection patterns (McCullough 1971).

Resource selection studies of reintroduced populations are rare but critical to future reintroduction successes (Dolev et al. 2002, Bar-David et al. 2005). Tule elk were reintroduced to the Tomales Point Elk Reserve (Tomales) at Point Reyes National Seashore (Pt. Reyes), California in 1978 as part of a state-wide effort to return the formerly threatened subspecies to its original range. Elk at Tomales exhibited exponential growth for the first 20 years; growing from 10 elk to over 400 (Gogan 1982, Howell et al. 2002). Six herds of elk now exist at Pt. Reyes: 4 high-density, fenced herds inhabiting a designated wilderness area; a low-density, open population inhabiting a designated wilderness area; and a low-density, open population on actively managed ranchland. This situation allows for an examination of potential differences in resource selection among adjacent herds at different densities inhabiting landscapes with varying combinations of habitats.

Resource selection patterns are the spatial manifestation of an animal's basic needs: feeding, reproducing and avoiding death. Elk resource selection is influenced by a number of biotic and abiotic factors, including: the abundance and distribution of high quality forage (Langvatn and Hanley 1993), changes in forage abundance and quality due to temporal variations in precipitation (Borkowski and Furubayashi 1998, Ager et al. 2003, Boyce et al. 2003), density-related intraspecific competition (Young et al. 2009) and human disturbance (Cole et al. 1997, Clair and Forrest 2009, Naylor et al. 2009). As selective foragers, elk maximize their energy intake per unit time by selecting high protein forage (Wickstrom et al. 1984). Habitats at Pt. Reyes consist of a matrix of grassland, scrubland and forests. The diet of Pt. Reyes tule elk is composed primarily of grasses and forbs (Gogan and Barrett 1995), suggesting selection for grassland habitats. Cervids in northern seasonal environments seasonally shift their diets and resource use in response to plant phenology and temperature (Parker and Robbins 1984, Dumont et al. 2005). In the more mild climate of Pt. Reyes, tule elk shift their diets from grasses during the wet winter periods, to more shrubs and trees during the dry summer (Gogan and Barrett 1995), but it is not understood how these seasonal diet shifts translate into spatial changes in resource selection. High population density in herding species can cause intraspecific competition and increased evidence of resource selection in heterogeneous environments (Kie and Bowyer 1999, Svanback and Bolnick 2007), but this relationship has not been thoroughly investigated for elk. Following the Ideal Free Distribution

Theory (Fretwell 1972), elk should distribute themselves relative to the quality of habitat patches and lower quality patches should be selected in a stepwise manner as density increases. Therefore, habitat selection intensity (the number of habitat variables selected and the degree of selection) is expected to be inversely related to population density. Although red deer (*Cervus elaphus*) (Clutton-Brock et al. 1987) and domestic sheep (Mobaek et al. 2009) have exhibited increased use of low quality habitat at high densities, few studies have simultaneously quantified habitat selection among adjacent wild large herbivore herds at different densities.

In addition to causing widespread undesirable environmental impacts (Augustine and McNaughton 2004, Johnson and Cushman 2007, Tremblay et al. 2007), elk in high density populations experience increased intraspecific competition that can promote emigration to unoccupied habitat (Van Dyke 2007). When high density elk populations border human developments, these range expansions can lead to human-wildlife conflict in the form of economic losses (Hegel et al. 2009, Messmer 2009), changes in human's perceptions of wildlife (Lacey et al. 1993, Heydlauff et al. 2006), and even injury or death (Conover et al. 1995). The 2 low density tule elk herds at Pt. Reyes are predicted to grow (Chapter 4) and exhibit concurrent range expansions that may result in increased human-wildlife conflict. Maps of resource selection can be used to identify areas of high probability of elk use and forecast areas of likely range expansion. This information allows resource managers make informed decisions that may reduce potential conflicts.

The goals of this chapter were to: 1) Quantify tule elk habitat use and availability at Pt. Reyes 2) Determine whether tule elk habitat use varied seasonally (wet versus dry) 3) Quantify tule elk resource selection at the herd and population levels and 4) Apply tule elk resource selection information in a Geographic Information System (GIS) to forecast the relative probability of tule elk occurrence and potential areas of human-elk conflict at Pt. Reyes. The results of my study will provide a detailed understanding of tule elk resource selection patterns, which will provides insight in the underlying processes affecting the persistence of this formerly threatened subspecies and aid in their future management and conservation.

METHODS

Radio Telemetry

Radio-marking is currently the most effective method of monitoring individual animals in a free-ranging situation to determine population parameters (Millspaugh and Marzluff 2001, Mech and Barber 2002). Between January 10, 2005 and January 12, 2005, 32 adult female tule elk were immobilized using helicopter net-gunning (Leading Edge Aviation LLC, Lewiston, ID 83501). Captured elk were hobbled, blindfolded, given a low-dose nasal sedative of xylazine. Captured elk were fitted with a uniquely numbered ear tag (Nasco, Modesto, CA 95352) and with a mortality-sensing VHF radio-telemetry collar (MOD-500HC, Telonics Inc., Mesa, AZ 85204). Each collar had a unique combination of color bands which allowed field researchers to visually identify individual elk. Following the initial helicopter operation, I immobilized 10 additional adult female elk by ground darting using a mixture of ketamine and metatomidine, and reversed with atipamezole (Arnemo et al. 1994). These elk were also fitted with a mortality-sensing VHF radio-telemetry collar and an ear tag.

I attempted to get a visual fix on instrumented elk on foot or by horseback 2-times per week for 3 consecutive years (April 1, 2005 – April 1, 2008), unless there was a mechanical failure in the radio collar, or the animal was confirmed dead. An elk "group" was defined as elk within 50 m of each other that shared similar activity patterns (Clutton-Brock et al. 1982). I attempted group counts and classifications (Smith and McDonald 2002) by age and sex (cow, bull, yearling male, or calf) on all groups containing radio-collared elk. I recorded the fix of an elk group containing radio-collared elk as a point on a 7.5 minute U.S. Geological Survey Digital Raster Graphic (DRG) (http://topomaps.usgs.gov/drg/) paper map. I later manually digitized and stored radio-collared fixes in a GIS (ArcGIS 9.3) (ESRI 2008). When groups moved away while conducting observations, I moved to the former center of the target group and recorded an additional paired fix using a handheld GPS unit (Garmin Etrex, Garmin, Olathe, KS 66062). Since I recorded GPS fixes only after the GPS unit displayed an estimated fix precision of <10 m, I assumed that GPS fixes were "true" locations of elk groups. To calculate the spatial precision and identify any potential spatial bias of paper-mapped fixes, I quantifying the Euclidian distances (m) between pairs of paper-mapped and GPS-obtained fixes (Beyer 2006).

Habitat Variables

Using studies of elk habitat selection as a guide (Unsworth et al. 1998, Rowland et al. 2000), I identified 6 *a priori* classes of predictor variables that could describe elk resource selection: vegetation, slope, aspect, relative solar radiation, and distances from roads and trails. I examined vegetation classes instead of a primary productivity index (eg. Normalized Difference Vegetation Index) (Ryan et al. 2006) so that I could directly apply my results to specific vegetation classes at a finer spatial scale and avoid the inherent limitations of remotely-sensed indices (soil, spectral and atmospheric effects). I determined the vegetation composition of the study area using a vector-based GIS vegetation coverage (http://www.nps.gov/gis) jointly produced by the National Park Service and the U.S. Geologic Survey as part of a national USGS-NPS mapping program (Schirokauer et al. 2003). The map was created by interpreting 1:24,000 color aerial photographs taken in 1994, and utilized a hierarchical classification system. For the purposes of this study, I selected the "life form" classification level because of the ecological relevance of this classification to elk and because of the ability to extrapolate results to other classifications and regions. The life form classification had an overall thematic accuracy of 84% (Schirokauer et al. 2003). I clipped the vegetation layer to the boundary of Pt. Reyes, which I defined as the study area. The resulting layer had three habitat classes: grass, scrub, and forest (Figure 1). Habitats not falling within these classes (development, water, marsh) composed less than 5% of the mapping area.

I derived elevation, slope and aspect from a 1/3 Arc-second USGS National Elevation Dataset (NED, 10-m^2 pixels) layer of the study area (http://seamless.usgs.gov) using 3D Analyst Tool in ArcGIS 9.3 (ESRI 2008) (Figure 1). Elevation was quantified in meters above sea level and slope was measured in degrees from horizontal. I created 4 aspect categories from the original data (northwest, southwest, southeast, northeast) (Figure 1). I considered pixels with less than 5 degrees slope as flat and without any defined aspect.

I created a solar radiation index (SRI) raster layer of the study area using the raster calculator function in ArcGIS 9.2 (Keating et al. 2007). Pixel values had the potential to vary from 0 to 1, with increasing average exposure to sunlight (Figure 1). The formula used was:

$$SRI = cos(latitude)cos(slope) + sin(latitude)sin(slope)cos(180^o - aspect)$$

I created vector layers depicting road and trail locations by interpreting road locations from Digital Raster Graphics (DRGs) for Pt. Reyes (http://www.nps.gov/gis/). I converted NPS road and trail vector layers (http://www.nps.gov/gis) into raster layers of distance in meters to the nearest road and trail using the NEAR function in ArcGIS 9.2 (ESRI 2006) (Figure 2).

I resampled layers to the 10-m pixel scale and stored them in the Universal Transverse Mercator (UTM) coordinate system, North American Datum 1983, zone 10. I buffered each pixel by a circular radius equivalent to the average radio telemetry spatial error (70 m). I extracted the proportion of vegetation, the average SRI, the average distance from road and trail, the average elevation, and the majority value for aspect from within the buffered regions using Spatial Analysis in ArcGIS 9.3 (ESRI 2008).

Habitat Use and Availability

I defined elk habitat use as the proportion of fixes within a given habitat type. I examined habitat use at the herd level (Chapter 1 for herd delineation methods) and population level over 2 temporal scales: the entire study period (April 2005 – March 2008) and seasonally. I classified seasons as wet (May – October) and dry (November – April) according to average monthly precipitation during the study period (Bodega Ocean Observing Node, University of California Davis, http://bmlsc.ucdavis.edu/boon/ index.shtml, Figure 5). Annual precipitation averaged 14.21 cm (SE = 3.01) during the wet season and 1.67 cm (SE = 0.71) during the dry season. For habitat use, I used the majority vegetation value within the 70-m buffered region surrounding each radio telemetry fix. I compared habitat use among herds and seasons using Kruskal-Wallis chi-square (KW χ^2) tests (R Core Development Team, 2008).

At the population level, I defined available habitats as Tomales and two 100% minimum convex polygons (MCPs) containing all elk telemetry fixes at Limantour and D Ranch. I quantified and rejected other commonly used home range metrics (kernel and least squared convex hull) to define habitat availability because they led to overly constrained estimates of available habitat. I created 5,000 random fixes within these regions and extracted habitat values. To insure an equal sampling of use among herds, I randomly sub-sampled herd telemetry points using the sample size from the least sampled herd (D Ranch). I combined herd samples and intersected the combined data with the buffered habitat raster layers to extract the underlying habitat information.

At the herd level, I restricted available habitats to MCPs containing all elk telemetry fixes for each herd (Figures 3 and 4). I created 5,000 random fixes within each herd's MCP ("available") and extracted the underlying habitats using Hawth's Tools (Beyer 2006) in ArcGIS 9.3 (ESRI 2008). I did not quantify distance to road predictors for herds that did not have roads within their home range (Plateau and North herds). I compared habitat availability among herds using Kruskal-Wallis chi-square (KW χ^2) tests (R Core Development Team, 2008).

To decide what habitat variables to include in resource selection models, I determined whether elk were exhibiting selection for habitat variables. I tested for selection by comparing the proportion of used habitats to the proportion of available habitats with KW χ^2 tests (R Core Development 2008). Habitat variables were retained was evidence of selection occurring ($p < 0.05$).

Resource Selection

I randomly divided telemetry data ("used") into testing and training data. I used logistic regression-based resource selection function (RSF) analyses to compare the used training data to the available data at the population level and for each herd (Manly et al. 2002). The RSF [$w(x)$] had the general form:

$$w(x) = exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \ldots)$$

I employed a backward stepwise approach to model selection and evaluated ecologically plausible interactions between predictor variables in the most parsimonious models (R Core Development 2008). I quantified support between competing candidate models and addressed model uncertainty using Akaike's information criterion (AIC) and Akaike weights (w_i) (Burnham and Anderson 2002). I selected the most parsimonious RSF model for each herd and created GIS raster layers of relative RSF values using the Raster Calculator function in Spatial Analyst (ESRI 2008). I reclassified pixels from relative RSF values into 10 ordinal bins representing increasingly selected habitat types using quantile breakdowns in the Spatial Analysis extension (ESRI 2008). I calculated a utilization value [$U(x_i)$] for each bin using the formula:

$$U(x_i) = w(x_i)A(x_i) / \sum w(x_j)A(x_j),$$

where $w(x_i)$ is the midpoint RSF of bin *i* and $A(x_i)$ is the area of bin *i* (Boyce and McDonald 1999). I quantified the number of testing data that fell within each RSF bin and the expected number of validation observations within each bin (N_i) using the formula:

$$N_i = N * U(x_i),$$

where N is the number of testing data used. I assessed the fit of RSF models by comparing the observed and expected observations with linear regression and Spearman rank correlation tests.

RESULTS

Radio Telemetry

I recorded a total of 3,749 elk group fixes (Table 1). The number of group fixes ranged among herds from 326 (D Ranch) to 886 (White Gulch). Elk were located on average every 3.68 days (min = 1, max = 19, SE = 0.02) for a maximum period of 1,095 days (April 1, 2005-March 31, 2008). Forty two radio-collared elk were relocated 9,953 times for a total of 36,005 individual elk days. Ten (23.3%) radio-collared elk died during the study. Each radio-collared elk was monitored for a average period of 857 days (SE = 52.07) and located an average of 237 times (SE = 14.29). See Chapter 1 for a more detailed description of elk group results.

Herd MCPs averaged 550 ha ($N = 6$, SE = 181, Table 1, Figures 3 and 4). The smallest herd MCP was the North herd (257 ha) and the largest herd was Limantour (1,435 ha). The population-level MCP size was 3,034 ha.

A total of 1,059 (28%) paired fixes were paper-mapped and recorded with a GPS unit. Most ($\geq$ 50%) of paper-mapped fixes were < 70 m (SE = 1.8) from paired GPS fixes (Figure 6). I buffered all group fixes by 70 m for RSF analysis.

Habitat Use and Availability

At the population level, elk used grassland more than any other vegetation type (51%) (Table 2). Although habitat use of vegetation varied among herds (Figure 7), all herds except Limantour used grassland the most ($\bar{x}$ = 55.2%, SE = 5.9), followed by scrub ($\bar{x}$ = 43.1%, SE = 5.0) and forest ($\bar{x}$ = 1.7%, SE = 1.3). Elk use of slopes, aspects and road and trail distances varied among herds (Table 2). At the population level, elk used an average slope of 12 degrees (SE = 0.6). The Plateau elk herd used the steepest ($\bar{x}$ = 14 degrees, SE = 0.3) and the North herd used the flattest ($\bar{x}$ = 10 degrees, SE = 0.2) terrain. Northeast-facing slopes were used most, except for the Limantour and South herds, where northwest-facing slopes were used most often. Elk used habitats that averaged 648-m from the nearest road and 486-m from the nearest trail. Elk used habitats averaging 236-m (South, SE = 7) to 1,138-m (Limantour, SE = 23) from the nearest road, and 160-m (North, SE = 3) to 1264-m (D Ranch, SE = 24) from the nearest trail. SRI values were fairly constant across herds (0.73 - 0.78).

Elk habitat use varied seasonally. Elk used shrubbier habitats, lower elevations, steeper slopes, areas with less solar radiation, more southeastern aspects and areas further from trails during dry seasons (Table 3). Although all elk herds used steeper slopes and areas further from trails during dry seasons, differences were not statistically significant in the D Ranch ($p = 0.18$) and Limantour ($p = 0.31$) herds. All herds used lower elevations during dry seasons, however the difference was not statistically significant in the South herd ($p = 0.56$).

The most available vegetation type within elk herd ranges at the population level was scrub (63%), followed by grassland (28%) and forest (8%) (Table 2). Most herd ranges were dominated by scrub, except D Ranch where grassland (59.8%) was dominant (Figure 7). The Limantour herd had the most scrub (72.8%) and the least grassland available (17.4%). The topography within elk herd ranges averaged 14 degrees and by herd varied only slightly from 11 degrees (SE = 0.07) at the D Ranch herd to 17 degrees (SE = 0.11) at the Plateau herd. Aspects were consistent between herds. The nearest roads and trails averaged 903 m and 546 m at the population level, respectively. At the herd level, average distances from the nearest road ranged from 393 m (White Gulch, SE = 4) to 903 m (Limantour, SE = 9) and average distances to the nearest trail ranged from 212 m (North, SE = 2) to 1,318 m (D Ranch, SE = 7).

KW χ^2 tests revealed habitat selection at the herd scale, but the degree and direction of selection varied among herds (Table 4). All herds used a greater proportion of grassland than available (KW $\chi^2 = 305.79$, $p_{\text{all}} < 0.03$). All herds used less scrub and lower slopes than were available, although the difference was not statistically significant at D Ranch (KW $\chi^2 = 2.12$, $p_{\text{scrub}} = 0.15$; KW $\chi^2 = 1.81$, $p_{\text{slope}} = 0.18$). The D Ranch herd showed the lowest habitat selection intensity, with only four of ten available habitat types selected ($\alpha \leq 0.05$). Selections of other habitat types were generally inconsistent among herds.

Resource Selection

The most parsimonious RSF model for Pt. Reyes included grassland, scrub, forest, slope, SRI and distance to the nearest trail as predictor variables (Table 5). According to this model, grassland was the most selected vegetation type, followed by scrub and then forest. The relative probability of elk using a particular location increased with greater grassland composition ($ß_{\text{grass}} = 8.51$, SE = 1.38), and declined as the proportions of scrub ($ß_{\text{scrub}} = 6.85$, SE = 1.39) and forest ($ß_{\text{forest}} = 4.98$, SE = 1.44) habitats increased (Figure 8). The relative probability of elk use declined with increasing slope and in areas with greater exposure to sun (high SRI values). Elk avoided habitats closer to trails at the population level.

The most parsimonious herd-level RSF models produced inconsistent results (Tables 6 and 7, Appendix), which further indicated that elk resource selection varied at the herd range scale. The D Ranch and North herds showed little habitat selection (two habitat predictors) compared to other herds (four to nine habitat predictors). Steep slopes were avoided by all herds except D Ranch, and grassland was selected by all herds except D Ranch and Plateau. Scrub was selected by the Limantour and South elk herds, but at a lower intensity than grassland. However, scrub and grass habitats were equally selected at the White Gulch herd ($\beta_{grass} = 3.41$, $\beta_{scrub} = 3.43$). Roads were avoided by elk at D Ranch and Limantour, but the South herd selected areas closer to roads. Areas near trails were avoided by the Plateau and White Gulch herds.

RSF Model Assessment

RSF models generally showed high levels of correlation between the testing and training data (Table 8), which indicated good model fits. Spearman rank correlation test results showed the South, White Gulch, and population-level RSF models to have the best model fits ($r_s = 0.988$). All RSF models except D Ranch ($r_s = 0.48$, $p = 0.16$) showed a statistically significant correlation between the testing and training data ($p < 0.01$). The low correlation levels at D Ranch indicated that this model may have a poor predictive potential.

Linear regression tests of observed against expected binned-RSF values suggested that RSF models fit well overall (Table 8). Excluding D Ranch, linear regression tests revealed a strong correlation between observed and expected data for all herds ($R^2_{\text{average}} = 0.88$, $p_{average} < 0.01$). There was a poor fit and a weak relationship between the observed and expected data at D Ranch ($R^2 = 0.14$, $p = 0.28$), indicating weak habitat selection and poor habitat selection predictive ability.

RSF Predictor Maps

The population-level RSF map predicted high probabilities of elk use on the western grassland and ranching regions of Pt. Reyes and low probabilities of use on the eastern forested, wilderness habitats (Figure 9). Cattle ranches composed of 32% of Pt. Reyes but were over 68% of the land in the RSF bin with the highest relative probable of use and less than 6% of the land in the RSF-bin with the lowest probability of use (Figure 10). Herd-level RSF models produced inconsistent spatial predictions of elk use at Pt. Reyes, therefore, predictor maps using herd-level RSF results were not produced much beyond the extent of herd ranges (Figures 11 and 12).

DISCUSSION

The first goals of this chapter were to quantify tule elk habitat use and availability at Pt. Reyes, and determine whether tule elk habitat use varied seasonally (wet versus dry). I found that elk used grassland more than any other habitat type, even though scrub habitat was most dominant. Elk generally used moderate, north-facing slopes the most. Elk used shrubbier habitats, lower elevations, steeper southeastern slopes, areas with less solar radiation and areas further from trails during dry seasons than during the dry seasons. The second goal was to quantify tule elk resource selection at the herd and population levels. Elk resource selection results were inconsistent among herds, but at the population-level, elk selected flat grassland habitats and avoided areas near trails. By incorporate these results into a GIS, I found that ranchlands were highly selected habitats for elk at Pt. Reyes, and likely areas of future herd range expansion.

As expected, tule elk at Pt. Reyes exhibited shifts in habitat use that corresponded with seasonal precipitation levels. The population used lower elevations, steeper slopes and more scrub vegetation during the dry season (May – October). Although seasonal shifts in habitat use have been identified in northern populations of elk, this is one of the first studies to quantify small-scale seasonal shifts for a population of elk in a maritime-Mediterranean climate. Large herbivores in northern climates often exhibit seasonal shifts in elevation related to forage availability, thermal regulation, and predation pressure (Mao et al. 2005, Rice 2008). Rocky Mountain elk in Idaho use steeper slopes with the progression of winter (Hershey and Leege 1982) and elk in a non-forested region of Wyoming used lower elevations and more southerly aspects during the winter (Sawyer et al. 2007). Red deer select grasses when available (summer) and switch their diet to shrubs and forbs when grasses were unavailable (Dumont et al. 2005). Given the relatively stable Mediterranean climate at Pt. Reyes and lack of large predators capable of regulating the elk population, thermal regulation and predation pressure are not likely associated with the seasonal elevation shifts at Pt. Reyes. However, seasonal shifts in habitat use in this study do correspond with observed seasonal shifts in Pt. Reyes elk diets, suggesting that forage availability does influence elk spatial patterns at Pt. Reyes. Pt. Reyes elk foraged primarily on grasses during the wet season and scrub vegetation during the dry season (Gogan and Barrett 1995). This energy maximizing strategy is most likely driven by plant phenology and has been attributed to seasonal shifts in elevation by other cervids (Albon and Langvatn 1992). Large scale seasonal movements of stable, warm climate large herbivores such as wildebeest have been reported and are thought to be driven by temporal changes in the spatial distribution of newly emergent grasses due to rainfall (Wilmshurst et al. 1999).

Elk at Pt. Reyes generally selected grassland-dominated habitats over scrub and forest habitats, which is consistent with other studies of elk resource selection (Jones and Hudson 2002, Sawyer et al. 2007, Wolf et al. 2009). This finding also supports the theory of a proportional relationship between the time that a large herbivore resides in a particular forage type and the available quantity and quality of that forage (Bailey et al. 1996). There are currently no other studies on tule elk resource selection from which to compare my results, but in general elk typically select grass when available both for habitat and diet (Weckerly 2005, Christianson and Creel 2007). Consuming increased proportions of grass can improve maintenance of elk body mass (Christianson and Creel 2009), which is related to improved survival and reproduction (Bender et al. 2008). Elk at Pt. Reyes fed mainly on grasses and forbs (Gogan and Barrett 1995, Roberts 2000), with approximately 77% of their diet composed of two grass and two forb species that are found within the grassland habitat type (Roberts 2000). Coupled with my results, this finding supports the theory that tule elk have evolved features (enlarged jaws) for a specialized diet composed of limited grass species (McCullough 1971).

Steep slopes were generally avoided by elk at Pt. Reyes, like other populations (Sawyer et al. 2007, Wolf et al. 2009). Topography, along with soil and climate, can create microhabitats by altering nutrient contents, water availability, and solar radiation. At Pt. Reyes, steeper slopes were generally associated with mature coyote brush stands that were more difficult to traverse, obscured the field of view and contained lower quality forage. Steeper slopes were not avoided by elk at D Ranch where slopes have been cleared of woody vegetation for cattle grazing. Together these findings suggest that flatter areas selected by Pt. Reyes elk were tied to areas of higher quality forage.

Resource selection varied among adjacent herds of tule elk at Pt. Reyes, suggesting that the abundance and distribution of available habitat types affected elk resource selection patterns. The Pt. Reyes elk herd that showed the least resource selection intensity (D Ranch herd, two habitat variables) had the most available grassland, much of which was actively managed dairy pastures fertilized with manure and grazed by cattle. These pastures likely contained higher quality forage than nearby non-fertilized, wild grassland (Lee et al. 2000), but quantifying forage quality among Pt. Reyes elk herd ranges was beyond the scope of this study. Conversely, the Pt. Reyes herd with the least proportion of grassland habitat available to them (Limantour herd) showed one of the strongest habitat selection intensity (seven habitat variables). Thus, elk habitat selection intensity at Pt. Reyes appears to generally increase in areas with poorer forage availability. Home range size has been linked to resource availability and distribution for a number of foraging species (Kie et al. 2002), but fewer studies compared intensity of resource selection to habitat availability (Willems and Hill 2009). Additional data further supports this conclusion: elk at Pt. Reyes from herds with greater proportions of available grassland habitat had elevated adult survival rates and fecundity during all three years of this study. These results should be considered when attempting to extrapolate resource selection results to areas containing different proportions of available habitat.

I found some evidence that elk resource selection intensity was positively associated with herd density at Pt. Reyes, as reported elsewhere (Hobbs and Hanley 1990). The D Ranch herd had the lowest herd density (0.005 elk/ ha grassland) and exhibited little resource selection, while higher density herds [White Gulch (1.81 elk/ha grass) and South (2.49 elk/ha grass)] displayed strong resource selection. However, this pattern was not consistent between all herds, suggesting that either herd density may affect resource selection intensities only at the extreme values or possibly at a different scale than was quantified in this study. Biologists have understood that population density affects space use of wildlife for some time (Fretwell and Lucas 1969, Morris 2003), but it has not been until recently that population density is included in studies quantifying resource selection with RSFs (Mobaek et al. 2009, McLoughlin et al. 2010). Contrary to this study, domestic sheep showed less selection at higher densities (Mobaek et al. 2009). My results lend partial support for the prediction that resource selection increases with population density as a result of increased intraspecific competition, but future work is needed to further clarify the relationship between large herbivore population density and intensity of habitat selection.

The differences between herd-level RSF predictor maps at Pt. Reyes exemplify the potential danger in extrapolating RSF predictions far beyond the region used to generate the predictions. This is especially true if the habitats beyond the current range are substantially different than those used in the model. Researchers should attempt to examine habitat selection across all available habitats within the boundaries of the predicted region when possible. In my study, the population level RSF incorporated all existing available elk habitat, and is favored over the herd-level RSFs for population-level habitat selection predictions. Quantifying habitat selection across a study area might not be feasible if the target species inhabits a heterogeneous and patchy landscape, or if the population has a relatively small range within the study area. Potential solutions include choosing coarser habitat delineations or limiting habitat selection estimations to the currently usable region (e.g. within the existing home ranges). Similar landscapes with different population densities may have different habitat selection predictions, as demonstrated by the Tomales elk herds in this study. Studies attempting to predict future population expansion should make an effort to take into account the effects of population density on habitat selection. RSF predictor maps can be used to prepare wildlife managers for future conditions if the proper steps are taken to avoid erroneous extrapolations.

Most herds of elk at Pt. Reyes showed avoidance of roads and trails, but the effects were less uniform than other regions where elk avoid human development throughout their range (Rowland et al. 2000, St. Clair and Forrest 2009). Human disturbances can alter activity and movements (Conner et al. 2001, Naylor et al. 2009), reduce survival rates (Cole et al. 1997), change habitat selection patterns (Millspaugh et al. 2000) and increase physiological stress levels (Creel et al. 2002) of elk. However, elk exposed to high levels of human activity in protected areas may become habituated and gain a fitness benefit by associating with human development, thereby avoiding predators and hunters (Schultz and Bailey 1978, Thompson and Henderson 1998). Pt. Reyes receives some of the highest levels of annual visitation of any NPS unit (approximately 2 million visitors annually), and it is estimated that at least half visit Tomales (John Dell'Osso, NPS, personal statement). Elk avoidance of trails at Tomales was associated with distance from the trailhead: herds closer to the trailhead (White and South) avoiding areas near trails and herds further from the trailhead (Plateau and North) not exhibiting any selection relating to trail distance. This finding can be explained by my observations of the distribution of visitors at Tomales: hikers often did not complete the entire length of trail and therefore did not come into contact with herds further from the trailhead. Although most herds avoided habitat closer to roads as expected, the South herd showed a slight attraction to areas near roads. This finding may have been due to the central location of the road within this herd's small home range, the close proximity of a large portion of the available flat grassland to the road and the herd's level of habituation to traffic due to year-round high level of exposure with little associated aversive effects.

Although elk and cattle currently have limited spatial overlap at Pt. Reyes, ranchland habitats were selected by elk according to RSF model results. Based on these results, I predict that Limantour and D Ranch herd growth and concurrent range expansions (Chapter 4) will occur primarily onto adjacent cattle ranchlands where human-wildlife conflict may arise. Conflict between government agencies and ranchers over property damages is not uncommon in regions where elk and ranching overlap (Edge and Marcum 1990, Van Tassell et al. 1999, Brook 2009, Hegel et al. 2009). At Pt. Reyes, ranchers within the D Ranch herd's range have already voiced concern and frustration to the National Park Service (NPS) over elk damages to fences and a perceived reduction in forage (N. Gates, personnel communication). Elk and cattle use similar areas and consume similar forage (Torstenson et al. 2006) and elk at high densities can compete for and reduce forage availability for cattle (Hobbs et al. 1996), leading to economic losses for ranchers. Tule elk may be especially susceptible to forage competition with cattle because of their relatively narrow diet selection compared to other elk subspecies (McCullough 1971). In addition to direct forage competition, disease transmission between elk and cattle increase with closer proximity. Elk at Tomales harbor Johne's disease (*Mycobacterium paratuberculosis*), which was believed to be transmitted from cattle when they were initially reintroduced. There is currently no information on Johne's disease prevalence in Pt. Reyes cattle.

Though RSF models indicate that Pt. Reyes elk select for ranchland habitat, elk were observed avoiding pastures when cattle were present and cattle were seen chasing elk from pastures on multiple occasions. These observations were supported by concurrent GPS collar data that showed Pt. Reyes tule elk almost entirely avoided pastures occupied by cattle (unpublished data). Cattle can cause increased levels of vigilance and decreased feeding rates in wild ungulates (Brown et al. 2010) and can competitively exclude elk from pastures (Coe et al. 2001, Stewart et al. 2002) resulting in spatial displacement and potentially increased intraspecific resource competition in adjacent areas. Interactions between cattle and elk at Pt. Reyes can be expected to increase with increasing elk population density, and predicted overlap between cattle and elk at Pt. Reyes may be complicated by spatial repulsion between the two species. NPS managers at Pt. Reyes are encouraged to alleviate future conflict between ranchers and tule elk by developing a proactive elk-rancher management plan that would prioritize management efforts based on my RSF map prediction results and forecasts of future elk population growth (Chapter 4).

CONCLUSIONS

The resource use and selection patterns of tule elk at Pt. Reyes were largely explained by their forage needs. Elk at Pt. Reyes selected for grasslands with little slope, which contain preferred forage. Elk shifted to lower elevations and increased their use of scrub habitat during dry seasons possibly as a result of spatial shifts in the caloric values of forage across the landscape. Elk resource selection varied among adjacent herds, which may be due to differences in habitat availability or intraspecific competition for forage related to differences in herd densities. Elk in herd ranges with higher proportions of preferred habitat tended to exhibit lower resource selection intensities. According to RSF model results, cattle pastures bordering existing elk ranges were areas of high probability of elk use and potential sources of future conflict if the elk population continues to increase as predicted. I encourage wildlife managers to continue to use RSF modeling results to forecast potential future human-wildlife conflict and begin a proactive management strategy in areas of potential conflict.

LITERATURE CITED

Ager, A. A., B. K. Johnson, J. W. Kern, and J. G. Kie. 2003. Daily and seasonal movements and habitat use by female Rocky Mountain elk and mule deer. Journal of Mammalogy 84:1076-1088.

Albon, S. D., and R. Langvatn. 1992. Plant phenology and the benefits of migration in a temperate ungulate. Oikos 65:502-513.

Arnemo, J. M., T. Negard, and N. E. Soli. 1994. Chemical capture of free-ranging red deer (*Cervus elaphus*) with medetomidine-ketamine. Rangifer 14:123-127.

Augustine, D. J., and S. J. McNaughton. 2004. Regulation of shrub dynamics by native browsing ungulates on East African rangeland. Journal of Applied Ecology 41:45-58.

Bailey, D. W., J. E. Gross, E. A. Laca, L. R. Rittenhouse, M. B. Coughenour, D. M. Swift, and P. L. Sims. 1996. Mechanisms that result in large herbivore grazing distribution patterns. Journal of Range Management 49:386-400.

Bar-David, S., D. Saltz, and T. Dayan. 2005. Predicting the spatial dynamics of a reintroduced population: the Persian fallow deer. Ecological Applications 15:1833.

Bender, L. C., J. G. Cook, R. C. Cook, and P. B. Hall. 2008. Relations between nutritional condition and survival of North American elk *Cervus elaphus*. Wildlife Biology 14:70-80.

Beyer, H. 2006. Hawth's Analysis Tools v. 3.27. Available at http://www.spatialecology.com/htools.

Borkowski, J., and K. Furubayashi. 1998. Seasonal changes in number and habitat use of foraging sika deer at the high altitude of Tanzawa Mountains, Japan. Acta Theriologica 43:95-106.

Boyce, M. S., J. S. Mao, E. H. Merrill, D. Fortin, M. G. Turner, J. Fryxell, and P. Turchin. 2003. Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. Ecoscience 10:421-431.

Boyce, M. S., and L. L. McDonald. 1999. Relating populations to habitats using resource selection functions. Trends in Ecology and Evolution 14:268-272.

Brook, R. K. 2009. Historical review of elk-agriculture conflicts in and around Riding Mountain National Park, Manitoba, Canada. Human-Wildlife Conflicts 3:72-87.

Brown, N. A., K. E. Ruckstuhl, S. Donelon, and C. Corbett. 2010. Changes in vigilance, grazing behaviour and spatial distribution of bighorn sheep due to cattle presence in Sheep River Provincial Park, Alberta. Agriculture Ecosystems and Environment 135:226-231.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference. 2nd edition. Springer, New York, NY.

Christianson, D., and S. Creel. 2009. Effects of grass and browse consumption on the winter mass dynamics of elk. Oecologia 158:603-613.

Christianson, D. A., and S. Creel. 2007. A review of environmental factors affecting elk winter diets. Journal of Wildlife Management 71:164-176.

Clair, C. C. S., and A. Forrest. 2009. Impacts of vehicle traffic on the distribution and behaviour of rutting elk, *Cervus elaphus*. Behaviour 146:393-413.

Clutton-Brock, T., F. Guinness, and S. Albon. 1982. Red Deer: Behavior and Ecology of Two Sexes. Edinburgh University Press, Edinburgh, UK.

Clutton-Brock, T. H., G. R. Lason, and F. E. Guinness. 1987. Sexual segregation and density-related changes in habitat use in male and female red deer (*Cervus elaphus*). Journal of Zoology 211:275-289.

Coe, P. K., B. K. Johnson, J. W. Kern, S. L. Findholt, J. G. Kie, and M. J. Wisdom. 2001. Responses of elk and mule deer to cattle in summer. Journal of Range Management 54:A51-A76.

Cole, E. K., M. D. Pope, and R. G. Anthony. 1997. Effects of road management on movement and survival of Roosevelt elk. Journal of Wildlife Management 61:1115-1126.

Conner, M. M., G. C. White, and D. J. Freddy. 2001. Elk movement in response to early-season hunting in northwest Colorado. Journal of Wildlife Management 65:926-940.

Conover, M. R., W. C. Pitt, K. K. Kessler, T. J. Dubow, and W. A. Sanborn. 1995. Review of human injuries, illnesses, and economic losses caused by wildlife in the United States. Wildlife Society Bulletin 23:407-414.

Creel, S., J. E. Fox, A. Hardy, J. Sands, B. Garrott, and R. O. Peterson. 2002. Snowmobile activity and glucocorticoid stress responses in wolves and elk. Conservation Biology 16:809-814.

Dolev, A., D. Saltz, S. Bar-David, and Y. Yom-Tov. 2002. Impact of repeated releases on space-use patterns of Persian fallow deer. Journal of Wildlife Management 66:737-746.

Dumont, B., P. C. Renaud, N. Morellet, C. Mallet, F. Anglard, and H. Verheyden-Tixier. 2005. Seasonal variations of red deer selectivity on a mixed forest edge. Animal Research 54:369-381.

Edge, W. D., and C. L. Marcum. 1990. Elk and cattle on public lands: a new look at an old conflict. Western Wildlands 16:12-15.

ESRI. 2008. ArcGIS 9.3. Redlands, CA.

Fretwell, S. D. 1972. Populations in a seasonal environment. Princeton University Press, Princeton, NJ.

Fretwell, S. D., and H. L. J. Lucas. 1969. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheoretica 19:16-52.

Gogan, P. 1982. Ecology of the tule elk range, Point Reyes National Seashore, California. Dissertation, University of California, Berkeley.

Gogan, P. J. P., and R. H. Barrett. 1995. Elk and deer diets in a coastal prairie-scrub mosaic, California. Journal of Range Management 48:327-335.

Gordon, I. J., A. J. Hester, and M. Festa-Bianchet. 2004. The management of wild large herbivores to meet economic, conservation and environmental objectives. Journal of Applied Ecology 41:1021-1031.

Hegel, T. M., C. C. Gates, and D. Eslinger. 2009. The geography of conflict between elk and agricultural values in the Cypress Hills, Canada. Journal of Environmental Management 90:222-235.

Hershey, T. J., and T. A. Leege. 1982. Elk movements and habitat use on a managed forest in north-central Idaho. Wildlife Bulletin, Idaho Department of Fish and Game:25 pp.

Heydlauff, A. L., P. R. Krausman, W. W. Shaw, and S. E. Marsh. 2006. Perceptions regarding elk in northern Arizona. Wildlife Society Bulletin 34:27-35.

Hobbs, N. T., D. L. Baker, G. D. Bear, and D. C. Bowden. 1996. Ungulate grazing in sagebrush grassland: Mechanisms of resource competition. Ecological Applications 6:200-217.

Hobbs, N. T., and T. A. Hanley. 1990. Habitat evaluation - do use availability data reflect carrying-capacity? Journal of Wildlife Management 54:515-522.

Howell, J. A., G. C. Brooks, M. Semenoff-Irving, and C. Greene. 2002. Population dynamics of tule elk at Point Reyes National Seashore, California. Journal of Wildlife Management 66:478-490.

Johnson, B. E., and J. H. Cushman. 2007. Influence of a large herbivore reintroduction on plant invasions and community composition in a California grassland. Conservation Biology 21:515-526.

Jones, P. F., and R. J. Hudson. 2002. Winter habitat selection at three spatial scales by American Elk, *Cervus elaphus*, in west-central Alberta. Canadian Field-Naturalist 116:183-191.

Keating, K. A., P. J. P. Gogan, J. M. Vore, and L. R. Irby. 2007. A simple solar radiation index for wildlife habitat studies. Journal of Wildlife Management 71:1344-1348.

Kie, J. G., and R. T. Bowyer. 1999. Sexual segregation in white-tailed deer: Density-dependent changes in use of space, habitat selection, and dietary niche. Journal of Mammalogy 80:1004-1020.

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.

Lacey, J. R., K. Jamtgaard, L. Riggle, and T. Hayes. 1993. Impacts of big game on private land in south-western Montana - landowner perceptions. Journal of Range Management 46:31-37.

Langvatn, R., and T. A. Hanley. 1993. Feeding-patch choice by red deer in relation to foraging efficiency - an experiment. Oecologia 95:164-170.

Lee, H. S., I. D. Lee, and H. S. Jeon. 2000. Effect of chemical fertilizer and cattle manure on dry matter yield, quality and botanical composition in pasture mixtures. Journal of Animal Science and Technology 42:719-726.

Manly, B. F. J., L. McDonald, D. L. Thomas, T. L. McDonald, and W. Erickson. 2002. Resource selection by animals. Kluwer Academic Publishers, Netherlands.

Mao, J. S., M. S. Boyce, D. W. Smith, F. J. Singer, D. J. Vales, J. M. Vore, and E. H. Merrill. 2005. Habitat selection by elk before and after wolf reintroduction in Yellowstone National Park. Journal of Wildlife Management 69:1691-1707.

McCullough, D. R. 1971. The tule elk: its history, behavior, and ecology. University of California Press, Berkeley, CA.

McLoughlin, P. D., D. W. Morris, D. Fortin, E. Vander Wal, and A. L. Contasti. 2010. Considering ecological dynamics in resource selection functions. Journal of Animal Ecology 79:4-12.

Mech, L. D., and S. M. Barber. 2002. A critique of wildlife radio-tracking and its use in national parks, a report to the U.S. National Park Service. Washington, D.C.

Messmer, T. A. 2009. Human-wildlife conflicts: emerging challenges and opportunities. Human-Wildlife Conflicts 3:10-17.

Millspaugh, J. J., G. C. Brundige, R. A. Gitzen, and K. J. Raedeke. 2000. Elk and hunter space-use sharing in South Dakota. Journal of Wildlife Management 64:994-1003.

Millspaugh, J. J., and J. M. Marzluff. 2001. Radio-tracking and animal populations: past trends and future needs. Pages 383-393 *in* J. J. Millspaugh, and J. M. Marzluff, editors. Radio tracking and animal populations. Academic Press, New York, NY.

Mobaek, R., A. Mysterud, L. Egil Loe, O. Holand, and G. Austrheim. 2009. Density dependent and temporal variability in habitat selection by a large herbivore: an experimental approach. Oikos 118:209-218.

Morris, D. W. 2003. Toward an ecological synthesis: a case for habitat selection. Oecologia 136:1-13.

Naylor, L. M., M. J. Wisdom, and R. G. Anthony. 2009. Behavioral responses of North American elk to recreational activity. Journal of Wildlife Management 73:328-338.

Parker, K. L., and C. T. Robbins. 1984. Thermoregulation in mule deer and elk. Canadian Journal of Zoology 62:1409-1422.

R-Core-Development-Team. 2008. R: A language and environment for statistical computing.

Rice, C. G. 2008. Seasonal altitudinal movements of mountain goats. Journal of Wildlife Management 72:1706-1716.

Roberts, S. L. 2000. Foraging ecology of tule elk at Tomales Point, Point Reyes National Seashore, California. MS thesis, University of Idaho, Boise, ID.

Rowland, M. M., M. J. Wisdom, B. K. Johnson, and J. G. Kie. 2000. Elk distribution and modeling in relation to roads. Journal of Wildlife Management 64:672-684.

Ryan, S. J., C. U. Knechtel, and W. M. Getz. 2006. Range and habitat selection of African buffalo in South Africa. Journal of Wildlife Management 70:764-776.

Sawyer, H., R. M. Nielson, F. G. Lindzey, L. Keith, J. H. Powell, and A. A. Abraham. 2007. Habitat selection of Rocky Mountain elk in a nonforested environment. Journal of Wildlife Management 71:868-874.

Schirokauer, D., T. Keeler-Wolf, J. Meinke, and P. Van der Leeden. 2003. Plant community mapping and classification project final report. National Park Service Report.

Schultz, R. D., and J. A. Bailey. 1978. Responses of National Park elk to human activity. Journal of Wildlife Management 42:91-100.

Smith, B. L., and T. L. McDonald. 2002. Criteria to improve age classification of antlerless elk. Wildlife Society Bulletin 30:200-207.

St. Clair, C. C., and A. Forrest. 2009. Impacts of vehicle traffic on the distribution and behaviour of rutting elk, *Cervus elaphus*. Behaviour 146:393-413.

Stewart, K. M., R. T. Bowyer, J. G. Kie, N. J. Cimon, and B. K. Johnson. 2002. Temporospatial distributions of elk, mule deer, and cattle: Resource partitioning and competitive displacement. Journal of Mammalogy 83:229-244.

Svanback, R., and D. I. Bolnick. 2007. Intraspecific competition drives increased resource use diversity within a natural population. Proceedings of the Royal Society 274:839-844.

Thompson, M. J., and R. E. Henderson. 1998. Elk habituation as a credibility challenge for wildlife professionals. Wildlife Society Bulletin 26:477-483.

Torstenson, W. L. F., J. C. Mosley, T. K. Brewer, M. W. Tess, and J. E. Knight. 2006. Elk, mule deer, and cattle foraging relationships on foothill and mountain rangeland. Rangeland Ecology and Management 59:80-87.

Toweill, D. E., and J. W. Thomas. 2002. North American elk: ecology and management. Smithsonian Institution Press, Washington.

Tremblay, J. P., J. Huot, and F. Potvin. 2007. Density-related effects of deer browsing on the regeneration dynamics of boreal forests. Journal of Applied Ecology 44:552-562.

Unsworth, J. W., L. Kuck, E. O. Garton, and B. R. Butterfield. 1998. Elk habitat selection on the Clearwater National Forest, Idaho. Journal of Wildlife Management 62:1255-1263.

Van Dyke, F. 2007. Colonization of non-traditional range in dispersing elk (*Cervus elaphus nelsoni*) populations. Canadian Field Naturalist 121:133-141.

Van Tassell, L. W., C. Phillips, and B. Z. Yang. 1999. Depredation claim settlements in Wyoming. Wildlife Society Bulletin 27:479-487.

Weckerly, F. W. 2005. Grass and supplemental patch selection by a population of Roosevelt elk. Journal of Mammalogy 86:630-638.

Wickstrom, M. L., C. T. Robbins, T. A. Hanley, D. E. Spalinger, and S. M. Parish. 1984. Food intake and foraging energetics of elk and mule deer. Journal of Wildlife Management 48:1285-1301.

Willems, E. P., and R. A. Hill. 2009. Predator-specific landscapes of fear and resource distribution: effects on spatial range use. Ecology 90:546-555.

Wilmshurst, J. F., J. M. Fryxell, B. P. Farm, A. R. E. Sinclair, and C. P. Henschel. 1999. Spatial distribution of Serengeti wildebeest in relation to resources. Canadian Journal of Zoology 77:1223-1232.

Wolf, M., J. Frair, E. Merrill, and P. Turchin. 2009. The attraction of the known: the importance of spatial familiarity in habitat selection in wapiti *Cervus elaphus*. Ecography 32:401-410.

Young, K. D., S. M. Ferreira, and R. J. van Aarde. 2009. The influence of increasing population size and vegetation productivity on elephant distribution in the Kruger National Park. Austral Ecology 34:329-342.

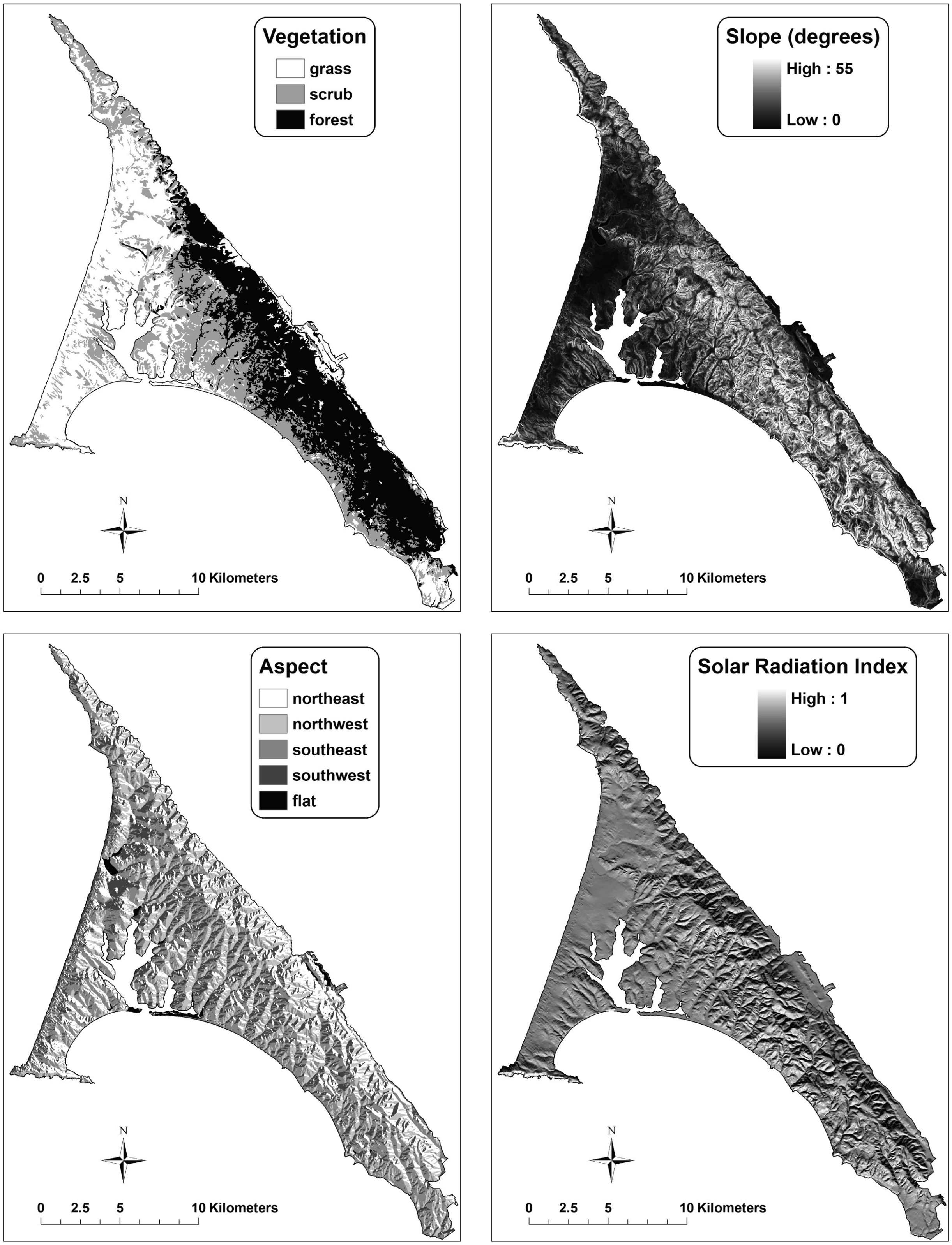

Figure 3. Maps of vegetation classes, aspect, slope and solar radiation (SRI) at Point Reyes National Seashore, CA.

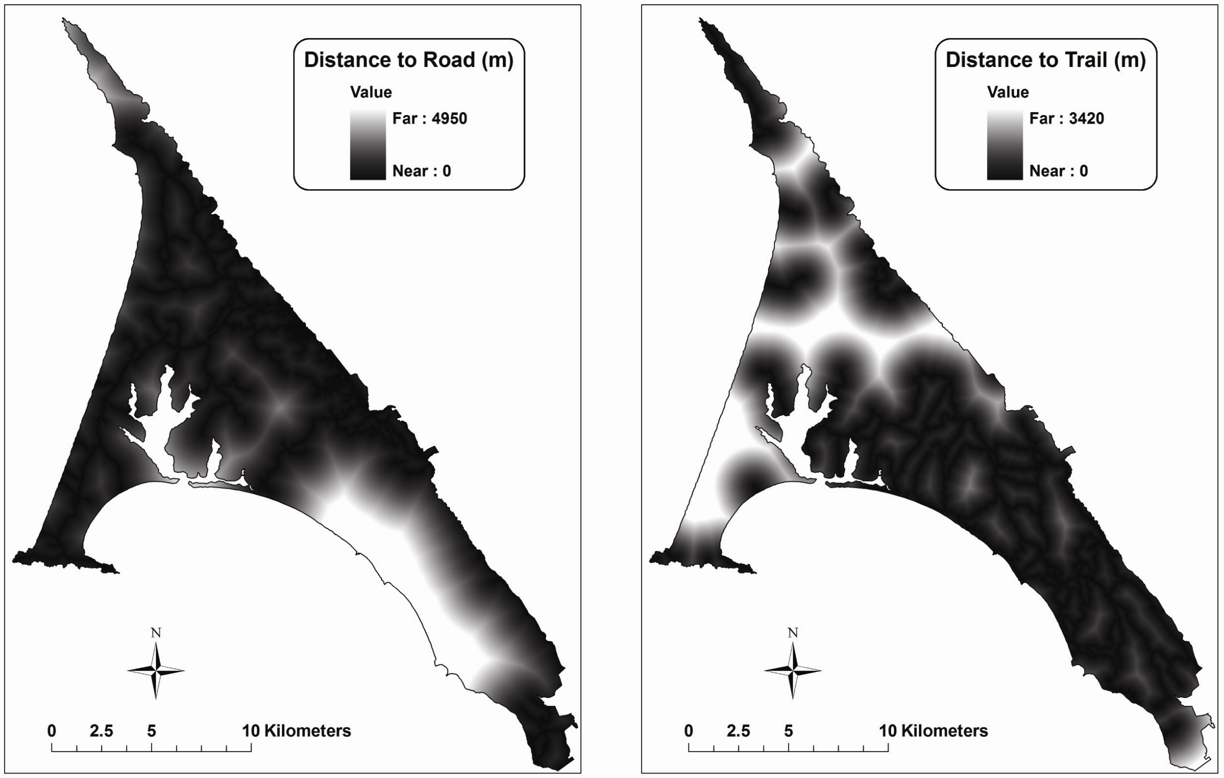

Figure 4. Maps of distance to nearest road (m) and distance to nearest trail (m) at Point Reyes National Seashore, California.

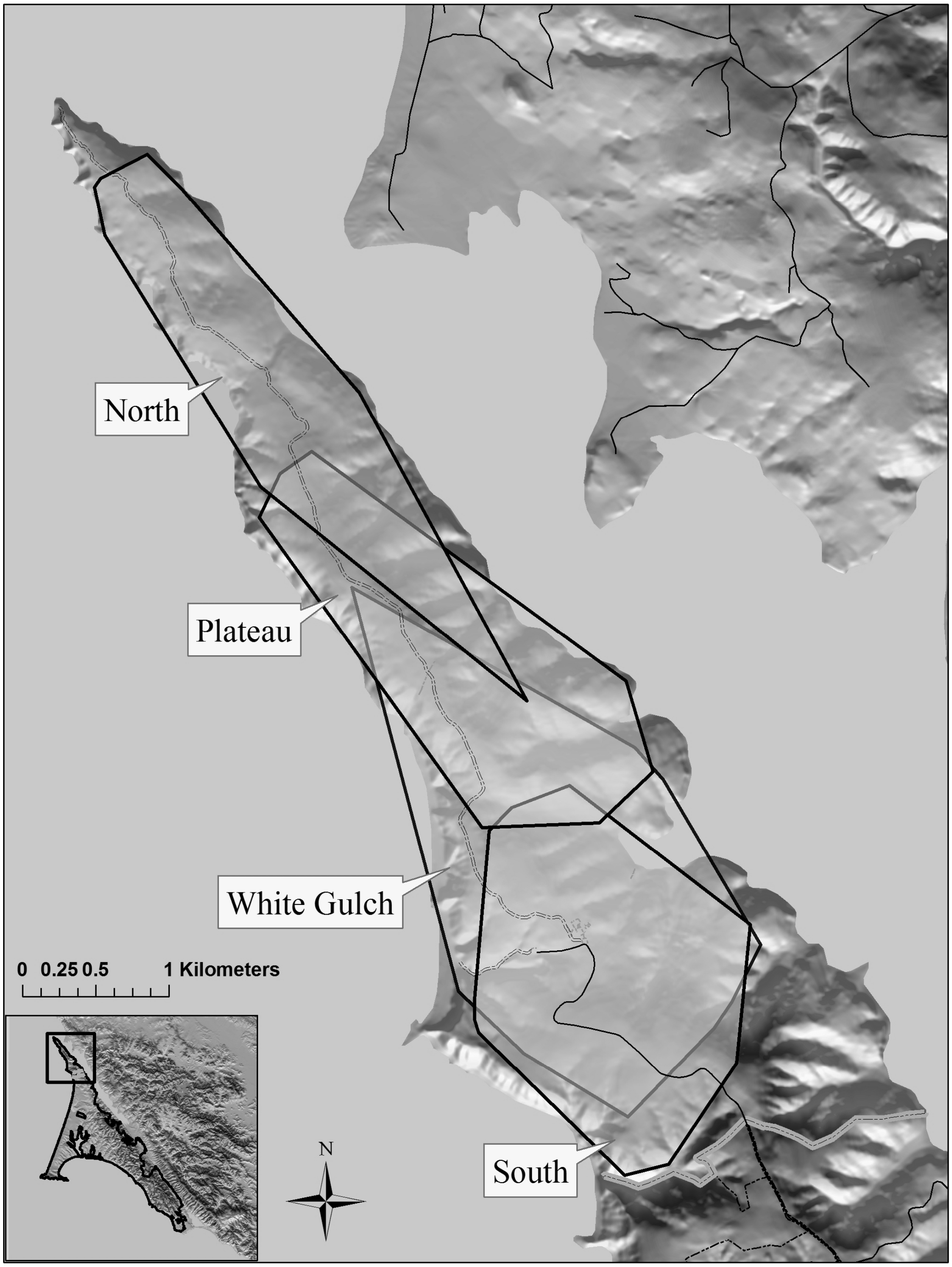

Figure 3. Minimum convex polygons (100% MCPs) of tule elk radio-telemetry data from North, Plateau, White Gulch and South herds at the Tomales Point Elk Reserve, Point Reyes National Seashore, CA, 2005 – 2008. MCPs define the extent of available habitats for resource selection function (RSF) estimations at the herd scale.

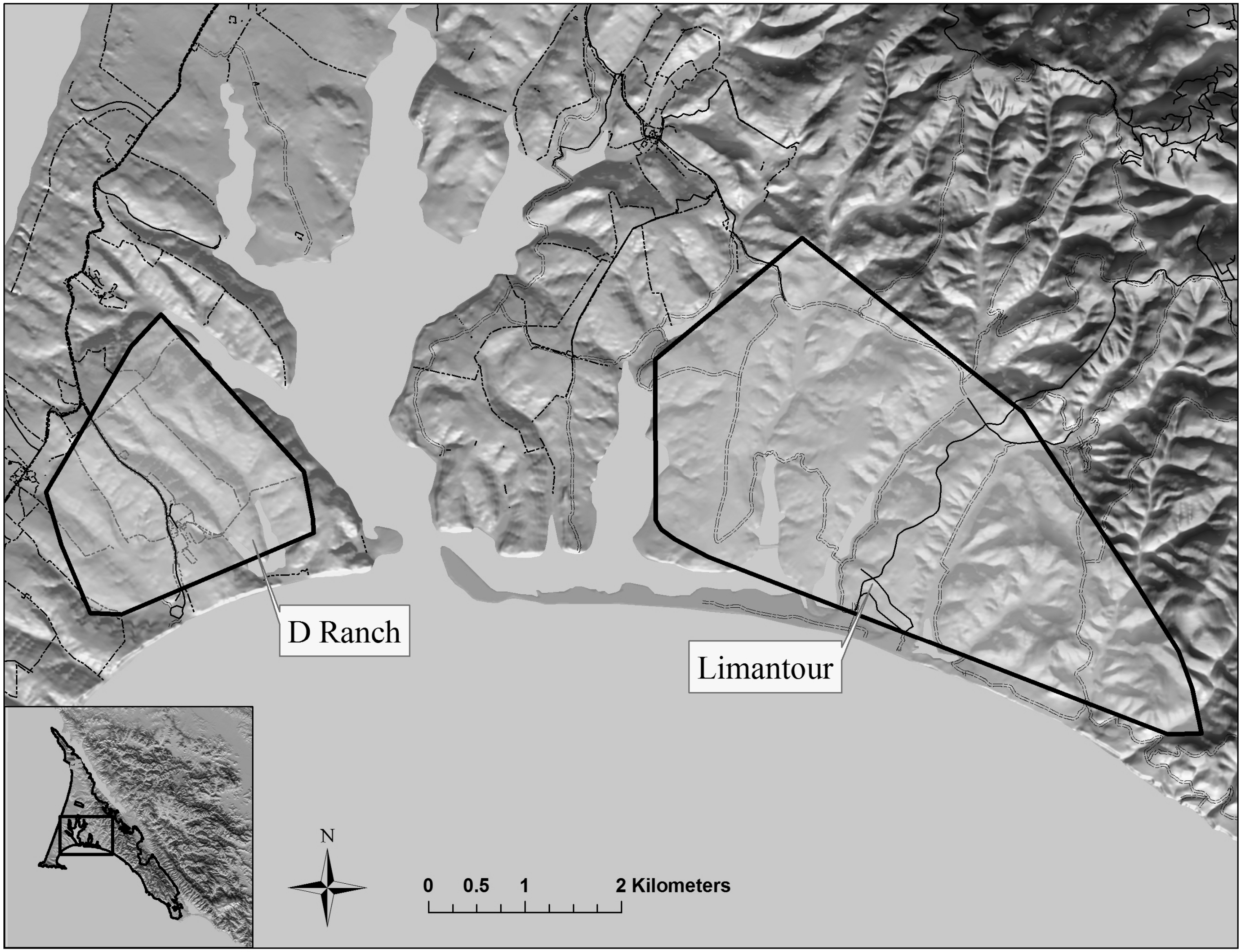

Figure 4. Minimum convex polygons (100% MCPs) of tule elk radio telemetry data at the D Ranch and Limantour herds. MCPs define the extent of available habitats for resource selection function (RSF) estimation at Point Reyes National Seashore, California.

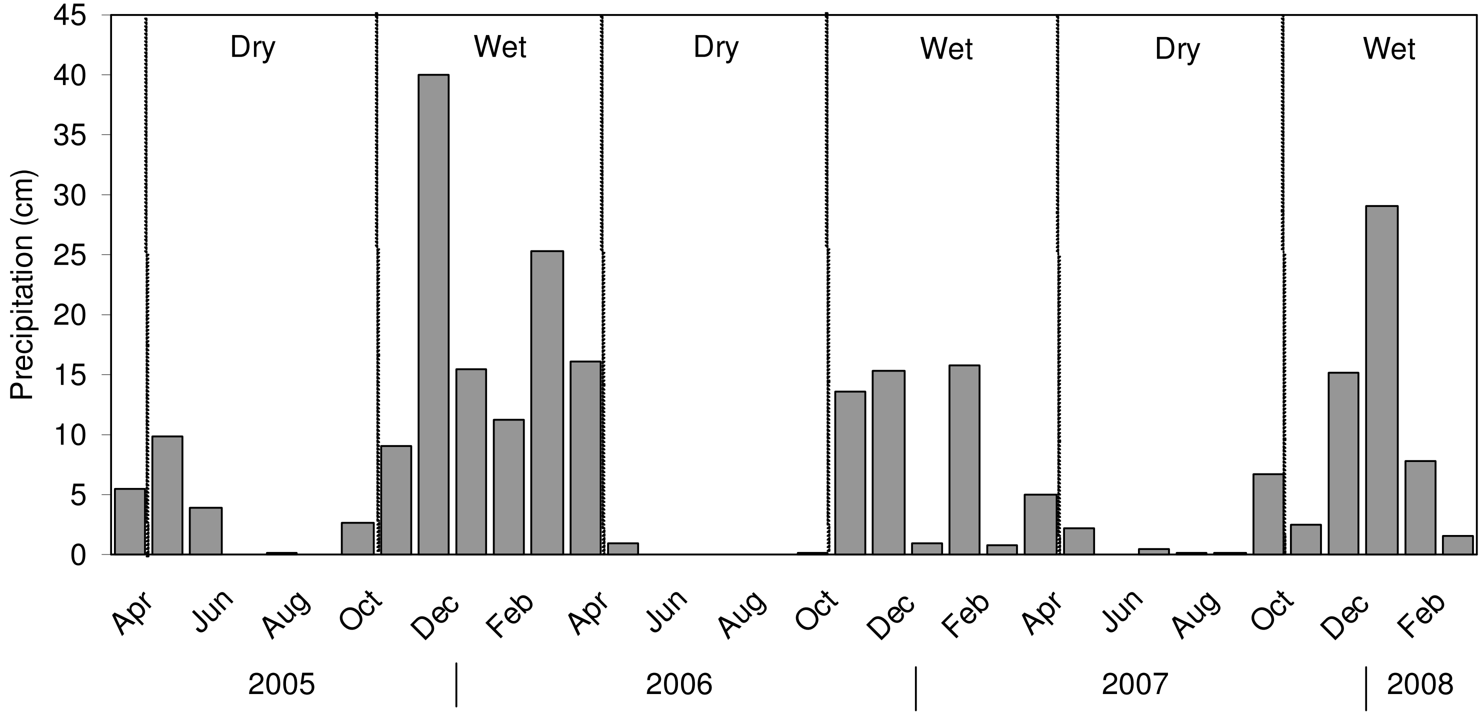

Figure 5. Monthly precipitation (cm) for Point Reyes National Seashore, California, April 2005 – April 2008. Data were compiled from the Bodega Ocean Observing Node, Bodega, CA. Dry seasons were from May to October, and wet seasons were from November to April.

Table 1. Summary of radio-telemetry results by tule elk herd, Point Reyes National Seashore, California, 2005-2008.

Herd	# of group fixes	100% MCP Area (ha)
D Ranch	326	499
Limantour	588	1435
North	663	257
Plateau	566	304
White Gulch	886	338
South	720	465
Population*	1956	3035

*326 group fixes randomly selected from each herd

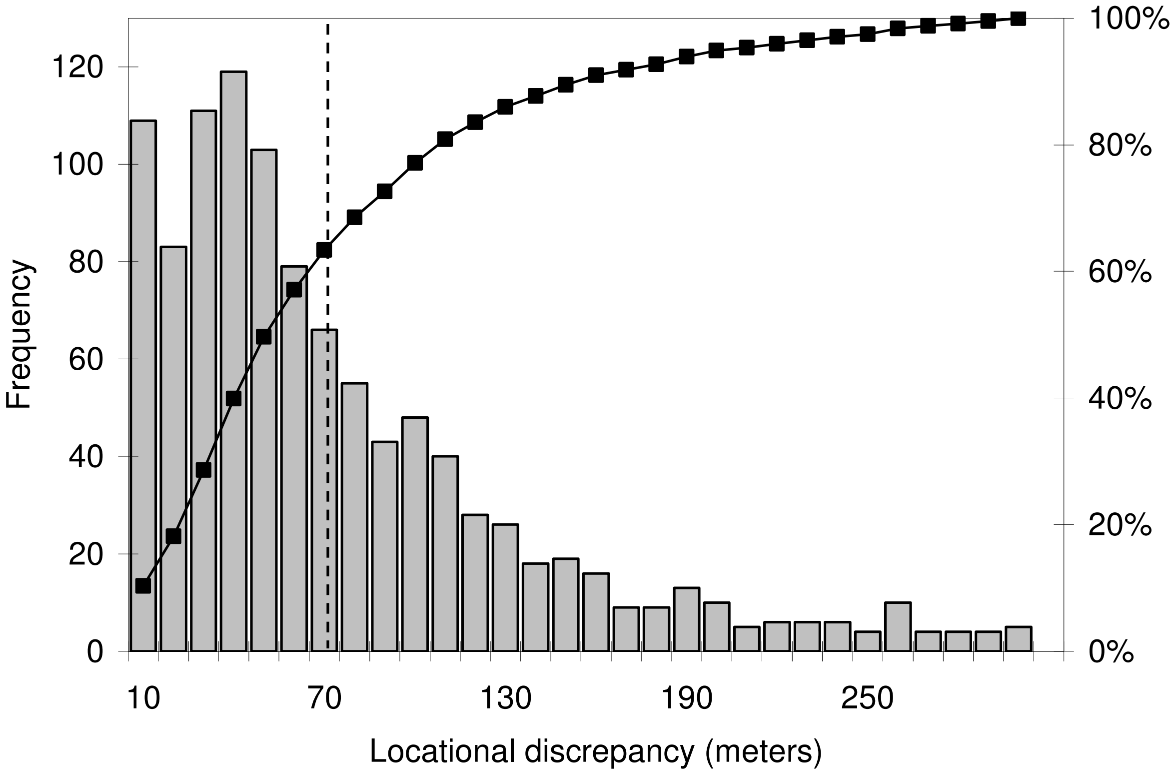

Figure 6. Histogram of the spatial discrepancy (m) between paper-mapped and GPS-recorded fixes of radio-collared tule elk, Point Reyes National Seashore, California, 2005-2008. The dashed line at 70 m indicates the radius that tule elk fixes were buffered for habitat selection analyses.

Table 2. Composition of average available and used tule elk habitats [slope, aspect, solar radiation index (SRI), distance from nearest road, and distance from near trail] at Point Reyes National Seashore, California, 2005 – 2008. Available habitats were quantified using random fixes within herd 100% minimum convex polygons. Used habitats were quantified using fixes of radio-collared tule elk. Vegetation types and aspects are proportions summing to one. Slope is measured in degrees from horizontal. Road and trail distance are in meters. "*NA*" indicates not available within that herd range. Asterisks indicate significant difference ($\alpha = 0.95$) between used and available habitats, according to Kruskal-Wallis chi-square tests.

		Vegetation type			Aspect							
Herd	Avail/Used	Grass	Scrub	Forest	NE	NW	SE	SW	Slope	SRI	Road	Trail
D Ranch	A	0.58	0.39	0.00	0.34	0.04	0.09	0.41	11	0.77	573*	1318
	U	0.66	0.33	0.00	0.35	0.02	0.11	0.40	11	0.78	472*	1264
Limantour	A	0.17*	0.71*	0.08	0.11	0.23	0.23	0.30	13*	0.76	903*	239*
	U	0.27*	0.65*	0.09	0.13	0.24	0.21	0.30	11*	0.77	1138*	272*
North	A	0.27*	0.72*	0.01	0.42	0.19	0.17	0.18	14*	0.72*	*NA*	212*
	U	0.40*	0.60*	0.00	0.44	0.17	0.19	0.16	10*	0.74*	*NA*	160*
Plateau	A	0.44*	0.55*	0.01	0.32	0.16*	0.25	0.24	17*	0.74*	*NA*	373*
	U	0.53*	0.46*	0.01	0.33	0.12*	0.23	0.27	14*	0.75*	*NA*	270*
White Gulch	A	0.46*	0.51*	0.01*	0.28*	0.29*	0.19*	0.17*	14*	0.74	393	641*
	U	0.64*	0.35*	0.01*	0.44*	0.12*	0.27*	0.12*	13*	0.75	747	378*
South	A	0.40*	0.57*	0.02*	0.26*	0.25*	0.18*	0.25	15*	0.74	804*	454*
	U	0.51*	0.49*	0.00*	0.15*	0.53	0.08*	0.16	11*	0.73	236*	571*
Population	A	0.28*	0.63*	0.06*	0.22*	0.19	0.19	0.29*	14*	0.75*	903*	546
	U	0.51*	0.47*	0.02*	0.31*	0.20	0.19	0.23*	12*	0.75*	935*	479

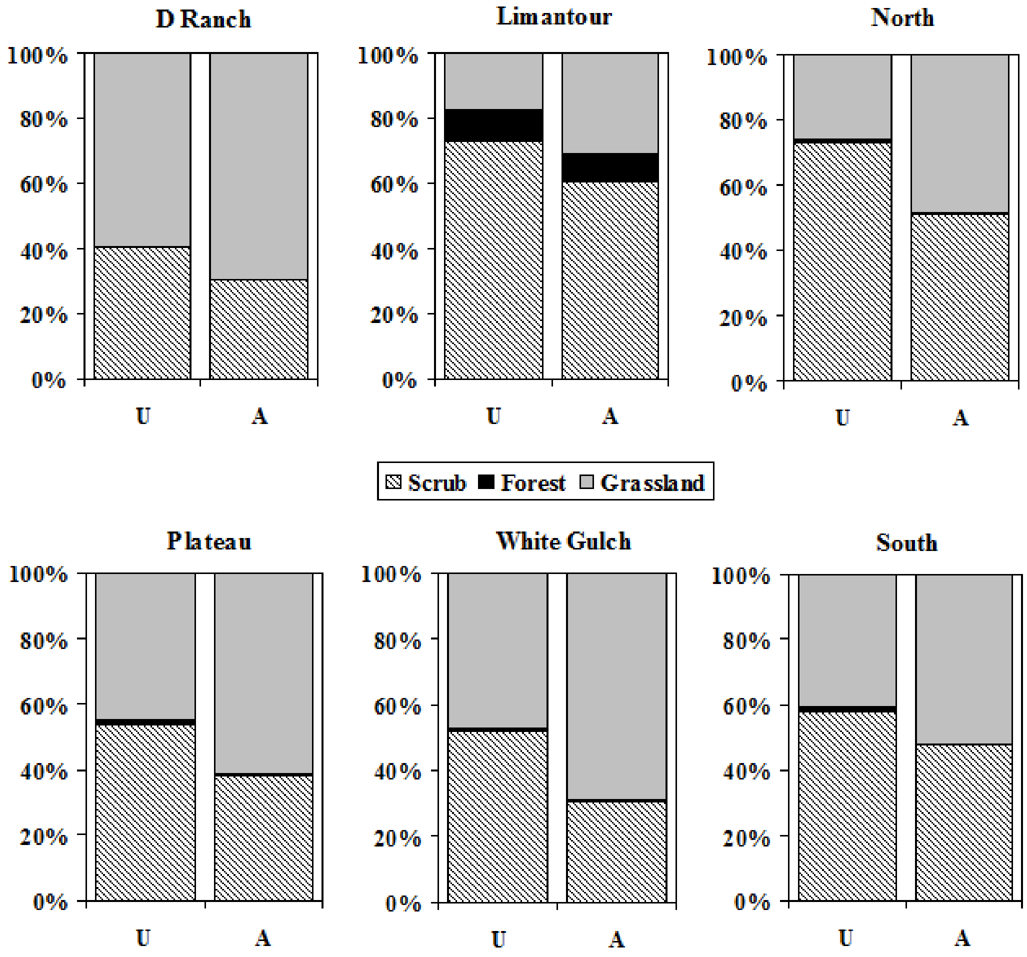

Figure 7. Composition of used (U) and available (A) grassland, forest, and scrub vegetation classes considered for tule elk resource selection function (RSF) modeling at Point Reyes National Seashore, California, 2005 – 2008. Used habitats were defined by fixes of radio-collared tule elk. Available habitats were random fixes within herd 100% minimum convex polygons (MCPs).

Table 3. Comparison of tule elk habitat use during wet (November – April) and dry (May – October) seasons, Point Reyes National Seashore, California, 2005 – 2008. "W" values indicate larger values during the wet season and "D" values indicate larger values during the dry season, according to Kruskal-Wallis chi-squre tests. The number of W/D's indicates statistical significance (p-value $<$ 0.001 is three W/D's, 0.001 $<$ p-value $>$ 0.05 is two W/D's, 0.05 $<$ p-value $>$ 0.10 is one W/D). *NA* indicates that habitat use was not quantified for the herd.

	D Ranch		Limantour		North		Plateau		White Gulch		South		Population	
Coefficent	+/-	*p*-value	+/-	*p*-value	+/-	*p*-value	+/-	*p*-value	+/-	*p*-value	+/-	*p*-value	+/-	*p*-value
Grass	W W	0.03		0.20		0.57	W W W	< 0.001	W	0.09		0.89	W W W	< 0.001
Shrub	D D	0.04	D	0.06		0.79	D D D	< 0.001		0.12		0.75	D D D	< 0.001
Forest		*NA*		0.76		0.18		0.40		0.25		0.68		0.88
Slope		0.31		0.18	D D D	< 0.001	D D D	< 0.001	D D D	< 0.001	D D D	< 0.001	D D D	< 0.001
Elevation	W W	0.00	W W W	< 0.001	W W W	< 0.001	W W W	< 0.001	W W W	< 0.001		0.56	W W W	< 0.001
SRI		0.09		0.84	W W	0.03	W W W	< 0.001	W W W	< 0.001		0.94	W W W	< 0.001
NE aspect		0.11	W W W	< 0.001		0.09		0.10		0.13		0.95		0.35
NW aspect		0.64	D D D	< 0.001		0.96	W W W	< 0.001	D	0.09	W W	0.01		0.11
SE aspect		0.63		0.23	D D	0.01	D D D	< 0.001		0.56	D D D	< 0.001	D D	0.01
SW aspect	D D	0.04		0.41	W W	0.00	W W W	< 0.001	D D	0.00	D D	0.01		0.18
Road	D D	0.01	W W	0.01		*NA*		*NA*	W W	0.01	D D D	< 0.001		0.86
Trail		0.68		0.27	D D D	< 0.001	D D D	< 0.001	D D D	< 0.001	D D D	< 0.001	D D D	< 0.001

Table 4. Kruskal-Wallis chi-square test results (p) for significant differences between habitat types used and available for tule elk at Point Reyes National Seashore, California, 2005-2008. Habitat coefficients with p-value < 0.05 were selected as candidate predictors in RSF models (italicized). “NA” indicates habitat was not available.

	Vegetation class			Aspect							
Herd	Grass	Scrub	Forest	NE	NW	SE	SW	Slope	SRI	Road	Trail
D Ranch	0.03*	0.15	NA	0.59	0.003*	0.005*	0.29	0.18	0.73	< 0.001**	0.057*
Limantour	< 0.001**	0.03*	0.11	0.75	0.009*	0.93	0.17	< 0.001**	0.80	< 0.001**	0.006*
North	< 0.001**	< 0.001**	0.09	0.10	0.24	0.12	0.57	< 0.001**	< 0.001**	NA	< 0.001**
Plateau	< 0.001**	< 0.001**	0.13	0.38	< 0.001**	0.46	0.17	< 0.001**	0.030*	NA	< 0.001**
South	< 0.001**	< 0.001**	< 0.001**	< 0.001**	< 0.001**	< 0.001**	0.08	< 0.001**	0.054*	< 0.001**	0.015*
White Gulch	< 0.001**	< 0.001**	0.04*	< 0.001**	< 0.001**	< 0.001**	< 0.001**	< 0.001**	0.43	0.55	0.002*
Population	< 0.001**	< 0.001**	< 0.001**	< 0.001**	0.59	0.22	< 0.001**	< 0.001**	0.012*	0.035*	0.49

Table 5. Population-level resource selection function (RSF) coefficient estimates for tule elk based on radio telemetry fix data, Point Reyes National Seashore, California, 2005-2008.

Coefficient	Estimate	SE	*p*-value
(Intercept)	-5.710	1.399	< 0.001
Grass	8.509	1.382	< 0.001
Scrub	6.852	1.378	< 0.001
Forest	4.976	1.442	0.001
Slope	-0.035	0.007	< 0.001
SRI	-3.446	0.477	< 0.001
Trail	0.001	< 0.001	< 0.001

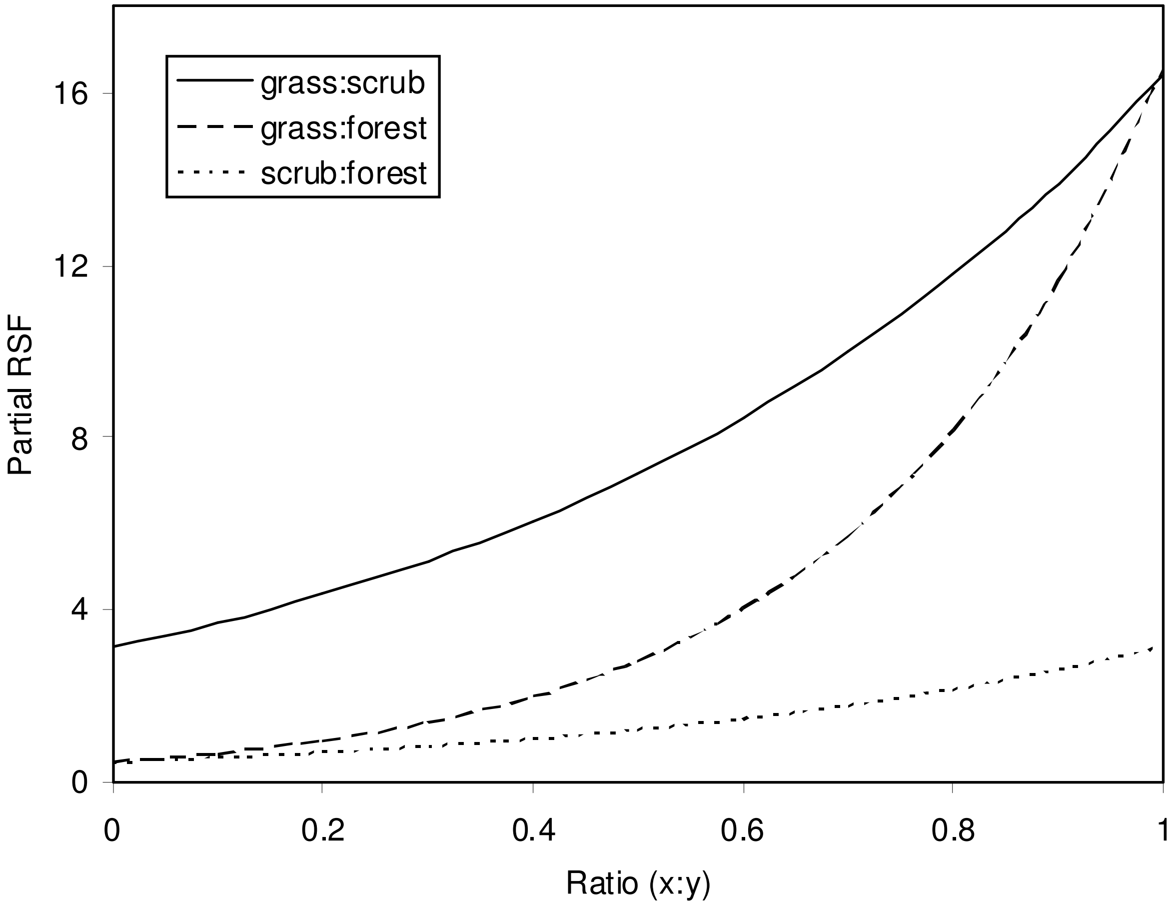

Figure 8. Relative elk selection of grassland, scrub, and forest proportions based the population-level resource selection function (RSF) model, Point Reyes National Seashore, California, 2005-2008. Vegetation proportions were quantified within 70-meter buffered regions. The relative probability of an elk selecting a particular location (RSF values) increased with greater proportions of grass relative to scrub and forest proportions.

Table 6. Herd-level and population-level resource selection function (RSF) models for tule elk herds, Point Reyes National Seashore, California, 2005 – 2008.

Herd	RSF
D Ranch	SE aspect + Road
Limantour	Grass + Scrub + NW aspect + Slope + Road + (Grass*Scrub)+ (Scrub*Road)
North	Grass + Slope
Plateau	NW aspect + Slope + Trail + (NW aspect * Slope)
White Gulch	Grass + Scrub + NE aspect + SE aspect + SW aspect + Slope + Trail + (Scrub*SE aspect) + (Grass*Slope)
South	Grass + Scrub + NW aspect + SE aspect + Slope + Road + (Grass*NW aspect) + (Grass*Scrub)
Population	Grass + Scrub + Forest + Slope + SRI + Trail

Table 7. Distribution of habitat coefficients in herd-level and population-level resource selection function (RSF) models for tule elk at Point Reyes National Seashore, California, 2005-2008. Positive selection is indicated with "+", negative selection with "-". Ranking of selection within vegetation classes and aspect classes (relative size of estimated β) is indicated by the number of signs. "*NA*" indicates habitat was not available.

	Vegetation class				Aspect						
Herd	Grass	Scrub	Forest	NE	NW	SE	SW	Slope	SRI	Road	Trail
D Ranch			NA			+				-	
Limantour	++	+			+			-		-	
North	+							-		NA	
Plateau					-			-		NA	-
South	++	+			+	-		-		+	
White Gulch	+	+		+		++	-	-			-
Population	+++	++	+					-	-		-

Table 8. Assessment of resource selection function (RSF) models by herd and population for tule elk at Point Reyes National Seashore, California, 2005 – 2008. RSF model results were applied to testing data and compared using Spearman rank correlations and linear regression analyses.

	Rank correlation		Regression (expected vs. observed)			
Herd	r_s	p	b_0	b_1	R^2	p
D Ranch	0.479	0.160	0.301	0.301	0.141	0.284
Limantour	0.939	< 0.001	0.007	0.930	0.893	< 0.001
North	0.855	0.003	0.019	0.808	0.764	0.001
Plateau	0.915	< 0.001	0.005	0.952	0.958	< 0.001
South	0.988	< 0.001	-0.002	1.017	0.831	< 0.001
White Gulch	0.988	< 0.001	-0.019	1.188	0.863	< 0.001
Population	0.988	< 0.001	-0.012	1.122	0.980	< 0.001

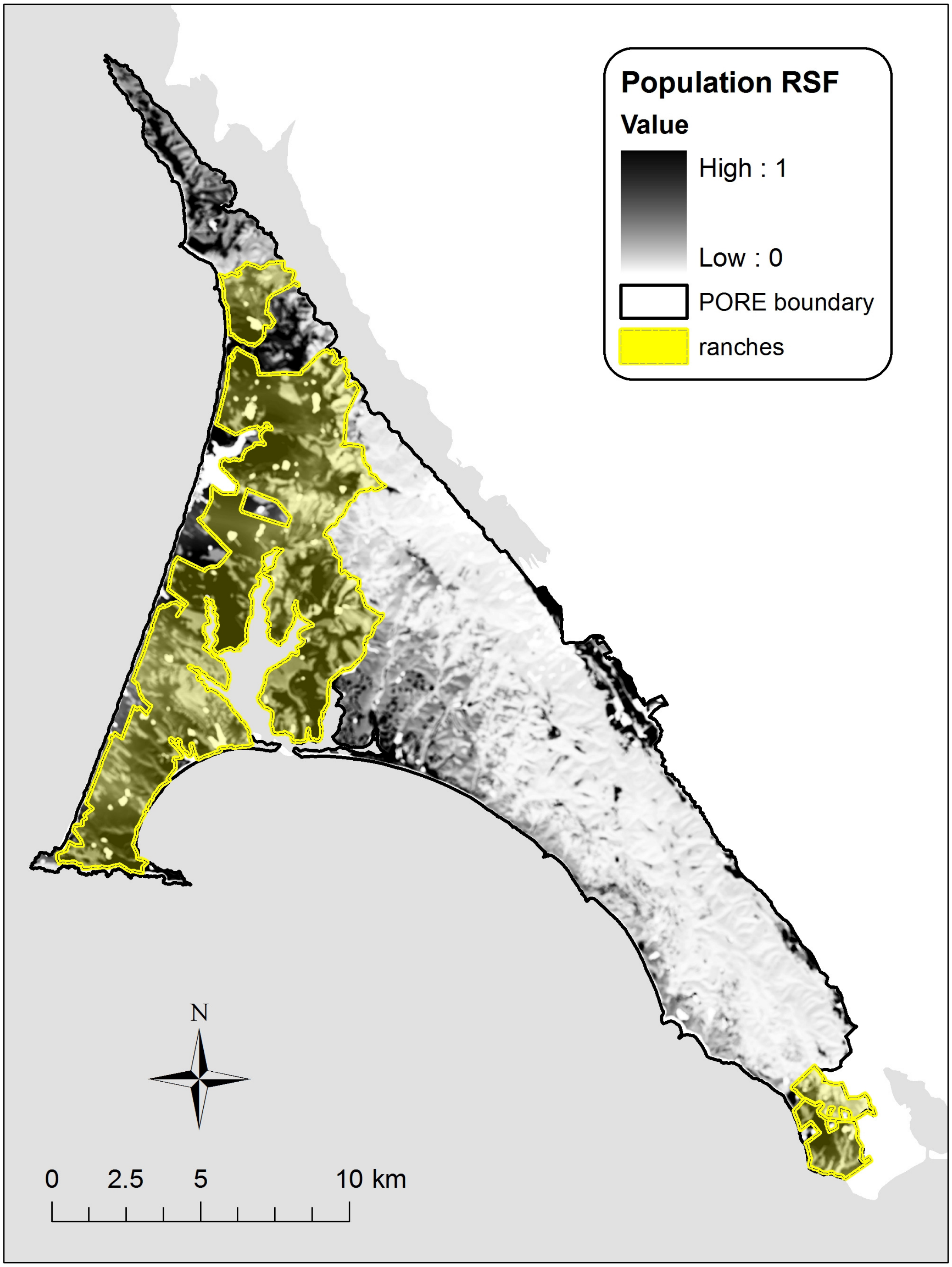

Figure 9. Predicted relative probability of tule elk use within Point Reyes National Seashore, California from binned-RSF values of population-level radio telemetry data, 2005- 2008. Higher RSF value equals greater probability of use. Existing leased cattle ranches within Point Reyes National Seashore, California are in yellow. Areas of high predicted probability of tule elk use overlaps with cattle ranch lands.

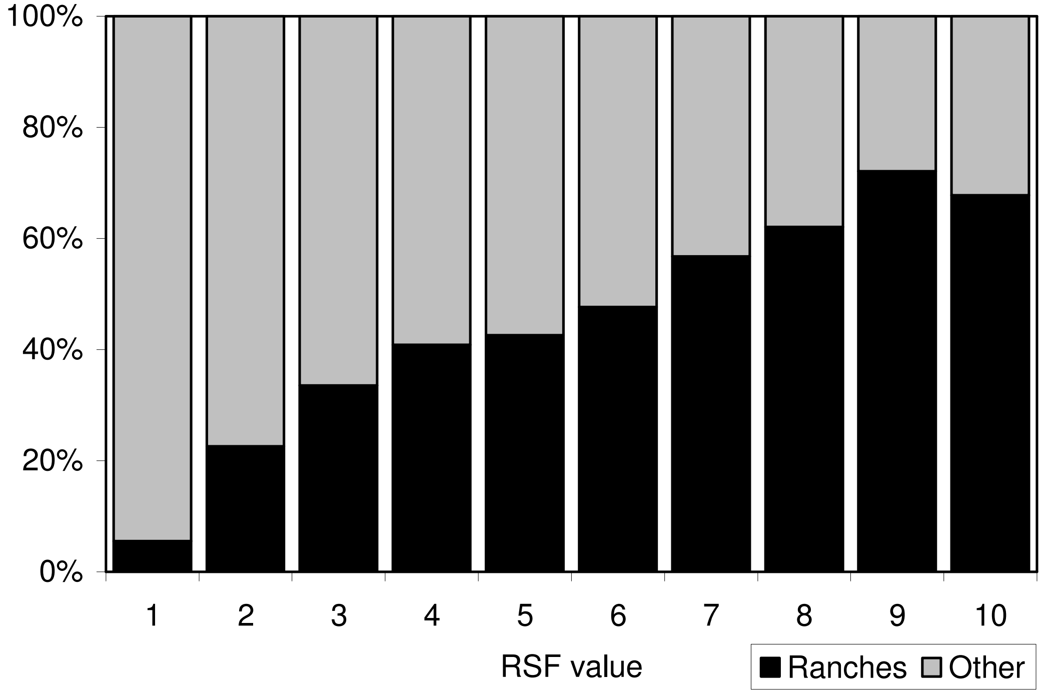

Figure 10. Distribution of the percentage of binned-RSF values for predicted relative probability of use by tule elk on ranchlands versus other habitats at Point Reyes National Seashore, California, 2005 – 2008. 1 = lowest, 10 = highest. Values are based on the most parsimonious population-level RSF model using radio telemetry data. Ranches composed 32% of Pt. Reyes.

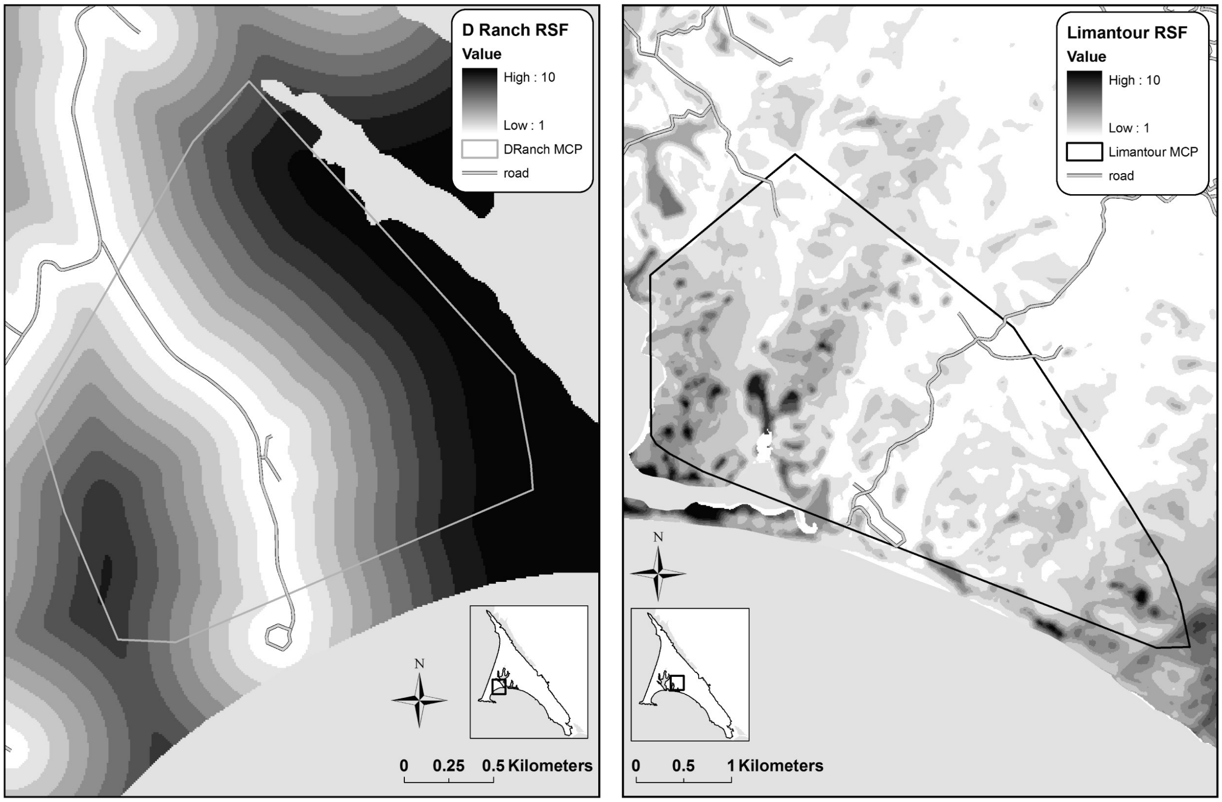

Figure 11. Maps of tule elk binned RSF values using herd-level radio-telemetry data at the D Ranch and Limantour herds, Point Reyes National Seashore, California, 2005 – 2008. Note that the scale of the Limantour map is twice that of other herds.

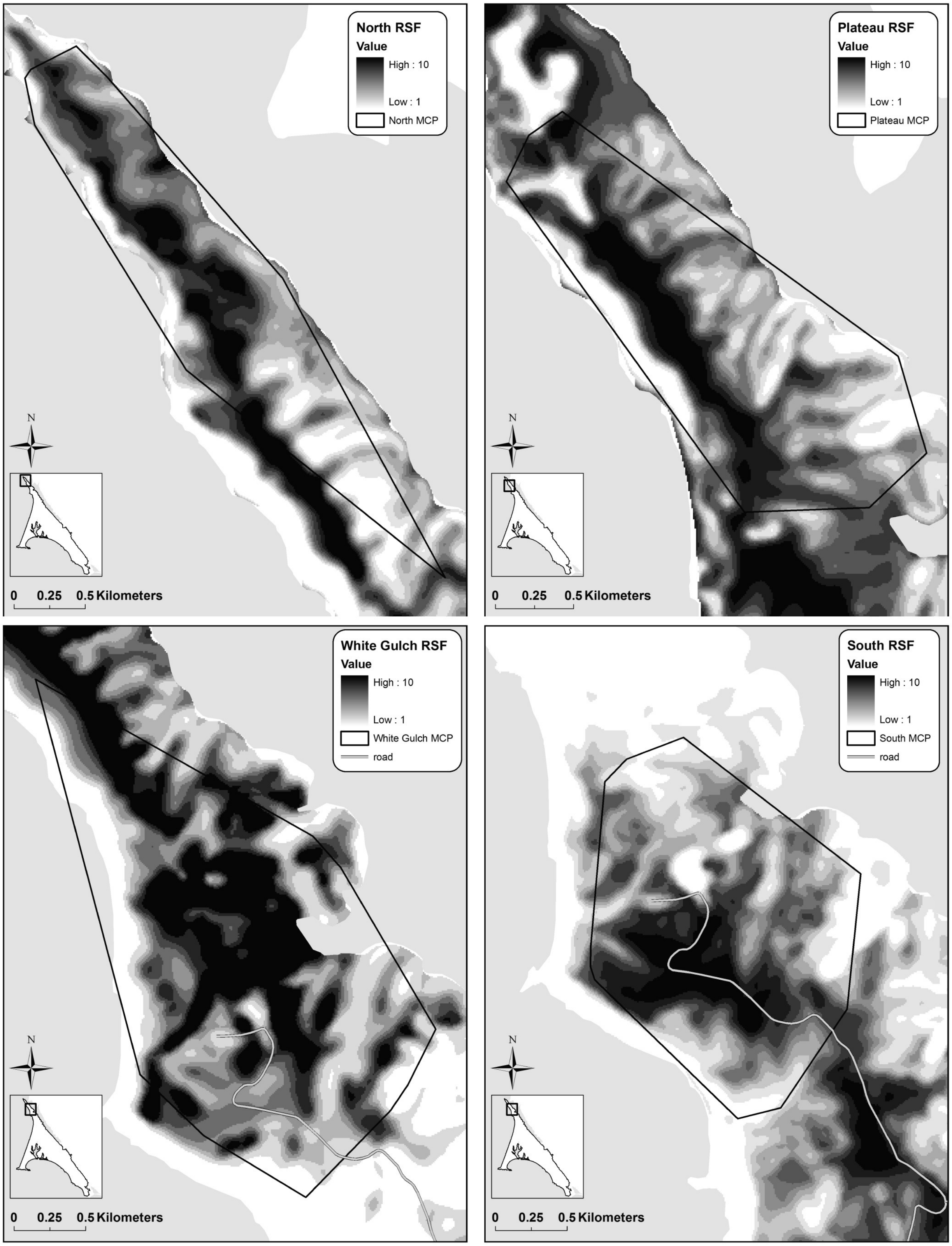

Figure 12. Maps of tule elk binned RSF values using herd-level telemetry data (North, Plateau, White Gulch, and South) at the Tomales Point Elk Reserve, Point Reyes National Seashore, California, 2005 – 2008.

CHAPTER 3

SMALL-SCALE MOVEMENT PATTERNS OF TULE ELK AT POINT REYES NATIONAL SEASHORE, CALIFORNIA

INTRODUCTION

The spatial distributions and movements of wildlife have received a great deal of attention (Schick et al. 2008) because they are central to the field of ecology and have both theoretical and applied importance. The pattern and shape of large herbivore movements are the results of fundamental interactions between landscape structure and individual behavioral decisions. Since movements are influenced by the environment and individual life histories (Wiens et al. 1997), understanding how an animal utilizes its habitats can also give insight into the ecological niche of the species and how changes in environmental factors may affect populations in the future (Turchin 1998). Despite efforts to examine these factors in a wide range of species, small-scale movement behaviors of large herbivores in Mediterranean climates, such as the tule elk (*Cervus elaphus nannodes*) in California, are not well understood (Morales et al. 2005).

Large herbivore movements follow a general pattern, at the small-scale, of repeated short movements in interspaced with longer movements (Morales et al. 2004). This pattern of movement varies temporally in response to scale-dependent biotic and abiotic drivers (Johnson et al. 2002a, Ager et al. 2003, Nams 2005). For many species, patterns of movement are influenced by the distribution of available habitats (Dussault et al. 2005, Morales et al. 2005, de Knegt et al. 2007), climate (Harper 1962), population density and human disturbances. The relative contribution of these factors on tule elk movement is unclear.

The availability and distribution of habitats play a central role in driving the distribution and spatial patterns of animals (Lima and Zollner 1996). Large herbivores, such as elk, adjust their movement speeds relative to habitat quality (Wiens et al. 1993) by slowing in high-value habitats and moving faster in poor quality habitats (Bartumeus et al. 2005, de Knegt et al. 2007). This behavioral strategy likely concentrates search efforts where resources are abundant, thereby increasing foraging efficiency (Marell et al. 2002). In addition to movements speeds, the shape of movement paths have also been associated with habitat quality and heterogeneity (Fryxell et al. 2008). Herbivores generally show more linear movements in habitats with low forage availability and more tortuous movements in habitats containing abundant forage (Etzenhouser et al. 1998, Klaassen et al. 2006). Increased habitat heterogeneity along movement paths generally leads to slower and more tortuous movements because of increased foraging search efforts (de Knegt et al. 2007), increased predation risks (Anderson et al. 2008) and greater energy required for movement (eg. patchy scrub/grassland habitats) (Johnson et al. 2002b).

Climate is known to influence large-scale annual migrations and habitat selection patterns, but the effects of local, small-scale weather on tule elk movement patterns are unclear. Cervids exhibit reduced activity levels and more tortuous movements during precipitation (Kamler et al. 2007, Webb et al. 2009). Wind can influence elk movements by decreasing the effective temperature of their environment, and reducing their ability to hear threats (Skovlin et al. 2002). High winds can decrease elk activity (Harper 1971), and cause them vacant high quality forage habitats to seek shelter (Beall 1974, Glushkov 1976). Large herbivores in northern climates adjust their movement patterns in response to seasonal limitations in forage

(Vander Wal and Rodgers 2009), but little is known about how annual movement patterns of large herbivores in Mediterranean climates, such coastal California.

Population density affects movement behaviors of many species (Clobert et al. 2009, Mobaek et al. 2009). Individuals at high density experience intraspecific competition for resources, which can simulate large-scale movements in the form of migration and dispersal (Taylor and Taylor 1977, Hawkes 2009). The role of population density in regulating small-scale movements of species such as elk is less understood, partly because long-term data on a single population or multiple comparable populations at different densities are rare.

As human developments continue to expand into wildlife habitat, it is increasingly important to understand the relationship between human-caused disturbances and wildlife populations. Movements of species are affected by human disturbances, which can have cascading effects on their population distributions, population dynamics and energetics (Hayward and Hayward 2009, Li et al. 2009, St. Clair and Forrest 2009). For elk specifically, road and trail traffic can lead to increased activity levels (Naylor et al. 2009) that cause elevated physiological stress levels (Creel et al. 2002) and lower survival rates and reproductive success (Sapolsky 1992). Understanding the effects of roads and trails on movement behaviors is especially important when examining expanding wildlife populations near urban areas.

Six distinct tule elk herds exist at Point Reyes National Seashore (Pt. Reyes), California, at varying densities and habitat configurations. The goals of this study were to quantify 1) the hourly and daily movements of tule elk at Pt. Reyes and 2) the influence of herd density, habitat availability and heterogeneity, human development (trail and road distance) and weather (wind and rain) on hourly and daily tule elk movements. Based on our understanding of large herbivore movement dynamics, I had a number of initial predictions. I predicted that elk movement would be elevated near roads and trails where visitors are most abundant. Since tule elk at Pt. Reyes live in a heterogeneous landscape composed of patchy habitats of varying quality (Gogan 1986), I expected elk to select high quality habitat through movement decisions at multiple temporal scales (Fryxell et al. 2008). Specifically, I expected that Pt. Reyes elk would move slower through high quality, heterogeneous habitat and movement speed would be inversely related to habitat heterogeneity. I predicted that Pt. Reyes elk herds at higher densities would move farther on hourly and daily scales compared to lower density herds. Finally, I predicted that elk at Pt. Reyes would decrease their hourly and daily movement distances during rainy and windy conditions.

METHODS

GPS

Two cow elk were immobilized using helicopter net-gunning (Leading Edge Aviation LLC, Lewiston, ID 83501) between January 10, 2005 and January 12, 2005. Net-gunned elk were hobbled, blindfolded, and given a low-dose nasal sedative of xylazine and an intragingival injection of lidocaine (Swift et al. 2002, Cattet et al. 2004). Eight additional cow elk were chemically-immobilized by ground darting (Pneu-dart, Williamsport, PA 17701) with medetomidine and ketamine between 2005 and 2007 (Bookhout 1996). All captured elk were fitted with a uniquely numbered ear tag (NASCO, Modesto, CA 95352) and a mortality-sensing Global Positioning Satellite (GPS) collar (Telonics Inc., Mesa, AZ 85204).

GPS collars were programmed to record a point location ("fix") every hour and to release near the end of the collars' battery life (10 – 12 months after deployment). Time and date were recorded at each fix. A percent dilution of precision (PDOP) value was recorded at each fix, which is a measurement of the geometric strength of satellite locations when a fix is attempted and can be used to gauge the precision of the GPS fix (D'Eon and Delparte 2005). Data were stored on the collars and downloaded after the collar was recovered ("store-on-board" GPS collars, Telonics TGW-3600), or downloaded remotely via a wireless modem to a nearby laptop computer in the field ("spread spectrum" GPS collars, TGW-3690).

GPS fixes were entered into a Geographic Information System (GIS) (ArcGIS 9.3), and stored in Universal Transverse Mercator (UTM) North American Datum (NAD) 1983 projection. Obvious spatially outlying fixes and two dimensional fixes with PDOP > 5 (D'Eon and Delparte 2005) were censored. Fixes collected within a week of capture were censored to avoid biased movement and behavioral data from capture-related stress (Cattet et al. 2008).

I calculated the Euclidian distance between consecutive hourly fixes (hourly step lengths) (Figure 1) and the sum of all hourly step lengths within a day (daily step lengths) using Hawth's Tools (Beyer 2006) in ArcGIS 9.3 (ESRI 2008). I estimated hourly step lengths for missing and censored fixes by dividing the missing time interval by the next available step length. Daily step lengths that included less than 23 hourly step lengths were removed from the analysis.

Predictor Variables

Based on past studies of large herbivore movement patterns (Ager et al. 2003, de Knegt et al. 2007, Fahrig 2007, Anderson et al. 2008), I selected 16 *a priori* predictor variables to quantify elk movement at the hourly and daily scale (Table 1). Grassland abundance and variation was selected as a measure of habitat quality and heterogeneity, based on previous work on elk resource selection patterns at Pt. Reyes (Chapter 2).

I obtained mean hourly wind speed and total hourly precipitation for the study period from the Bodega Oceanographic Observing Node (National Oceanographic and Atmospheric Administration, www.srrb.noaa.gov/ highlights/sunrise/ sunrise.html), and linked these data to associated hourly GPS step length data. Missing hourly weather data due to weather station malfunctions were excluded from the analysis (< 5%). I calculated mean daily wind and total daily precipitation using hourly weather data.

I quantified spatial predictors within a Geographic Information System (GIS) (ESRI 2008). I derived slope (degrees from horizontal) from a 1/3 Arc-second USGS National Elevation Dataset (NED) layer (10-m pixels, http://seamless.usgs.gov) using 3D Analyst Tool in ArcView 9.3 (ESRI 2008). I used a vector-based GIS vegetation coverage (http://www.nps.gov/gis/) jointly produced by the National Park Service (NPS) and the U.S. Geological Survey (USGS) to quantify grassland composition (Moritsch et al. 2003). The layer was created by interpreting 1:24,000 color aerial photographs taken in 1994, and utilized a hierarchical classification system. For the purposes of this study, I selected the "life form" classification level because of its ecological relevance to elk and overall thematic accuracy (84%). I isolated the grassland habitat category from the vegetation layer, and converted it to a binary 10-m pixel size raster layer. Vector layers depicting road and trail locations at Pt. Reyes were created by the NPS by interpreting road locations from Digital Raster Graphics (DRGs) (http://www.nps.gov/gis/). I used the road and trail layers to create 10-m pixel raster layers of distance (m) to road and trails using the NEAR function in ArcGIS 9.2 (ESRI 2006). I clipped all layers to the boundary of Pt. Reyes, which I defined as the study area. All layers were stored in the Universal Transverse Mercator (UTM) coordinate system, North American Datum 1983.

I quantified elk density by herd with data on radio telemetry collared cow elk (Chapters 2 and 3). I first estimated herd sizes by summing daily group counts within herds and selected the highest daily herd count for each month. I then averaged the monthly high herd counts annually across the study period for estimates of annual herd sizes. I combined elk group fixes within a herd for each study year and created 90% fixed kernel annual herd ranges using the Animal Movement Extension (Hooge and Eichenlaub 2002) in ArcView 3.2 (ESRI 1996). I calculated the smoothing parameter (h) individually for each elk using the least squared cross-validation (LSCV) method (Sain et al. 1994). I quantified grassland area within annual elk herd ranges by clipping kernel herd ranges to the grassland GIS layer. I divided annual herd sizes by grass availability to determine the number of elk per km^2 of grassland ("herd density").

To quantify the mean values for spatial predictors along hourly and daily step lengths, I buffered step length paths by 100 m and calculated length-weighted means (LWM) of the spatial predictors along the step length paths using Hawth's Tools (Beyer 2006). LWM ($\bar{x}$) was defined as:

$$\bar{x} = \sum_{1}^{i} [\frac{(l_i v_i)}{L}],$$

where l is the length of the path within the raster pixel, v is the value of the raster, and L is the step length.

To quantify the variation in spatial predictors along hourly and daily step lengths, I buffered step length paths by 100 m and calculated length-weighted standard deviations (LWSD) of the spatial predictors along the step length paths using Hawth's Tools (Beyer 2006). LWSD was defined as:

$$\delta = \sqrt{\frac{1}{n-1}\sum_{1}^{i}(x_i - \bar{x})^2(\frac{l_i}{L})},$$

where n is the number of segments, x_i is the raster cell value of segment i, $\bar{x}$ is the length-weighted mean, l_i is the length of segment i, and L is the total line length.

To quantify the shape of movements across the landscape, I calculated the turning angle of the hourly step lengths and the fractal dimension (FD) of the daily step lengths. Turning angles were defined as the angle (0 - 180 degrees) created between current and previous hourly step lengths (Figure 1). FD was defined as:

$$FD = \frac{\log(n)}{[\log(n) + \log(d + L)]},$$

where n is the number of hourly step lengths that make up the daily step length (23), d is the distance between the start and end points of the daily step length, and L is the total length of the daily step length. Larger turning angles and FD values indicated more tortuous movement path at the hourly and daily scales, respectively.

Movement Models

I assessed statistical independence between candidate predictor variables using a Spearman rank correlation coefficient matrix at the hourly and daily scales. Pairs of predictor coefficients with significant correlation ($r_s > 0.56$, p-value < 0.05) were examined independently in respective movement models (Zar 1998). I quantified the relationship between the response (hourly and daily step lengths) and predictor variables using generalized linear regression analyses. Hourly step lengths were log-transformed to achieve normality. I employed backwards stepwise selection and evaluated competing models using Akaike's Information Criteria (AIC) (Burnham and Anderson 2002). I evaluated ecologically plausible interactions between predictors in the most parsimonious model. All statistical analyses were performed in R (R Core Development Team, 2008).

RESULTS

Ten adult female elk were captured and fitted with GPS collars (Table 2) between January 17, 2005 and October 10, 2007. One adult female elk GPS-collared at Tomales in 2005 was re-captured in 2006 (ID = 477). Multiple attempts were made to capture additional elk from the D Ranch herd but efforts were unsuccessful due to the wariness of this herd.

Individual elk were GPS-collared for an average of 303 days (SE = 22) and for a total of 3,032 elk days. One (10%) GPS-collared elk (ID = 584) died 354 days after it was captured. The mean number of usable fixes recorded per elk was 7,114 (SE = 524.77), with a mean GPS fix success rate of 97.7% (SE = 0.43). After censoring, 72,771 GPS fixes were included in hourly step length analyses. I censored 968 daily step lengths with less than 23 hourly step lengths, leaving 1,982 usable daily step lengths.

Hourly movements

The median distance between consecutive hourly elk step lengths was 45 m, and the distribution of step lengths was positively skewed (Q1 = 12 m, Q3 = 120 m). Median hourly step lengths varied by herd (Figure 2) from 29 m at the Plateau herd to 55 m at the D Ranch herd. Collared elk movements varied by time of day, peaking in the morning (06:00) and evening (17:00) hours (Figure 3). The diel pattern of hourly step lengths was fairly consistent between herds, although crepuscular peaks in step lengths were most pronounced at the D Ranch herd, where grassland was most abundant (Figure 4).

Daily Movements

The overall median daily elk step length was 2,212 m, but the distribution of daily step lengths was positively skewed (Q1 = 1,655 m, Q3 = 2,902 m). Mean daily elk step lengths were longest at D Ranch (3,092) and shortest at Plateau (1,680 m) (Figure 5). Elk generally exhibited an annual cycle of daily step lengths that peaked in late winter/ early spring ($\text{median}_{\text{march}} = 2{,}672$ m), and were shortest in the fall ($\text{median}_{\text{october}} = 1{,}591$ m) (Figure 6).

Movement Models

Spearman rank correlation coefficient tests revealed little overall correlation between candidate predictor coefficients (Table 3). I found no statistically significant (p-value < 0.05) correlation between any predictor coefficient at the hourly scale and I found significant correlation between trail and road distance ($r_s = 0.57$), and trail distance and trail LWSD ($r_s = 0.69$) at the daily scale. Trail distance was least correlated with daily step length, therefore I excluded it from candidate models.

Hourly Movement- The most parsimonious model for hourly step length included all possible candidate predictors except rain, plus an interaction between road and trail distance (Table 4). This model was strongly selected over all other candidate models (Akaike's weight = 1), and explained 33% of the variation in hourly elk step lengths ($R^2 = 0.33$) (Table 5).

The strongest predictor of elk hourly movement distances from the most parsimonious model was wind speed. Elk moved approximately 5 m further every hour for every 10 km/h increase in wind speed ($\beta_{wind} = 0.54$, $p < 0.001$) (Figure 7). Hourly movements were correlated with distances, and variations in distance (LWSD), to roads and trails. Elk increased their hourly movements when traveling perpendicular to trails ($\beta_{trailLWSD} = 14.73$, $p < 0.001$) and decreased their hourly movements when traveling perpendicular to roads ($\beta_{roadLWSD} = -0.29$, $p < 0.001$) (Figure 8). Elk also had shorter hourly movements when far from trails, but this response was amplified when elk were also far from roads ($\beta_{road*trail} = -0.00002$, $p < 0.001$, Figure 9). Greater abundance and less variation in grass habitat was associated with shorter hourly movements ($\beta_{\text{grass}} = -16.68$, $p < 0.001$; $\beta_{grassLWSD} = 2{,}850$, $p < 0.001$; Figure 10). Similarly, hourly elk step lengths decreased approximately 8 m for every 10 degrees of increase in slope ($\beta_{slope} = -0.81$, $p < 0.001$) (Figure 11). Elk had straighter hourly movement paths when traveling further distances ($\beta_{turnAngle} = -0.20$, $p < 0.001$, Figure 12). Hourly elk step lengths were shorter at higher herd densities ($\beta_{density} = -2.2$, $p < 0.001$, Figure 13).

Daily Movement- The most parsimonious model for daily elk step length included month, herd, slope and LWSD, trail LWSD, wind, grass LWSD and road LWSD as candidate predictors (Table 6). This model was supported over all other candidate models (Akaike's weight = 0.62) and explained 39% of the variation in daily step length ($R^2 = 0.39$, Table 7). Grass, rain, herd density, fractal dimension, trail distance and road distance were not significant predictors of elk daily step length and were excluded from the best model.

According to the most parsimonious model, month was the strongest predictor coefficient of daily elk step length. Daily step lengths were predicted to significantly increase during March and July, and decrease from September to December compared to the rest of the year. The model predicted that daily step length varied by herd. Daily elk step lengths were also predicted to decrease over steeper slopes ($\beta_{slope} = -27.56$, $p < 0.001$) and in habitat with greater variation in topographic variation ($\beta_{slope\,\text{LWSD}} = -1854.74$, $p < 0.001$, Figure 14). Elk had longer daily step lengths in habitat with greater variation in road ($\beta_{roadLWSD} = 40.01$, $p < 0.001$) and trail distance ($\beta_{trailLWSD} = 37.86$, $p < 0.001$, Figure 15), which suggests that elk move faster when traveling perpendicular to road and trails versus parallel to roads and trails. Elk step lengths also increased with stronger average daily wind speed ($\beta_{wind} = 15.87$, $p < 0.001$, Figure 16). Finally, increased habitat heterogeneity was associated with shorter hourly elk movements ($\beta_{grassLWSD} = -24{,}015.94$, $p < 0.001$, Figure 17).

DISCUSSION

The goals of this study were to quantify the hourly and daily movements of tule elk at Pt. Reyes, and to determine the influence of herd density, habitat availability and heterogeneity, human development and weather on elk movement patterns. I found that elk moved a median distance of 45 m / hour and 2,122 m / day. Movement speeds varied among herds. Hourly movements of elk were affected by wind speed, slope, roads and trails and herd density. Daily movements of elk were affected by the time of year, wind, roads and trails and habitat heterogeneity.

Tule elk at Pt. Reyes displayed cycles in their hourly and daily movements, similar to other populations of elk (Green and Bear 1990, Kie et al. 2005, Olsson et al. 2007). Pt. Reyes elk increased their movements during the morning and evening hours. Elk did not remain stationary at night as previously assumed (Howell et al. 2002). Instead, diurnal and nocturnal movement distances were similar, indicating that the elk were moving and likely foraging at night. However, results from this study and others (Ager et al. 2003) suggest that although movements distance may be the similar between day and night elk, habitat use differs, possibly due to human avoidance during the day. Future research examining elk habitat selection should incorporate night-time data if possible or state the limitations of a day-time only dataset.

Elk movements at Pt. Reyes were longest during wet spring months and shortest during the dry fall months, and were generally correlated with annual grass senescence and selective pressures to conserve energy. Seasonal changes in daily elk movements have been observed elsewhere (Collins et al. 1978, Ager et al. 2003), and are likely dictated by the phenology of preferred forage (Gogan 1986). Herding behavior by rutting bull elk may have also been responsible for reducing cow elk movements by keeping cow groups spatially constrained to more easily defendable sub-regions within their annual home range. Increased movements during the spring season corresponded with elk calving (Chapter 5) and may have been related to parturition behavior. Daily movements by maternal elk can increase two-fold compared to barren elk during the pre-partum period (Vore and Schmidt 2001). Five of the 10 GPS-collared elk successfully calved during this study. Given the role of elk in regulating ecosystem processes, seasonal changes in elk movements like those observed in this study may have widespread effects on vegetative and nitrogen distributions across the landscape (Schoenecker et al. 2004).

Tule elk movement distances at Pt. Reyes were influenced by the abundance of and variation in grassland habitat. At the hourly scale, elk at Pt. Reyes slowed down in areas with high proportions of homogeneous grassland habitat, as predicted. Large herbivores slow their movements and spend more time in areas with greater forage availability, and pass quickly through low quality habitat or areas of high predation risk (Zollner and Lima 2005). Since grassland habitats held the majority of high quality forage for elk at Pt. Reyes (Roberts 2000), the observed shorter movements were likely associated with increased feeding behavior. Hourly movements likely captured small-scale patch selection related to foraging behavior. At the daily scale, Pt. Reyes elk movements were unaffected by grassland availability but elk slowed in heterogeneous habitat. Although this finding is contrary to my predictions, and previous study results (McIntyre and Wiens 1999), elk commonly exhibit multiple modes of movement over different spatiotemporal scales that are influenced by their associated motivational goals at each scale (Fryxell et al. 2008). Daily movements by elk at Pt. Reyes were less likely related to fine level foraging decisions and more likely affected by course level needs such as energy conservation and threat avoidance. Heterogeneous habitats at Pt. Reyes mainly consisted of a mixture of grassland and coyote brush that would have presented elk with additional obstacles when traveling, so by decreasing their daily movements in these habitats, elk may have conserved energy. Additionally, heterogeneous habitats of Pt. Reyes limited field of view and provided more hiding habitat which might have increased the cautiousness of elk and caused them to slow. Habitat heterogeneity can affect the large-scale distributions of large mammals (Clutton-Brock and Harvey 1978, Kie et al. 2002), which are the sum of all movements across the landscape during a given period. This study is one of the first to illustrate this relationship at smaller scales.

Topography influenced elk movements at Pt. Reyes at both the hourly and daily scale. Elk movements decreased in steeper terrain, as initially predicted, possibility because steeper slopes presented elk with added energetic demands the energetic cost of traveling upslope has been estimated to be over three-times that of traveling on flat terrain for elk (Parker et al. 1984), so Pt. Reyes elk may be reducing the energetic costs of travel by adjusting their movement speeds relative to topography. In Oregon, elk selected movement paths parallel to hillsides but overall movement distances were unaffected by topography (Kie et al. 2005). Traveling parallel to slopes may not be as efficient for Pt. Reyes elk because the landscape consists of nonlinear, rolling hills and numerous small valleys, although I did not quantify this specifically. Pt. Reyes elk reduced daily movements when traveling in habitats with greater topographic variation, further supporting the energy conservation hypothesis. Steeper terrain may limit the ability of elk to detect potential threats by obstructing their field of view, which may lead to more cautious and slower movements.

Elk at Pt. Reyes increased hourly and daily movements during windy conditions, as predicted. The effects of wind on small-scale ungulate behavior are not well understood, but reductions in movement from wind have been observed (Harper 1971, Beall 1974). Interest in wind effects on large herbivore spatial usage patterns has focused on thermal constraints (Merrill 1991) and insect avoidance (Mooring et al. 2003, Skarin et al. 2004), but these factors were not likely regulators of habitat use at Pt. Reyes. Wind can cause large herbivores to become hyper-vigilant to predation pressure (de Boer et al. 2004) and can lead to physiological reactions such as a faster heart rate, which is often correlated with greater movement and energy expenditure (Theil et al. 2004). High wind and changes in atmospheric pressure can cause elk herds to vacate prime feeding areas (Glushkov 1976), suggesting that elk avoid high winds if possible. It is likely that the increased Pt. Reyes elk movements during windy conditions were due to heightened predator vigilance because of olfactory deprivation. Although Pt. Reyes elk appeared more visually agitated, initiated flight from researchers at a greater distance, and fled for longer distances during windy conditions than during calm conditions, this was not specifically quantified as part of this study. Additionally, high winds at Pt. Reyes were often coupled with fog, which would have compounded sensory loss effects.

Contrary to my predictions, I found no evidence that precipitation affected elk movements at either the hourly or daily scale. I did not observe any noticeable behavioral reaction of elk to rain. Precipitation can play an important indirect role in the habitat selection and population regulation of elk by initiating rapid plant growth and increasing forage nutritional value (Coughenour and Singer 1996). Although precipitation can increase the range and movements (Bello et al. 2004) of ungulates at annual (Daleszczyk et al. 2007) and seasonal (Corp et al. 1998) scales, the effects of precipitation on hourly and daily movements of elk had not been quantified prior to this study. Unlike snow in seasonal northern environments that can physically restrict movements (Kamler et al. 2007) and reduce foraging efficiency, rain appeared to have little to no immediate impact on small-scale elk movements in Mediterranean climates. Additional research on the effects of precipitation on ungulate movements is needed. I recommend examining multiple temporal scales because a relationship may exist at a different scale than quantified in this study. Delayed behavioral responses to rain (week to month scale) due to changes in forage distributions and quality following rain events may also exist. The relationship between abiotic factors and animal behavior may be increasingly important and dynamic, especially given predicted future changes in the global climate.

Elk movements at Pt. Reyes increased near roads and trails, as predicted (Gagnon et al. 2007, Jiang et al. 2009). Roads and trails affect the behavior of large herbivores (Rowland et al. 2000, Rowland et al. 2004, Wisdom et al. 2004) and influence the abundance and dynamics of wildlife populations (Cole et al. 1997, Fahrig and Rytwinski 2009). Off-road recreation such as hiking and horseback riding can substantially increase elk movements and decrease feeding and resting (Naylor et al. 2009). My models supported these findings but also identified an interactive effect between trail and road proximity on elk movements: elk close to roads exhibited long hourly movements regardless of trail distance but those further from roads increased their movements only when near trails. Therefore, when considering the effects of a road/trail on elk movements, one must take into consideration the proximity of other nearby roads/trails. Increased activity and avoidance of humans can have a cumulative and long-term effects on body condition (Preisler et al. 2006), which can effect survival and reproductive potential. Hikers and horseback riders were the primary sources of human disturbance to elk at Pt. Reyes, although poaching may also be occurring (Gates, personal communication) which could have an effect on elk movement similar to natural predation (Proffitt et al. 2009). I observed that visitor traffic on Pt. Reyes trails decreased with increasing distance from the trailhead, suggesting that elk herds further from trailheads are less likely to be exposed to visitors than herds closer to trailheads. Previous studies have found that behavioral changes due to humans can depend on the relative abundance of visitors along travel corridors (Clair and Forrest 2009), but this may be the first study that quantifies a spatial gradient in the behavioral effect of trails and roads on elk movements.

The distance that Pt. Reyes elk traveled daily depended on the orientation of their movements relative to roads and trails. Elk increased their daily movements when traveling perpendicular to or across roadways and decreased their movements when moving parallel to roads. Radio telemetry data supported this conclusion: instrumented elk were generally found over one km to either side of the road bisecting the Limantour herd's home range and road crossing events were uncommon and occurred rapidly (< 24 hours). Elk in other herds were usually observed foraging at least 200 m from the nearest road. These findings further support the conclusion that roads substantially affect elk movements at Pt. Reyes.

I predicted that elk would travel straighter paths during long distance movements and more tortuous paths during shorter movements; my results supported this prediction at the hourly scale but not the daily scale. Shorter hourly step lengths were correlated with greater turning angle, indicating a relationship at the hourly scale. However, I found no correlation between daily step lengths and fractal dimensions, suggesting movement distance and shape were unrelated at the daily scale. Animal behaviors at the foraging scale are often characterized by short tortuous movements associated with feeding and resting, followed by longer movements to a new patch (Kareiva and Odell 1987, Viswanathan et al. 1996, Bartumeus et al. 2005). Elk at Pt. Reyes exhibited this pattern at the hourly scale, where foraging behaviors are most apparent.

The habitat use patterns of elk may relate to the shape complexity of elk hourly movements at Pt. Reyes. Elk habitat use is not be directed by residency time but by elk frequently returning to the same areas over time (Anderson et al. 2008). This may explain why shorter hourly movements of Pt. Reyes elk were generally associated with an increased tendency for an elk to return to the previous fix (less linear movement), but the shape complexity of larger scale daily movement paths are unrelated to daily movement distances. Pt. Reyes elk often revisited sites every few days but seldom remained in the same foraging patch for more than a few hours. By allowing plants to recover between foraging bouts, this behavior may benefit the population by diluting grazing intensity and promoting primary productivity and nitrogen cycling (Schoenecker et al. 2004).

Elk at Pt. Reyes moved shorter hourly distances in higher density herds but daily movement distances were unrelated to density, suggesting that herd density affected elk movements only at small temporal scales. These results partially supported my prediction that higher density herds of elk at Pt. Reyes would exhibit greater movement than lower density elk herds (Wickstrom et al. 1984, Bartmann et al. 1992). Population density can lead to changes in related aspects of elk ecology such as larger home range sizes (Kjellander et al. 2004), broader forage utilization (Fortin et al. 2008) and changes population dynamics (Gaillard et al. 2000). The movements and activity rates of white-tailed deer were affected by population density (Coulombe et al. 2008) but deer dispersal was unaffected (Skuldt et al. 2008). My study was unique because it compared small-scale movement patterns between adjacent wild large herbivore herds at different densities. In general, density dependent effects are scale dependent (Ray and Hastings 1996, Wang et al. 2006), but even quantifying density dependence can be difficult (Stiling et al. 1991). Density-dependent effects by elk are generally related to changes in habitat quality or increases in intraspecific competition. Although the diversity and abundance of vegetation within high density elk herd ranges at Pt. Reyes (Tomales) have been impacted by elk herbivory (McEachern et al. 2001, Johnson and Cushman 2007), how these changes have affected small-scale elk movements is unknown. High density herds at Pt. Reyes (Tomales) exhibited territorial aggression and had smaller home ranges than low density herds (Chapter 2), so inter-herd competition may have also reduced small-scale movements. Spatially explicit movement models are increasingly used to predict distributions of wildlife but have traditionally ignored density dependence. Given that population density affects small-scale movements, I recommend incorporating population density into future movement models. Movement models ignoring population density may produce overestimates of small scale movements; especially for populations with high variability in animal density between herds.

CONCLUSIONS

Small-scale movement models can address questions about how a species may spatially respond to its environment. Tule elk movements in the stable Mediterranean climate of Pt. Reyes exhibited seasonal fluctuations in movement that correlated with rainfall patterns, and were similar to elk in northern seasonal environments. Elk hourly movements were slower and more tortuous on homogeneous, grass habitats that contained high quality forage. Daily movements of elk were shorter during times of year with low forage availability, possibly because remaining forage more concentrated in few remaining areas (i.e. valley bottoms and riparian zones). The effect of grassland habitat heterogeneity on elk movements was scale dependent, and likely explained by motivations to meet their needs at each scale. Elk slowed on steep terrain at all scale, and when traveling over hilly terrain at a daily scale, which may be related to energy conservation. Wind increased elk movements at both the hourly and daily scales, possible due to sensory deprivation. Higher density herds exhibited reduced hourly movements, but herd density did not affect daily movements. Models of elk movement aiming at addressing management concerns should include appropriate habitat and abiotic predictors to achieve realistic predictions of movement patterns.

LITERATURE CITED

Ager, A. A., B. K. Johnson, J. W. Kern, and J. G. Kie. 2003. Daily and seasonal movements and habitat use by female Rocky Mountain elk and mule deer. Journal of Mammalogy 84:1076-1088.

Anderson, D. P., J. D. Forester, and M. G. Turner. 2008. When to slow down: elk residency rates on a heterogeneous landscape. Journal of Mammalogy 89:105-114.

Bartmann, R. M., G. C. White, and L. H. Carpenter. 1992. Compensatory mortality in a Colorado mule deer population. Wildlife Monographs:1-39.

Bartumeus, F., M. G. E. Da Luz, G. M. Viswanathan, and J. Catalan. 2005. Animal search strategies: A quantitative random walk analysis. Ecology 86:3078-3087.

Beall, R. C. 1974. Winter habitat selection and use by a western Montana elk herd. Dissertation, University of Montana, Missoula.

Bello, J., S. Gallina, and M. Equihua. 2004. Movements of the white-tailed deer and their relationship with precipitation in Northeastern Mexico. Interciencia 29:357-361.

Beyer, H. 2006. Hawth's Analysis Tools v. 3.27. Available at http://www.spatialecology.com/htools.

Bookhout, T. A. 1996. Research and management techniques for wildlife and habitats. 5th edition. The Wildlife Society, Bethesda, MD.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference. 2nd edition. Springer, New York, NY.

Cattet, M., J. Boulanger, G. Stenhouse, R. A. Powell, and M. J. Reynolds-Hogland. 2008. An Evaluation of Long-term Capture Effects in Ursids: Implications for Wildlife Welfare and Research. Journal of Mammalogy 89:973-990.

Cattet, M. R. L., N. A. Caulkett, C. Wilson, T. Vandenbrink, and R. K. Brook. 2004. Intranasal administration of xylazine to reduce stress in elk captured by net gun. Journal of Wildlife Diseases 40:562-565.

Clair, C. C. S., and A. Forrest. 2009. Impacts of vehicle traffic on the distribution and behaviour of rutting elk, *Cervus elaphus*. Behaviour 146:393-413.

Clobert, J., J. F. Le Galliard, J. Cote, S. Meylan, and M. Massot. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. Ecology Letters 12:197-209.

Clutton-Brock, T. H., and P. H. Harvey. 1978. Mammals, resources and reproductive strategies. Nature 273:191-195.

Cole, E. K., M. D. Pope, and R. G. Anthony. 1997. Effects of road management on movement and survival of Roosevelt elk. Journal of Wildlife Management 61:1115-1126.

Collins, W. B., P. J. Urness, and D. D. Austin. 1978. Elk diets and activities on different lodgepole pine habitat segments. Journal of Wildlife Management 42:799-810.

Corp, N., A. Spalton, and M. L. Gorman. 1998. The influence of rainfall on range in a female desert ungulate: the Arabian oryx (*Oryx leucoryx*) in the Sultanate of Oman. Journal of Zoology 246:369-377.

Coughenour, M. B., and F. J. Singer. 1996. Elk population processes in Yellowstone National Park under the policy of natural regulation. Ecological Applications 6:573-593.

Coulombe, M. L., S. D. Cote, and J. Huot. 2008. Experimental influence of population density and vegetation biomass on the movements and activity budget of a large herbivore. Behaviour 145:1167-1194.

Creel, S., J. E. Fox, A. Hardy, J. Sands, B. Garrott, and R. O. Peterson. 2002. Snowmobile activity and glucocorticoid stress responses in wolves and elk. Conservation Biology 16:809-814.

D'Eon, R. G., and D. Delparte. 2005. Effects of radio-collar position and orientation on GPS radio-collar performance, and the implications of PDOP in data screening. Journal of Applied Ecology 42:383-388.

Daleszczyk, K., M. Krasinska, Z. A. Krasinski, and A. N. Bunevich. 2007. Habitat structure, climatic factors, and habitat use by European bison (*Bison bonasus*) in Polish and Belarusian parts of the Bialowieza Forest, Poland. Canadian Journal of Zoology 85:261-272.

de Boer, H. Y., L. van Breukelen, M. J. M. Hootsmans, and S. E. van Wieren. 2004. Flight distance in roe deer (*Capreolus capreolus)* and fallow deer (*Dama dama)* as related to hunting and other factors. Wildlife Biology 10:35-41.

de Knegt, H. J., G. M. Hengeveld, F. van Langevelde, W. F. de Boer, and K. P. Kirkman. 2007. Patch density determines movement patterns and foraging efficiency of large herbivores. Behavioral Ecology 18:1065-1072.

Dussault, C., R. Courtois, J. P. Ouellet, and I. Girard. 2005. Space use of moose in relation to food availability. Canadian Journal of Zoology 83:1431-1437.

ESRI. 1996. ArcView 3.2. Redlands, CA.

_____. 2008. ArcGIS 9.3. Redlands, CA.

Etzenhouser, M. J., M. K. Owens, D. E. Spalinger, and S. B. Murden. 1998. Foraging behavior of browsing ruminants in a heterogeneous landscape. Landscape Ecology 13:55-64.

Fahrig, L. 2007. Non-optimal animal movement in human-altered landscapes. Functional Ecology 21:1003-1015.

Fahrig, L., and T. Rytwinski. 2009. Effects of roads on animal abundance: an empirical review and synthesis. Ecology and Society 14:21.

Fortin, D., D. W. Morris, and P. D. McLoughlin. 2008. Habitat selection and the evolution of specialists in heterogeneous environments. Israel Journal of Ecology and Evolution 54:311-328.

Fryxell, J. M., M. Hazell, L. Borger, B. D. Dalziel, D. T. Haydon, J. M. Morales, T. McIntosh, and R. C. Rosatte. 2008. Multiple movement modes by large herbivores at multiple spatiotemporal scales. Proceedings of the National Academy of Sciences 105:19114-19119.

Gagnon, J. W., T. C. Theimer, N. L. Dodd, S. Boe, and R. E. Schweinsburg. 2007. Traffic volume alters elk distribution and highway crossings in Arizona. Journal of Wildlife Management 71:2318-2323.

Gaillard, J. M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toigo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31:367-393.

Glushkov, V. M. 1976. Reasons for daily movements of elk. Ekologiya:85-87.

Gogan, P. 1986. Ecology of the tule elk range, Point Reyes National Seashore, California. Ph.D. dissertation, University of California, Berkeley.

Green, R. A., and G. D. Bear. 1990. Seasonal cycles and daily activity patterns of Rocky Mountain elk. Journal of Wildlife Management 54:272-279.

Harper, J. A. 1962. Daytime feeding habits of Roosevelt elk on Boyes Prairie, California. Journal of Wildlife Management 26:97-100.

_____. 1971. Ecology of Roosevelt elk. Oregon State Game Commission. PR W-59-R. Portland, OR.

Hawkes, C. 2009. Linking movement behaviour, dispersal and population processes: is individual variation a key? Journal of Animal Ecology 78:894-906.

Hayward, M. W., and G. J. Hayward. 2009. The impact of tourists on lion (*Panthera leo)* behaviour, stress and energetics. Acta Theriologica 54:219-224.

Hooge, P. N., and B. Eichenlaub. 2002. Animal movement extension for ArcView. USGS, Biological Science Office. Anchorage, AK.

Jiang, G. S., J. Z. Ma, M. H. Zhang, and P. Stott. 2009. Effects of human activities on the spatial distribution of eastern roe deer (*Capreolus pygargus bedfordi*) in the Lesser Khingan Mountains, northeastern China. Acta Theriologica 54:61-76.

Johnson, B. E., and J. H. Cushman. 2007. Influence of a large herbivore reintroduction on plant invasions and community composition in a California grassland. Conservation Biology 21:515-526.

Johnson, C. J., K. L. Parker, D. C. Heard, and M. P. Gillingham. 2002a. Movement parameters of ungulates and scale-specific responses to the environment. Journal of Animal Ecology 71:225-235.

_____. 2002b. A multiscale behavioral approach to understanding the movements of woodland caribou. Ecological Applications 12:1840-1860.

Kamler, J. F., B. Jedrzejewska, and W. Jedrzejewski. 2007. Activity patterns of red deer in Bialowieza National Park, Poland. Journal of Mammalogy 88:508-514.

Kareiva, P., and G. Odell. 1987. Swarms of predators exhibit preytaxis if individual predators use area-restricted search. American Naturalist 130:233-270.

Kie, J. G., A. A. Ager, and R. T. Bowyer. 2005. Landscape-level movements of North American elk (*Cervus elaphus*): effects of habitat patch structure and topography. Landscape Ecology 20:289-300.

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.

Kjellander, P., A. J. M. Hewison, O. Liberg, J. M. Angibault, E. Bideau, and B. Cargnelutti. 2004. Experimental evidence for density-dependence of home range size in roe deer (*Capreolus capreolus L.*): a comparison of two long-term studies. Oecologia 139:478-485.

Klaassen, R. H. G., B. A. Nolet, and D. Bankert. 2006. Movement of foraging tundra swans explained by spatial pattern in cryptic food densities. Ecology 87:2244-2254.

Li, C. W., Z. G. Jiang, Z. J. Feng, X. B. Yang, J. Yang, and L. W. Chen. 2009. Effects of highway traffic on diurnal activity of the critically endangered Przewalski's gazelle. Wildlife Research 36:379-385.

Lima, S. L., and P. A. Zollner. 1996. Towards a behavioral ecology of ecological landscapes. Trends In Ecology & Evolution 11:131-135.

Marell, A., J. P. Ball, and A. Hofgaard. 2002. Foraging and movement paths of female reindeer: insights from fractal analysis, correlated random walks, and Levy flights. Canadian Journal of Zoology 80:854-865.

McEachern, K., M. Semenoff-Irving, and A. Atkinson. 2001. Control/exclosure monitoring of tule elk effects on Tomales Point vegetation, Point Reyes National Seashore, 1998-1999. U.S. Geological Survey. Point Reyes National Seashore, CA.

McIntyre, N. E., and J. A. Wiens. 1999. Interactions between landscape structure and animal behavior: the roles of heterogeneously distributed resources and food deprivation on movement patterns. Landscape Ecology 14:437-447.

Merrill, E. H. 1991. Thermal constraints on use of cover types and activity time of elk. Applied Animal Behaviour Science 29:251-267.

Mobaek, R., A. Mysterud, L. Egil Loe, O. Holand, and G. Austrheim. 2009. Density dependent and temporal variability in habitat selection by a large herbivore: an experimental approach. Oikos 118:209-218.

Mooring, M. S., T. A. Fitzpatrick, I. C. Fraser, J. E. Benjamin, D. D. Reisig, and T. T. Nishihira. 2003. Insect-defense behavior by desert bighorn sheep. Southwestern Naturalist 48:635-643.

Morales, J. M., D. Fortin, J. L. Frair, and E. H. Merrill. 2005. Adaptive models for large herbivore movements in heterogeneous landscapes. Landscape Ecology 20:301-316.

Morales, J. M., D. T. Haydon, J. Frair, K. E. Holsiner, and J. M. Fryxell. 2004. Extracting more out of relocation data: Building movement models as mixtures of random walks. Ecology 85:2436-2445.

Moritsch, B. J., L. J. Allen, S. Allen, and T. Keeler-Wolf. 2003. Plant community mapping and classification at Point Reyes National Seashore and Golden Gate Recreational Area. National Park Service. Point Reyes National Seashore, CA.

Nams, V. O. 2005. Using animal movement paths to measure response to spatial scale. Oecologia 143:179-188.

Naylor, L. M., M. J. Wisdom, and R. G. Anthony. 2009. Behavioral responses of North American elk to recreational activity. Journal of Wildlife Management 73:328-338.

Olsson, P. M. O., J. J. Cox, J. L. Larkin, D. S. Maehr, P. Widen, and M. W. Wichrowski. 2007. Movement and activity patterns of translocated elk (*Cervus elaphus nelsoni*) on an active coal mine in Kentucky. Wildlife Biology in Practice 3:1-8.

Parker, K. L., C. T. Robbins, and T. A. Hanley. 1984. Energy expenditures for locomotion by mule deer and elk. Journal of Wildlife Management 48:474-488.

Preisler, H. K., A. A. Ager, and M. J. Wisdom. 2006. Statistical methods for analysing responses of wildlife to human disturbance. Journal of Applied Ecology 43:164-172.

Proffitt, K. M., J. L. Grigg, K. L. Hamlin, and R. A. Garrott. 2009. Contrasting Effects of Wolves and Human Hunters on Elk Behavioral Responses to Predation Risk. Journal of Wildlife Management 73:345-356.

Ray, C., and A. Hastings. 1996. Density dependence: Are we searching at the wrong spatial scale? Journal of Animal Ecology 65:556-566.

Roberts, S. L. 2000. Foraging ecology of tule elk at Tomales Point, Point Reyes National Seashore, California. MS thesis, University of Idaho, Boise, ID.

Rowland, M. M., M. J. Wisdom, B. K. Johnson, and J. G. Kie. 2000. Elk distribution and modeling in relation to roads. Journal of Wildlife Management 64:672-684.

Rowland, M. M., M. J. Wisdom, B. K. Johnson, and M. A. Penninger. 2004. Effects of road pattern and density on elk distributions: implications for management in forested ecosystems. Pages 491-508 *in* Proceedings of 69th North American Wildlife and Natural Resources Conference, 17 March-21 March 2004, Spokane, WA.

Sain, S. R., K. A. Baggerly, and D. W. Scott. 1994. Cross-validation of multivariate densities. Journal of the American Statistical Association 89:807-817.

Sapolsky, R. 1992. Neuroendocrinology of the stress response. Pages 287-324 *in* J. B. Becker, S. M. Breedlove, and D. Crews, editors. Behavioral Endocrinology. MIT Press, Cambridge.

Schick, R. S., S. R. Loarie, F. Colchero, B. D. Best, A. Boustany, D. A. Conde, P. N. Halpin, L. N. Joppa, C. M. McClellan, and J. S. Clark. 2008. Understanding movement data and movement processes: current and emerging directions. Ecology Letters 11:1338-1350.

Schoenecker, K. A., F. J. Singer, L. C. Zeigenfuss, D. Binkley, and R. S. C. Menezes. 2004. Effects of elk herbivory on vegetation and nitrogen processes. Journal of Wildlife Management 68:837-849.

Skarin, A., O. Danell, R. Bergstrom, and J. Moen. 2004. Insect avoidance may override human disturbances in reindeer habitat selection. Rangifer 24:95-103.

Skovlin, J. M., P. Zager, and B. K. Johnson. 2002. Elk habitat selection and evaluation. *in* D. E. Toweill, and D. L. Thomas, editors. North American Elk: ecology and management. Smithsonian Institution Press, Washington, D.C.

Skuldt, L. H., N. E. Mathews, and A. M. Oyer. 2008. White-tailed deer movements in a chronic wasting disease area in south-central Wisconsin. Journal of Wildlife Management 72:1156-1160.

St. Clair, C. C., and A. Forrest. 2009. Impacts of vehicle traffic on the distribution and behaviour of rutting elk, *Cervus elaphus*. Behaviour 146:393-413.

Stiling, P., A. Throckmorton, J. Silvanima, and D. R. Strong. 1991. Does spatial scale affect the incidence of density dependence - a field test with insect parasitoids. Ecology 72:2143-2154.

Swift, P. K., V. C. Bleich, T. R. Stephenson, A. E. Adams, B. J. Gonzales, B. M. Pierce, and J. P. Marshal. 2002. Tooth extraction from live-captured mule deer in the absence of chemical immobilization. Wildlife Society Bulletin 30:253-255.

Taylor, L. R., and R. A. J. Taylor. 1977. Aggregation, migration and population mechanics. Nature 265:415-421.

Theil, P. K., A. E. Coutant, and C. R. Olesen. 2004. Seasonal changes and activity-dependent variation in heart rate of roe deer. Journal of Mammalogy 85:245-253.

Turchin, P. 1998. Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Sinauer Associates, Sunderland, UK.

Vander Wal, E., and A. R. Rodgers. 2009. Designating seasonality using rate of movement. Journal of Wildlife Management 73:1189-1196.

Viswanathan, G. M., V. Afanasyev, S. V. Buldyrev, E. J. Murphy, P. A. Prince, and H. E. Stanley. 1996. Levy flight search patterns of wandering albatrosses. Nature 381:413-415.

Vore, J. M., and E. M. Schmidt. 2001. Movements of female elk during calving season in northwest Montana. Wildlife Society Bulletin 29:720-725.

Wang, G. M., N. T. Hobbs, R. B. Boone, A. W. Illius, I. J. Gordon, J. E. Gross, and K. L. Hamlin. 2006. Spatial and temporal variability modify density dependence in populations of large herbivores. Ecology 87:95.

Webb, S. L., S. K. Riffell, K. L. Gee, and S. Demarais. 2009. Using fractal analyses to characterize movement paths of white-tailed deer and response to spatial scale. Journal of Mammalogy 90:1210-1217.

Wickstrom, M. L., C. T. Robbins, T. A. Hanley, D. E. Spalinger, and S. M. Parish. 1984. Food intake and foraging energetics of elk and mule deer. Journal of Wildlife Management 48:1285-1301.

Wiens, J. A., R. L. Schooley, and R. D. Weeks. 1997. Patchy landscapes and animal movements: Do beetles percolate? Oikos 78:257-264.

Wiens, J. A., N. C. Stenseth, B. Vanhorne, and R. A. Ims. 1993. Ecological mechanisms and landscape ecology. Oikos 66:369-380.

Wisdom, M. J., A. A. Ager, H. K. Preisler, N. J. Cimon, and B. K. Johnson. 2004. Effects of off-road recreation on mule deer and elk. Pages 531-550 *in* Proceedings of 69th North American Wildlife and Natural Resources Conference, 17 March-21 March, 2004, Spokane, WA.

Zar, J. H. 1998. Biostatistical analysis. Volume 4.Prentice Hall, Upper Saddle River, NJ.

Zollner, P. A., and S. L. Lima. 2005. Behavioral tradeoffs when dispersing across a patchy landscape. Oikos 108:219-230.

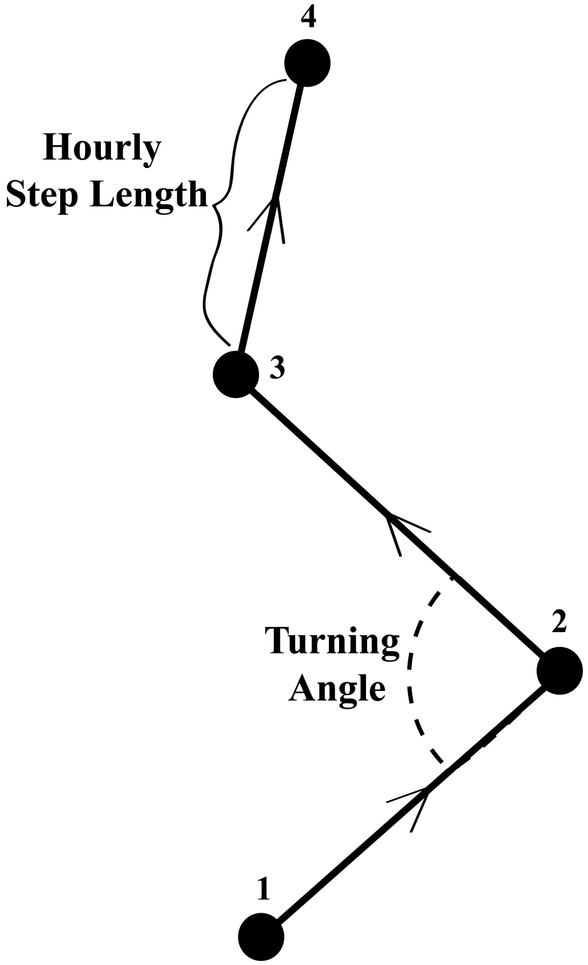

Figure 1. Depiction of hourly step lengths and turning angles calculated using fixes from GPS-collared tule elk, Point Reyes National Seashore, California from 2005 – 2008. Points (numbered) represent consecutive hourly fixes from a GPS collar. Arrows depict hourly step lengths between fixes. The angle formed by two consecutive hourly step lengths is the turning angle, measured in degrees.

Table 1. Summary of predictor coefficients in candidate model set for quantifying hourly (H) and daily (D) step lengths of tule elk at Point Reyes National Seashore, California, 2005-2008.

Category	Predictor Variable	Temporal Scale	Description
Habitat	Grass	H, D	Length weighted mean of grassland within 100-m of step length path
	Grass LWSD	H, D	Length weighted standard deviation of grassland within 100-m of step length path
	Slope	H, D	Length weighted mean of dominant slope within 100-m of step length path
	Slope LWSD	H, D	Length weighted standard deviation of dominant slope within 100-m of step length path
Human disturbance	Road	H, D	Length weighted mean of distance to road from step length path
	Road LWSD	H, D	Length weighted mean of standard deviation of distance to road from step length path
	Trail	H, D	Length weighted mean of distance to trail from step length path
	Trail LWSD	H, D	Length weighted mean of standard deviation of distance to trail from step length path
Density	Density	H, D	Annual herd density (elk/ha grassland)
Herd	Herd	H, D	Name of the herd (factor)
Weather	Rain	H, D	Rain (cm), hourly or daily totals
	Wind	H, D	Wind speed (km per hour), hourly or daily mean
Movement shape	FD	D	Fractal dimension of the step length path
	Turn angle	H	Turning angle from previous fix
Time	Hour	H	Hour of day (factor)
	Month	H, D	Month (factor)

Table 2. Summary of GPS collar data for tule elk at Point Reyes National Seashore, California, 2005 – 2008.

ID	Frequency	Herd	First Fix	Last Fix	Duration (days)	Fix Success	# of Fixes
482	172.175	D Ranch	1/19/2005	11/21/2005	306	98.0%	7180
8	172.175	Limantour	3/3/2006	11/9/2006	251	94.3%	5684
472	173.156	Limantour	8/21/2007	8/20/2008	365	97.2%	8515
476	172.125	North	2/9/2006	11/8/2006	272	98.5%	6433
624	172.175	North	10/10/2007	10/10/2008	366	98.5%	8649
584	173.420	Plateau	2/6/2007	1/30/2008	358	97.2%	8354
578	173.156	White Gulch	8/31/2006	1/23/2007	145	97.5%	3396
623	172.125	White Gulch	9/24/2007	9/24/2008	366	99.0%	8696
477	172.125	South	1/17/2005	11/4/2005	291	98.9%	6907
477	173.420	South	11/11/2005	9/19/2006	312	98.1%	7329

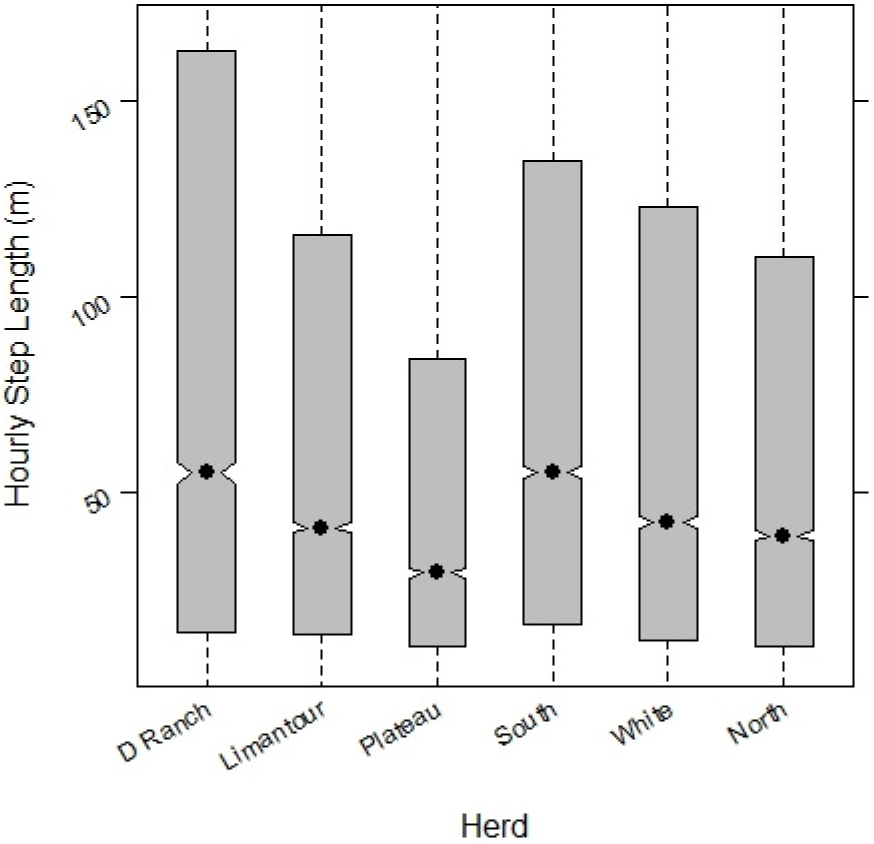

Figure 2. Notched box plot of distances between consecutive hourly tule elk GPS fixes (hourly step lengths) by herd for GPS-collared elk, Point Reyes National Seashore, California 2005 – 2008. Notches indicate 95% confidence interval around medians. Herds are listed in ascending ordered by density (elk/ha grass).

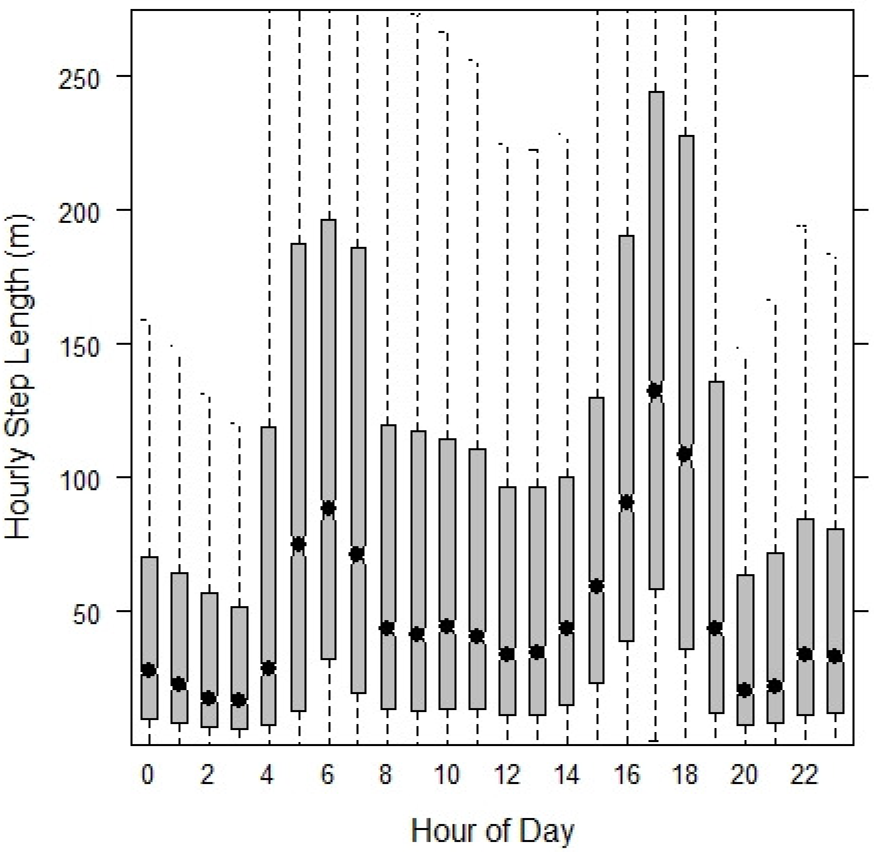

Figure 3. Notched box plot of distances between consecutive hourly tule elk GPS fixes (hourly step lengths) by hour of day for GPS-collared elk, Point Reyes National Seashore, California 2005 – 2008. Notches indicate 95% confidence interval around medians. Outliers have been removed from the figure for clarity, but were included in analyses.

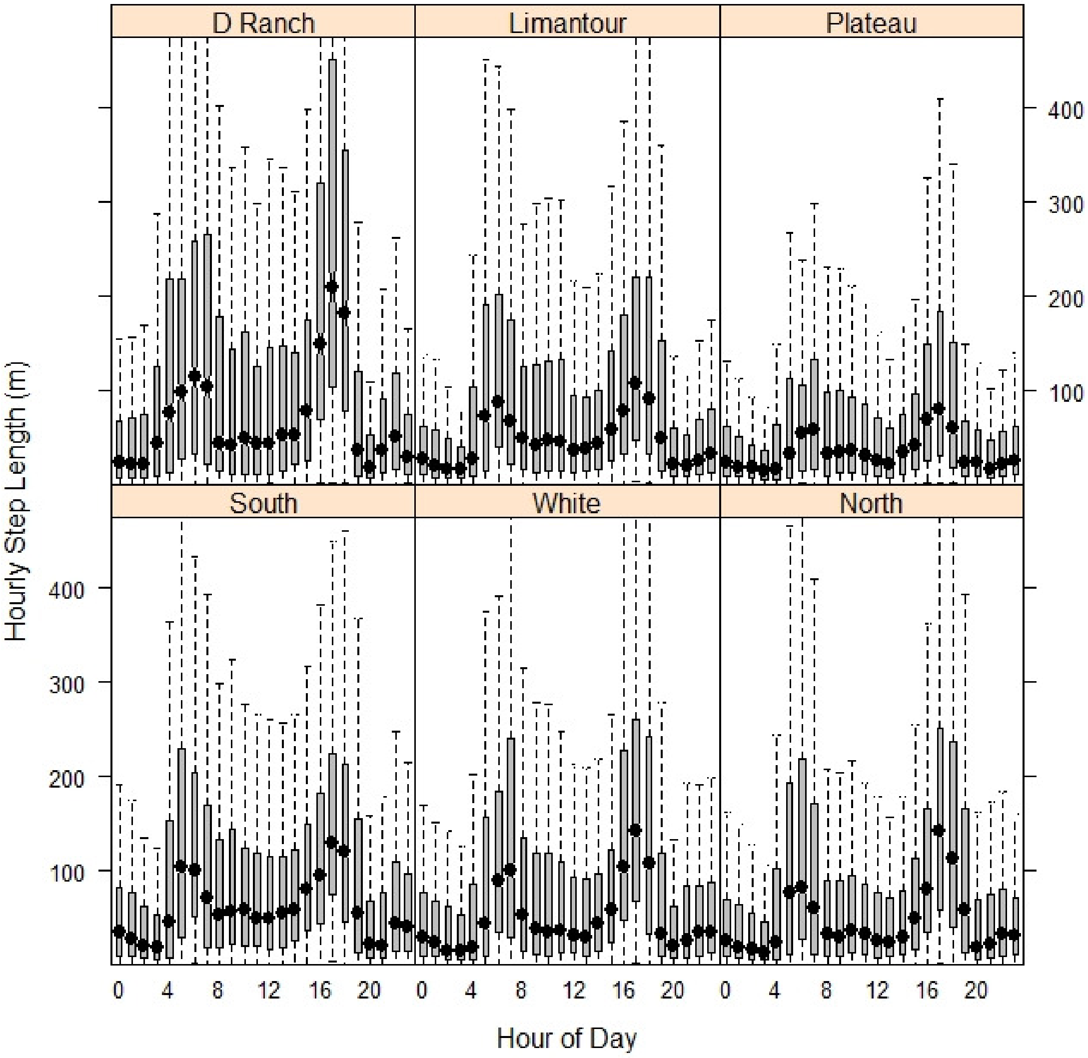

Figure 4. Notched box plots of distances between consecutive hourly tule elk GPS fixes (hourly step lengths) by herd for GPS-collared tule elk, Point Reyes National Seashore, California, 2005 – 2008. Notches indicate 95% confidence intervals around medians. Outliers have been removed from the figure for clarity, but were included in analyses. Herds are listed in ascending ordered by density (elk/ha grass), starting at the top left.

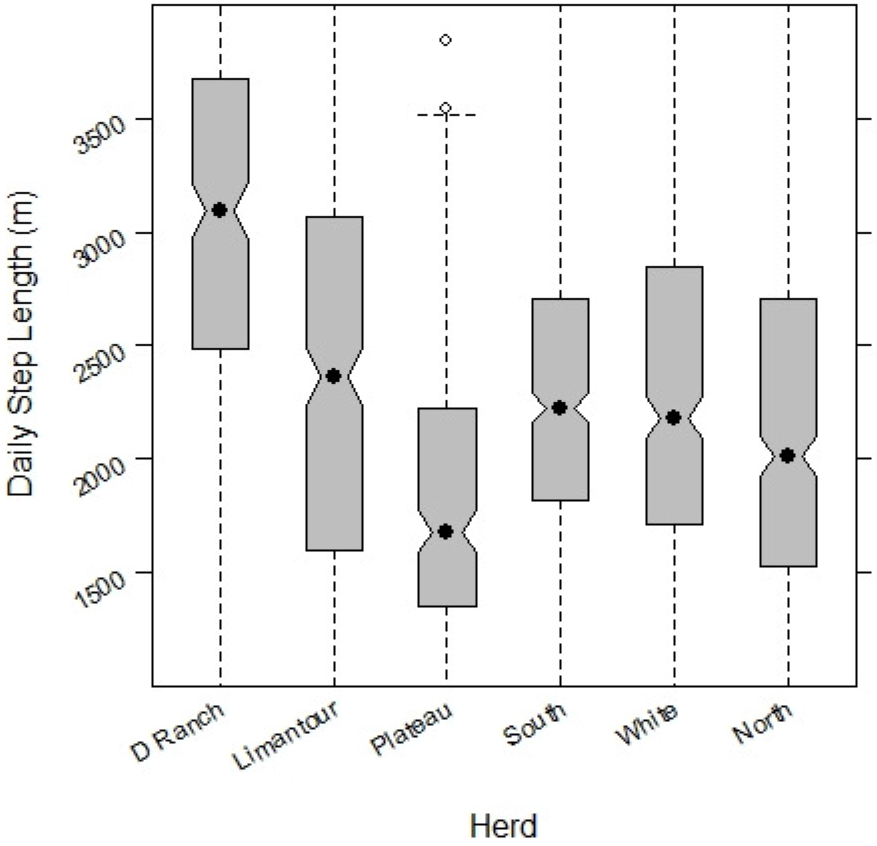

Figure 5. Notched box plots of distances between consecutive daily tule elk GPS fixes (daily step lengths) by herd for GPS-collared tule elk, Point Reyes National Seashore, California, 2005 – 2008. Notches indicate 95% confidence intervals around medians.

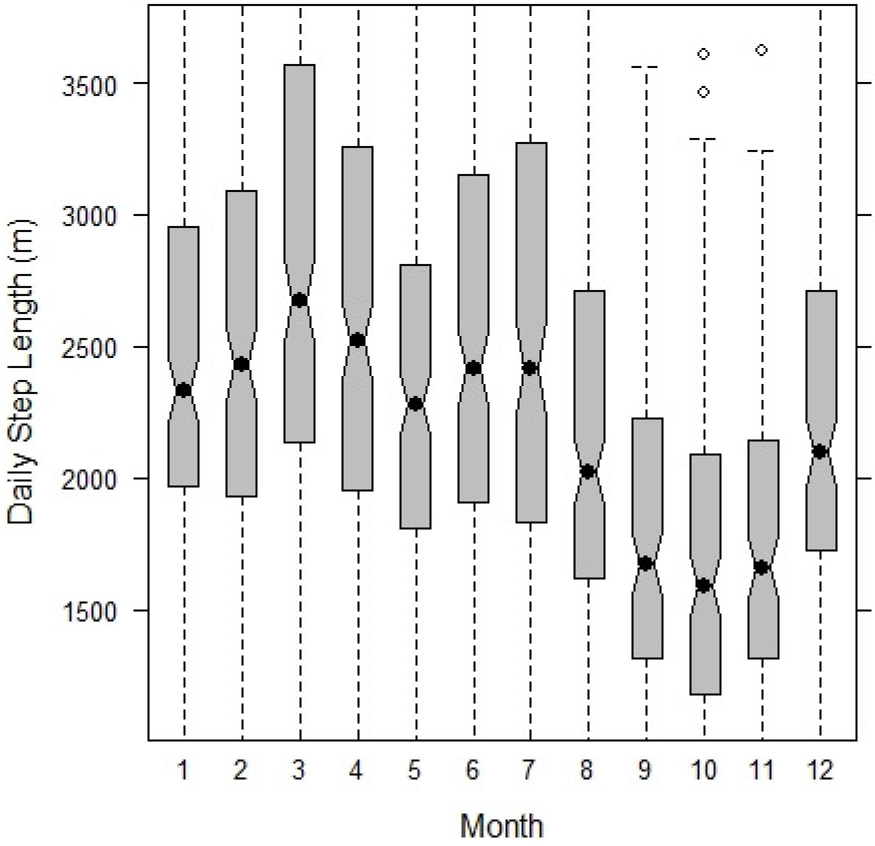

Figure 6. Notched box plots of distances between consecutive daily tule elk GPS fixes (daily step lengths) by month for GPS-collared tule elk at Point Reyes National Seashore, California, 2005 – 2008. Notches indicate 95% confidence intervals around medians.

Table 3. Spearman rank-order correlation coefficients (ρ) for predictor variables used in modeling hourly (a) and daily (b) tule elk step lengths, Point Reyes National Seashore, California, 2005-2008. Values over 0.55 are considered correlated highly correlated. Values with "**" indicate significant correlation between predictor coefficients (p-value < 0.05).

a)

	elk.grass	grass	grassLWSD	hour	rain	road	roadLWSD	slope	slopeLWSD	trail	trailLWSD	turnangle	wind
elk.grass	1.00	-0.21	-0.02	0.00	0.00	0.28	0.02	0.07	0.01	-0.37	-0.10	-0.02	-0.01
grass	-0.21	1.00	0.10	0.00	-0.01	-0.26	-0.04	-0.34	-0.04	0.17	0.03	-0.01	-0.03
grassLWSD	-0.02	0.10	1.00	0.04	0.02	-0.12	0.19	0.00	0.41	-0.02	0.41	-0.10	0.03
hour	0.00	0.00	0.04	1.00	0.00	0.00	0.01	0.05	0.05	0.01	0.05	-0.02	0.17
rain	0.00	-0.01	0.02	0.00	1.00	-0.04	0.00	0.05	0.01	0.01	0.03	0.02	0.17
road	0.28	-0.26	-0.12	0.00	-0.04	1.00	0.00	0.19	0.03	-0.45	-0.16	-0.01	0.02
roadLWSD	0.02	-0.04	0.19	0.01	0.00	0.00	1.00	0.00	0.52	-0.02	0.48	-0.04	0.01
slope	0.07	-0.34	0.00	0.05	0.05	0.19	0.00	1.00	0.22	-0.06	-0.01	0.02	0.10
slopeLWSD	0.01	-0.04	0.41	0.05	0.01	0.03	0.52	0.22	1.00	-0.03	0.44	-0.06	0.02
trail	-0.37	0.17	-0.02	0.01	0.01	-0.45	-0.02	-0.06	-0.03	1.00	0.18	0.03	0.00
trailLWSD	-0.10	0.03	0.41	0.05	0.03	-0.16	0.48	-0.01	0.44	0.18	1.00	-0.08	0.05
turnangle	-0.02	-0.01	-0.10	-0.02	0.02	-0.01	-0.04	0.02	-0.06	0.03	-0.08	1.00	0.01
wind	-0.01	-0.03	0.03	0.17	0.17	0.02	0.01	0.10	0.02	0.00	0.05	0.01	1.00

b)

	elk.grass	fd	grass	grassLWSD	month	rain	road	roadLWSD	slope	slopeLWSD	trail	trailLWSD	wind
elk.grass	1.00	0.05	-0.34	-0.12	0.12	-0.01	0.35	0.05	0.07	-0.02	-0.46	-0.43	-0.02
fd	0.05	1.00	-0.03	-0.01	0.00	0.03	0.05	-0.02	0.02	0.02	-0.09	-0.09	0.00
grass	-0.34	-0.03	1.00	0.22	-0.02	-0.02	-0.32	-0.16	-0.14	0.11	0.24	0.23	-0.03
grassLWSD	-0.12	-0.01	0.22	1.00	0.04	-0.03	-0.25	-0.13	-0.05	0.29	0.02	0.09	-0.06
month	0.12	0.00	-0.02	0.04	1.00	-0.08	0.04	-0.02	0.02	0.13	-0.04	-0.03	-0.25
rain	-0.01	0.03	-0.02	-0.03	-0.08	1.00	-0.06	0.03	0.04	-0.04	0.01	0.04	0.31
road	0.35	0.05	-0.32	-0.25	0.04	-0.06	1.00	0.12	0.19	0.13	-0.57**	-0.54	0.02
roadLWSD	0.05	-0.02	-0.16	-0.13	-0.02	0.03	0.12	1.00	0.12	0.00	-0.19	-0.06	0.05
slope	0.07	0.02	-0.14	-0.05	0.02	0.04	0.19	0.12	1.00	0.55	-0.15	-0.08	0.11
slopeLWSD	-0.02	0.02	0.11	0.29	0.13	-0.04	0.13	0.00	0.55	1.00	-0.13	-0.08	-0.03
trail	-0.46	-0.09	0.24	0.02	-0.04	0.01	-0.57**	-0.19	-0.15	-0.13	1.00	0.69**	0.02
trailLWSD	-0.43	-0.09	0.23	0.09	-0.03	0.04	-0.54	-0.06	-0.08	-0.08	0.69**	1.00	0.07
wind	-0.02	0.00	-0.03	-0.06	-0.25	0.31	0.02	0.05	0.11	-0.03	0.02	0.07	1.00

Table 4. List of candidate models quantifying hourly tule elk step length at Point Reyes National Seashore, California. Competing models were evaluated using Akaike Information Criteria (AIC). Delta AIC (dAIC) and Akaike's weights (*w)* indicate strength of the model relative to other candidate models. The best model is the listed on top.

Model	AIC	ΔAIC	*w*
wind + trailLWSD + grassLWSD + roadLWSD + road + slope + trail + grass + turningAngle + hour + month + herd + elk.grass	803788	0	1.00
wind + trailLWSD + grassLWSD + roadLWSD + road + slope + trail + grass + turningAngle + hour + month + herd + elk.grass	803828	40	0.00
wind + trailLWSD + grassLWSD + roadLWSD + road + slope + trail + grass + turningAngle + hour + month + herd + elk.grass	803829	41	0.00
wind	865595	61807	0.00
trailLWSD	876831	73043	0.00
grassLWSD	882948	79160	0.00
slopeLWSD	889347	85559	0.00
roadLWSD	891472	87684	0.00
road	894906	91118	0.00
slope	895051	91263	0.00
trail	895071	91283	0.00
grass	895202	91414	0.00
turningAngle	911021	107233	0.00
hour	927956	124168	0.00
month	931661	127873	0.00
herd	931858	128070	0.00
elk.grass	932543	128755	0.00
rain	932563	128775	0.00

Table 5. Summary of most parsimonious model for quantifying tule elk hourly step lengths at Point Reyes National Seashore, California, 2005-2008. Variables are listed from greatest to least explanatory power, based on relative AIC values.

Variable	Estimate	SE	*t*-value	*p*-value
(Intercept)	29.60	4.34	6.82	< 0.001
wind	0.54	0.08	6.76	< 0.001
trailLWSD	14.73	0.16	94.36	< 0.001
grassLWSD	2850.00	47.53	59.96	< 0.001
roadLWSD	-0.29	0.05	-5.44	< 0.001
road	0.01	0.00	7.20	< 0.001
slope	-0.81	0.11	-7.16	< 0.001
trail	0.00	0.00	-1.40	0.16
grass	-16.68	1.93	-8.64	< 0.001
turningAngle	-0.20	0.01	-22.18	< 0.001
hour[1]	0.07	3.27	0.02	0.98
hour[2]	-3.63	3.27	-1.11	0.27
hour[3]	-3.02	3.27	-0.92	0.36
hour[2]	19.11	3.28	5.82	< 0.001
hour[4]	45.00	3.30	13.64	< 0.001
hour[5]	47.25	3.32	14.25	< 0.001
hour[6]	39.72	3.32	11.97	< 0.001
hour[7]	8.89	3.31	2.69	0.01
hour[8]	12.28	3.30	3.72	< 0.001
hour[9]	12.33	3.30	3.74	< 0.001
hour[10]	14.68	3.30	4.45	< 0.001
hour[11]	9.13	3.30	2.77	0.01
hour[12]	8.35	3.30	2.53	0.01
hour[13]	4.17	3.31	1.26	0.21
hour[14]	9.91	3.31	2.99	0.00
hour[15]	29.48	3.32	8.88	< 0.001
hour[16]	62.04	3.33	18.65	< 0.001
hour[17]	56.54	3.31	17.10	< 0.001
hour[18]	24.84	3.28	7.58	< 0.001
hour[19]	-0.41	3.27	-0.13	0.90
hour[20]	-1.15	3.27	-0.35	0.73
hour[21]	0.60	3.28	0.18	0.85
hour[22]	0.07	3.27	0.02	0.98
month[2]	4.78	2.49	1.92	0.06
month[3]	12.52	2.36	5.31	< 0.001
month[4]	4.18	2.37	1.77	0.08
month[5]	-3.25	2.45	-1.33	0.18
month[6]	0.22	2.52	0.09	0.93
month[7]	0.24	2.51	0.09	0.93
month[8]	-10.04	2.39	-4.20	< 0.001
month[9]	-18.19	2.39	-7.61	< 0.001
month[10]	-17.13	2.44	-7.03	< 0.001
month[11]	-13.73	2.57	-5.34	< 0.001
month[12]	1.17	2.61	0.45	0.66
herd[D Ranch]	33.19	2.86	11.59	< 0.001
herd[North]	17.87	4.38	4.08	< 0.001
herd[Limantour]	6.95	2.68	2.59	0.01
herd[White]	14.19	2.07	6.86	< 0.001
herd[Plateau]	-12.38	2.86	-4.33	< 0.001
elk.grass	-2.23	0.93	-2.39	0.02
road:trail	0.00	0.00	-6.45	< 0.001

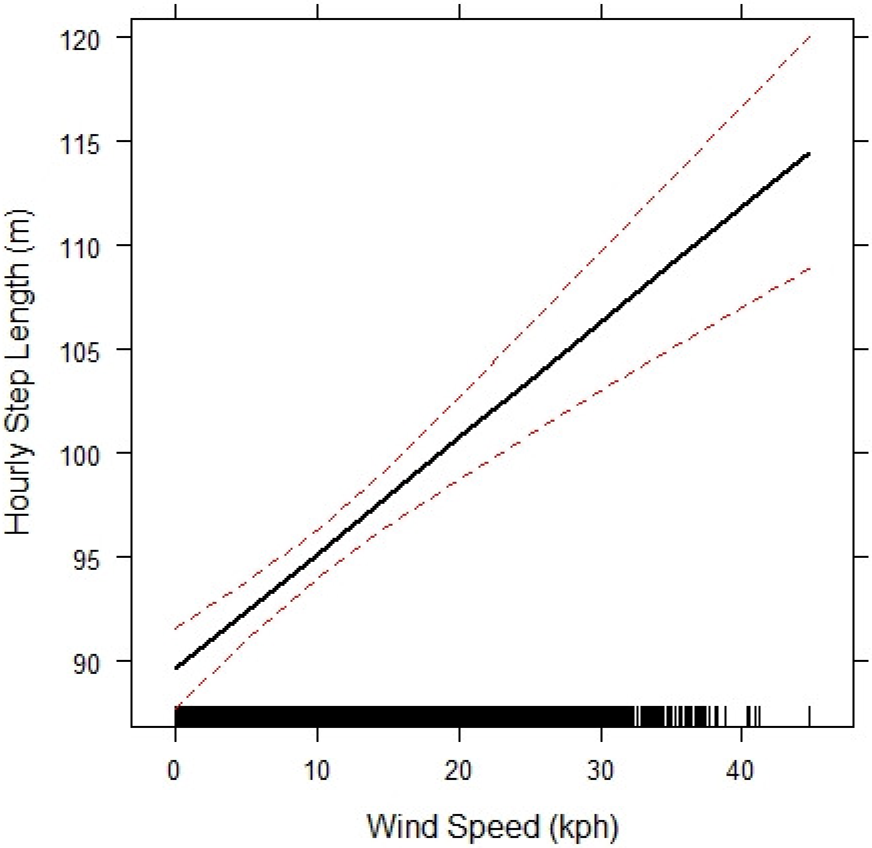

Figure 7. Plot of the model-predicted effect of wind speed (kph) on hourly step lengths of tule elk at Point Reyes National Seashore, CA 2005 – 2008. Dashed lines indicate 95% confidence intervals.

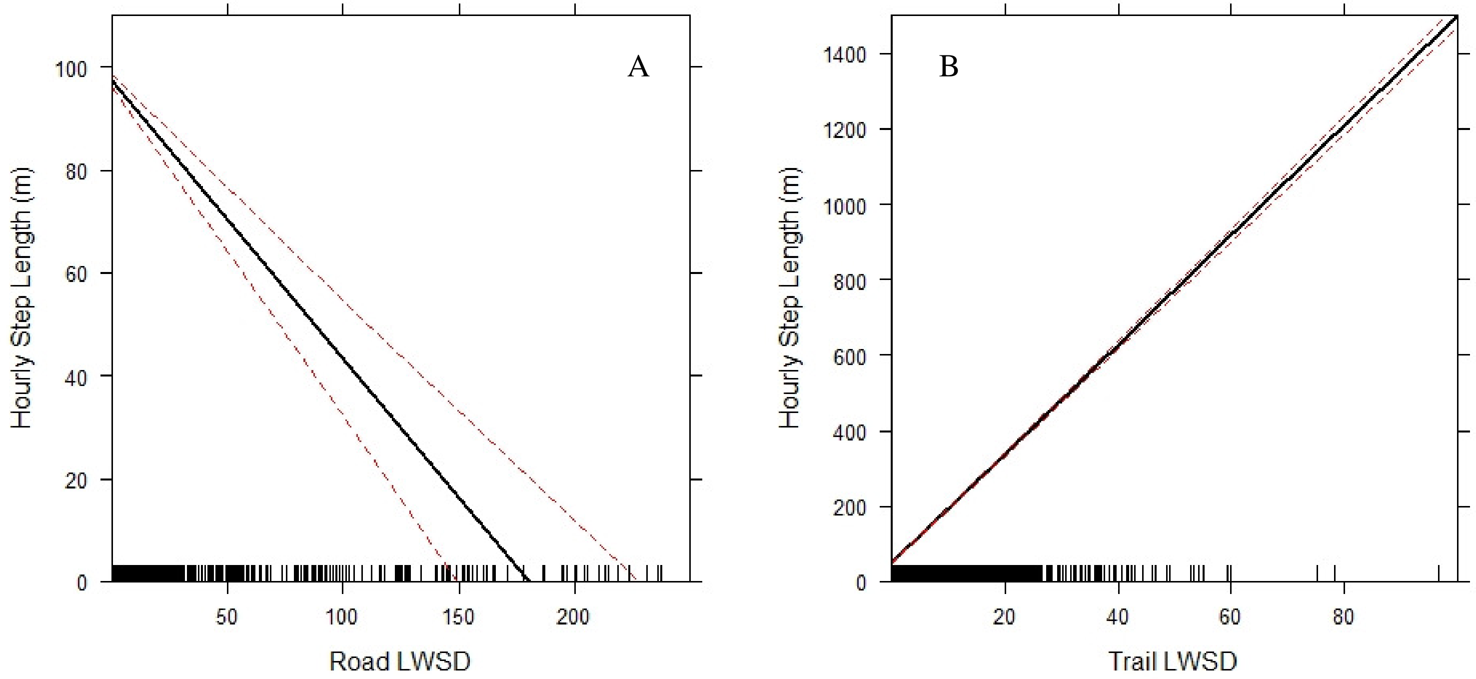

Figure 8. Plot of the model-predicted effect of the variation [line weighted standard deviation (LWSD)] in the distance to the nearest road (A) and trail (B) on hourly step lengths of tule elk at Point Reyes National Seashore, CA 2005 – 2008. Dashed lines indicate 95% confidence intervals.

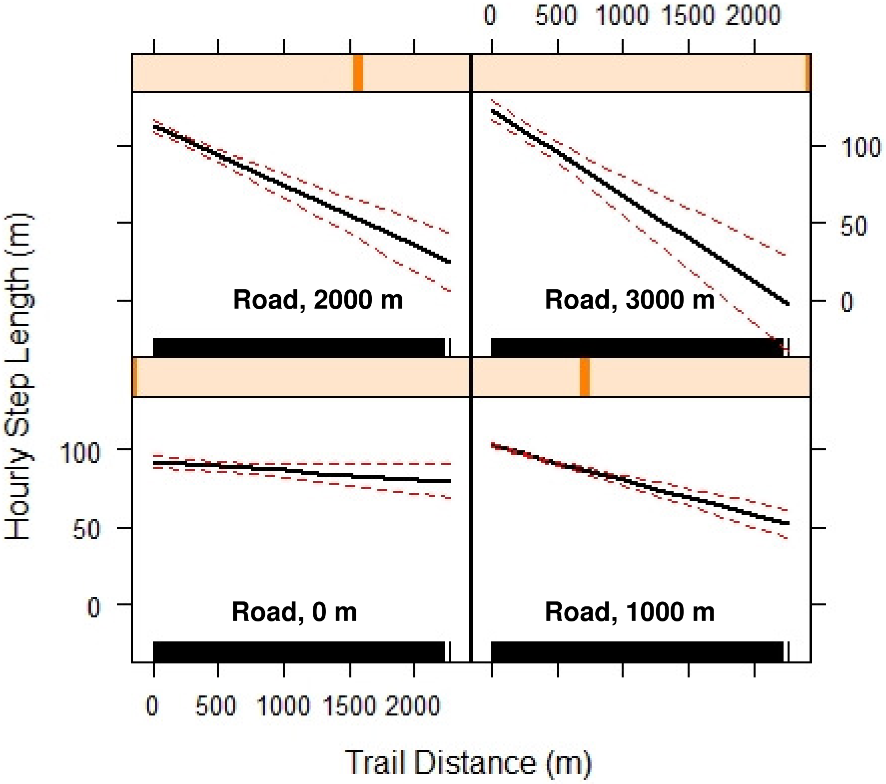

Figure 9. Plot of the model-predicted interactive effect of trail distance (m) on hourly step length of tule elk at road distances of 0, 1000, 2000 and 3000 m. Point Reyes National Seashore, California, 2005 – 2008. Dashed lines indicate 95% confidence intervals around the mean.

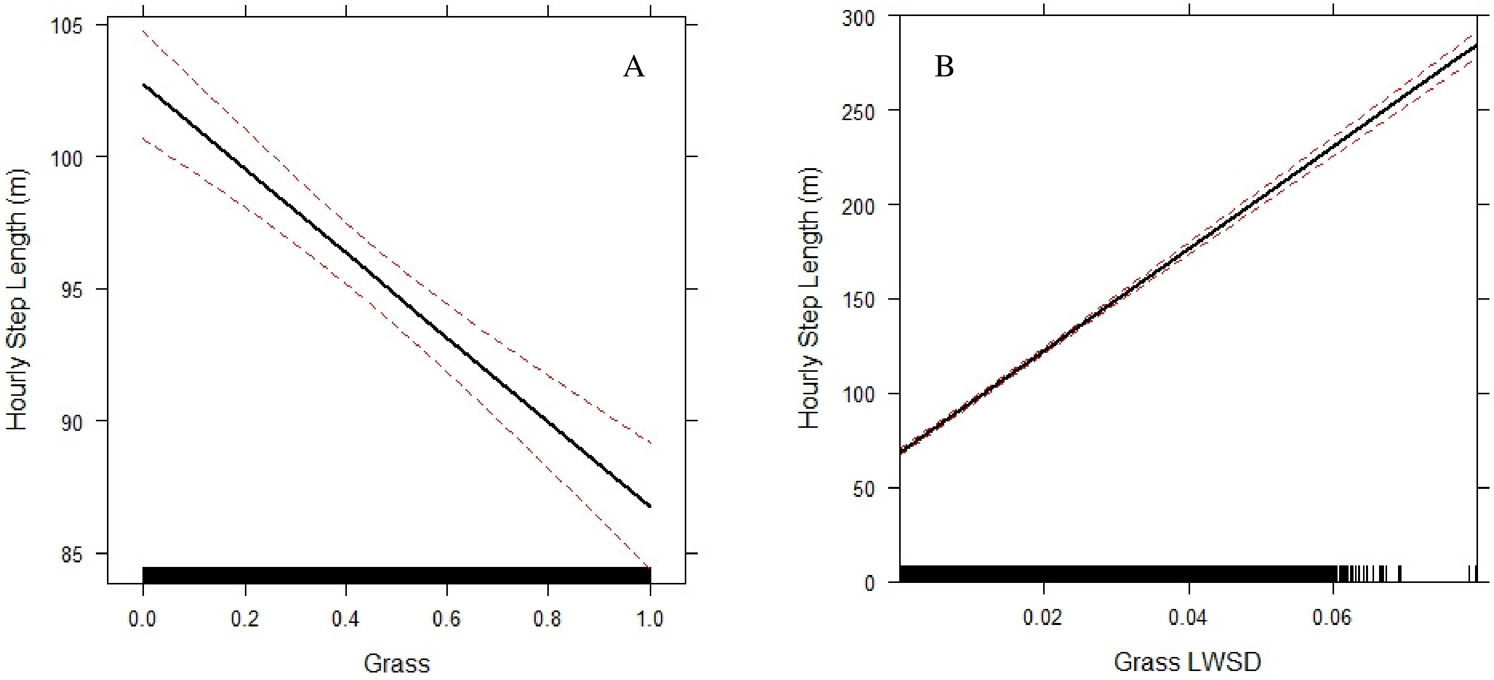

Figure 10. Plot of the model-predicted effect of the mean proportion of grass within 100 m of travel paths (A) and the variation in the proportion of grass habitat (B) on hourly step lengths of tule elk at Point Reyes National Seashore, CA 2005 – 2008. Dashed lines indicate 95% confidence intervals.

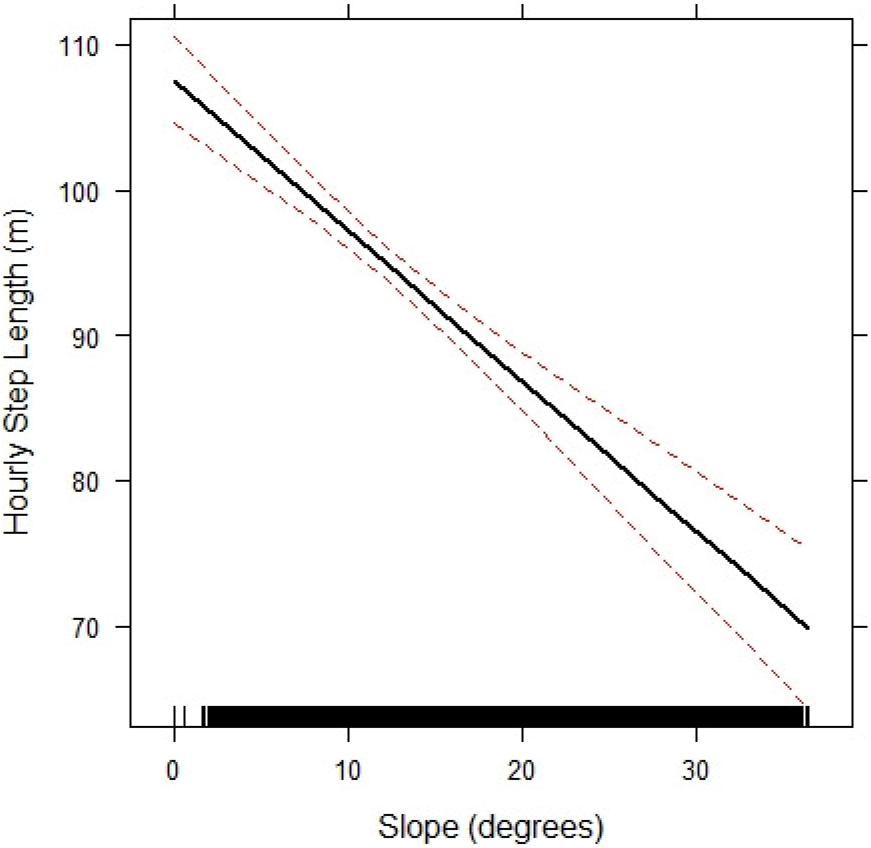

Figure 11. Plot of the model-predicted effect of slope (degrees) on hourly step lengths of tule elk at Point Reyes National Seashore, CA 2005 – 2008. Dashed lines indicate 95% confidence intervals.

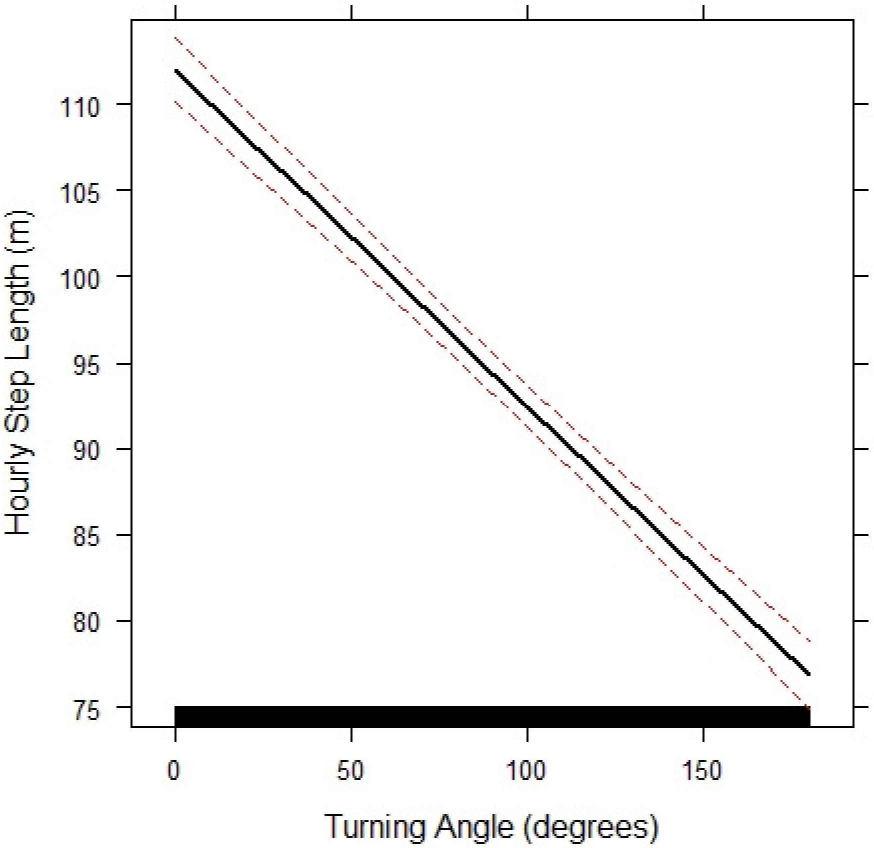

Figure 12. Plot of the model-predicted effect of turning angle (degrees from straight) on hourly step lengths of tule elk at Point Reyes National Seashore, CA 2005 – 2008. Dashed lines indicate 95% confidence intervals.

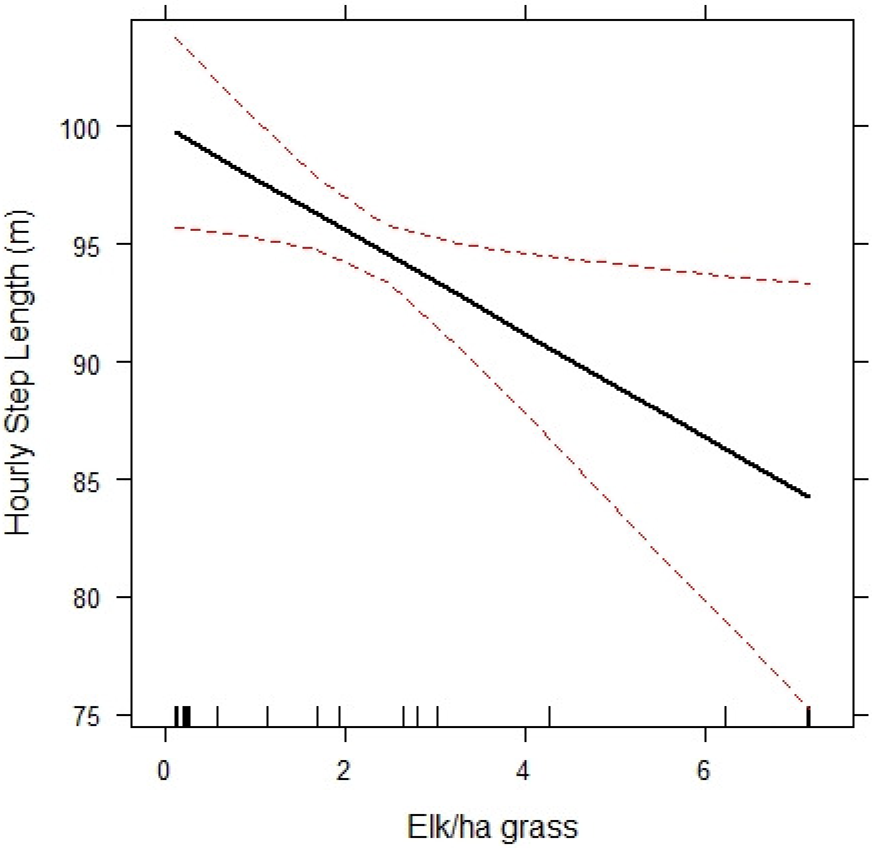

Figure 13. Plot of the model-predicted effect of elk density (elk / ha grassland habitat) on hourly step lengths of tule elk at Point Reyes National Seashore, CA, 2005 – 2008. Dashed lines indicate 95% confidence intervals.

Table 6. List of candidate models quantifying daily tule elk step length at Point Reyes National Seashore, California. Competing models were evaluated using Akaike Information Criteria (AIC). Delta AIC (dAIC) and Akaike's weights (*w)* indicate strength of the models relative to other candidate models. The most parsimonious model is listed first.

Predictors	AIC	ΔAIC	*w*
month + herd + slopeLWSD + trailLWSD + wind + slope + grassLWSD + roadLWSD	31908	0	0.62
month + herd + slopeLWSD + trailLWSD + wind + road + slope + grassLWSD + roadLWSD	31910	2	0.24
month + herd + slopeLWSD + trailLWSD + wind + road + slope + grassLWSD + roadLWSD + density	31912	4	0.09
month + herd + slopeLWSD + trailLWSD + wind + road + slope + grassLWSD + roadLWSD + density + rain	31914	6	0.03
month + herd + slopeLWSD + trailLWSD + wind + road + slope + grassLWSD + roadLWSD + density + rain + gras	31915	7	0.02
month + herd + slopeLWSD + trailLWSD + wind + road + slope + grassLWSD + roadLWSD + density + rain + gras	31917	9	0.01
month	32564	656	0.00
herd	32601	693	0.00
slopeLWSD	32612	704	0.00
trailLWSD	32633	725	0.00
trail	32721	813	0.00
wind	32738	830	0.00
road	32762	854	0.00
slope	32770	862	0.00
grassLWSD	32786	878	0.00
roadLWSD	32793	885	0.00
density	32802	894	0.00
rain	32834	926	0.00
grass	32839	931	0.00
FD	32843	934	0.00

Table 7. Summary of the most parsimonious model for quantifying tule elk daily step length at Point Reyes National Seashore, California, 2005-2008. Variables are listed from greatest to least explanatory power, based on AIC values.

Variable	Estimate	SE	*t*-value	*p*-value
(Intercept)	2510.72	149.67	16.78	< 0.001
month[2]	81.04	86.32	0.94	0.35
month[3]	334.01	82.87	4.03	< 0.001
month[4]	177.51	83.56	2.12	0.03
month[5]	-59.08	83.72	-0.71	0.48
month[6]	79.42	84.13	0.94	0.35
month[7]	285.66	87.62	3.26	< 0.001
month[8]	-42.46	86.51	-0.49	0.62
month[9]	-561.12	91.71	-6.12	< 0.001
month[10]	-602.96	87.65	-6.88	< 0.001
month[11]	-459.67	93.95	-4.89	< 0.001
month[12]	-69.64	90.12	-0.77	0.44
herd[White]	122.13	73.32	1.67	0.10
herd[South]	118.72	74.60	1.59	0.11
herd[D Ranch]	484.45	97.20	4.98	< 0.001
herd[Limantour]	-178.93	85.73	-2.09	0.04
herd[North]	-36.15	73.02	-0.50	0.62
slopeLWSD	-1854.74	221.67	-8.37	< 0.001
trailLWSD	37.86	4.95	7.64	< 0.001
wind	15.87	2.34	6.78	< 0.001
slope	-27.56	7.55	-3.65	< 0.001
grassLWSD	-24015.94	4246.62	-5.66	< 0.001
roadLWSD	40.01	3.94	10.17	< 0.001

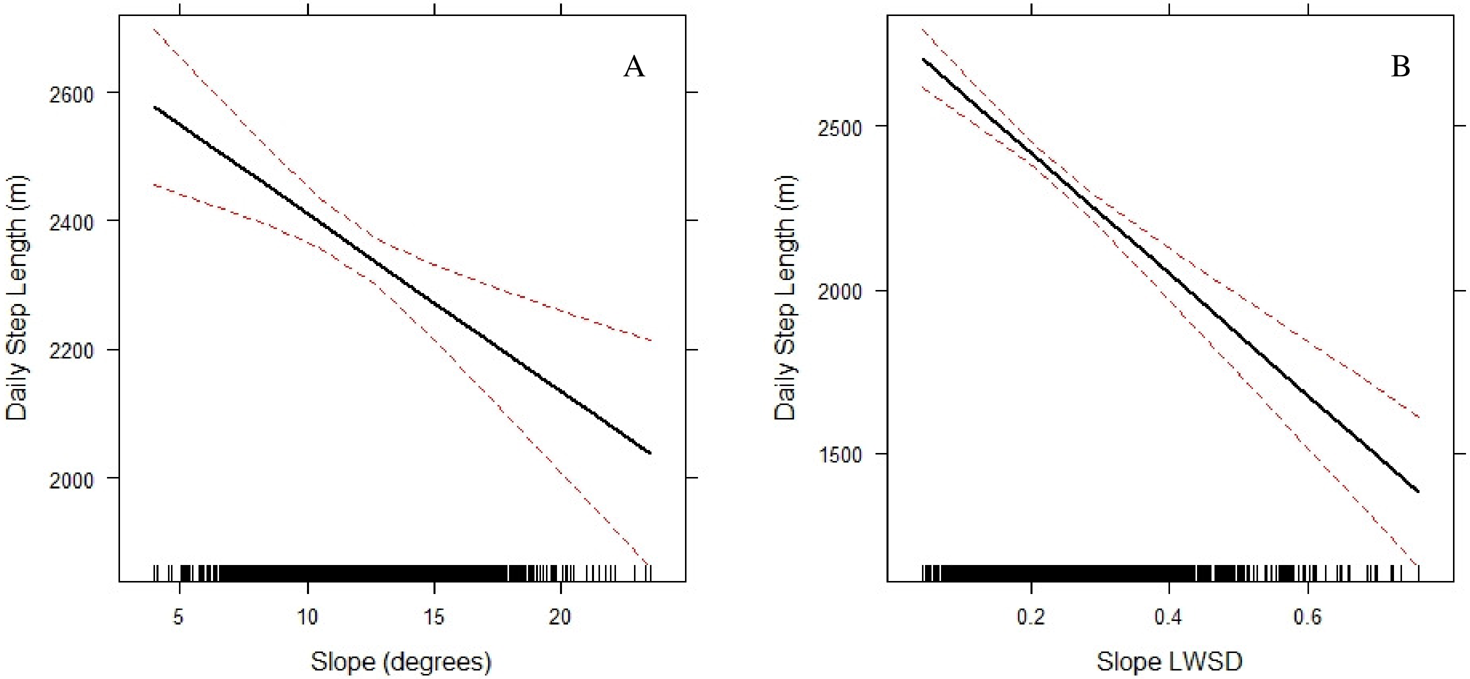

Figure 14. Model-predicted effect of majority value of slope within 100 m of step length paths (A) and variation in slope [line weighted standard deviation (LWSD)] on elk daily step lengths of tule elk at Point Reyes National Seashore, California, 2005 – 2008. Dashed lines indicate 95% confidence intervals. Note the difference scale between the two figures.

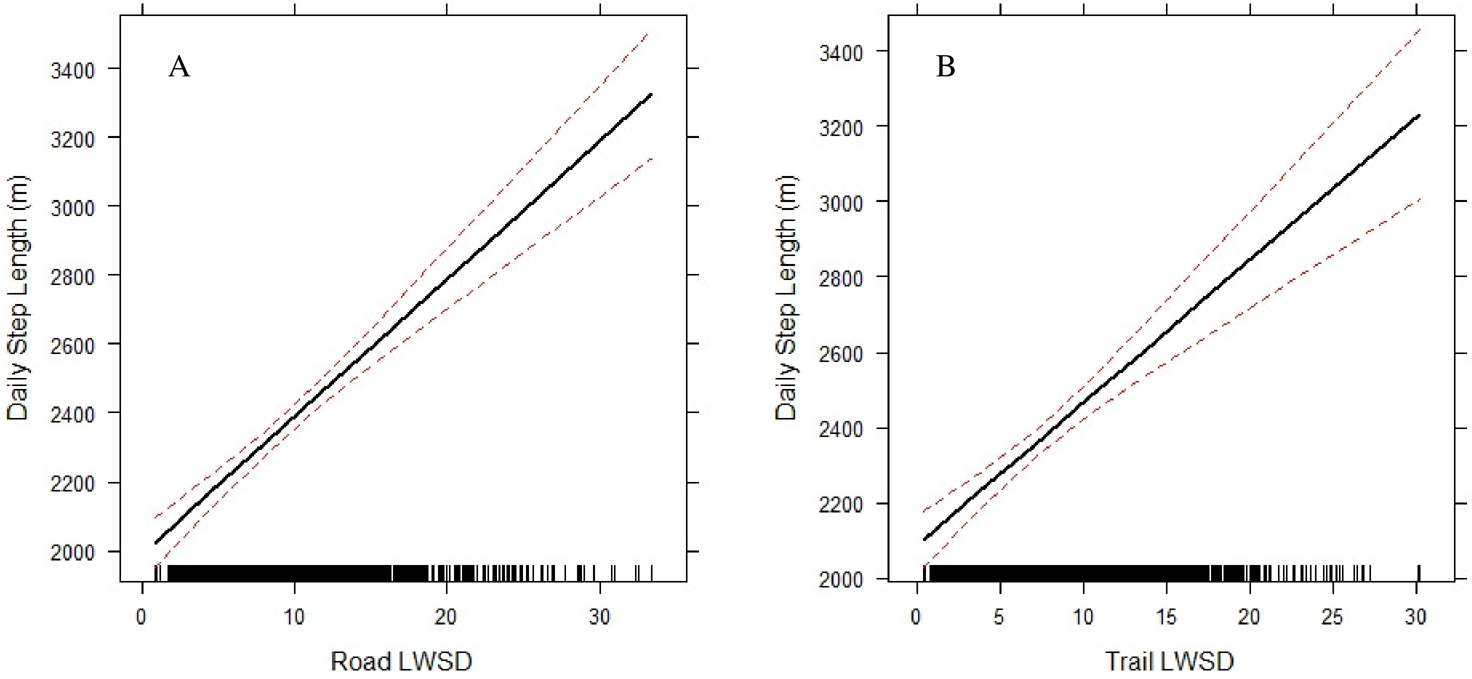

Figure 15. Model-predicted effect of variation in road distance (A) and trail distance (B) along tule elk daily step length paths [length weighted standard deviation (LWSD)] on daily step lengths of tule elk at Point Reyes National Seashore, California, 2005 – 2008. Dashed lines indicate 95% confidence interval.

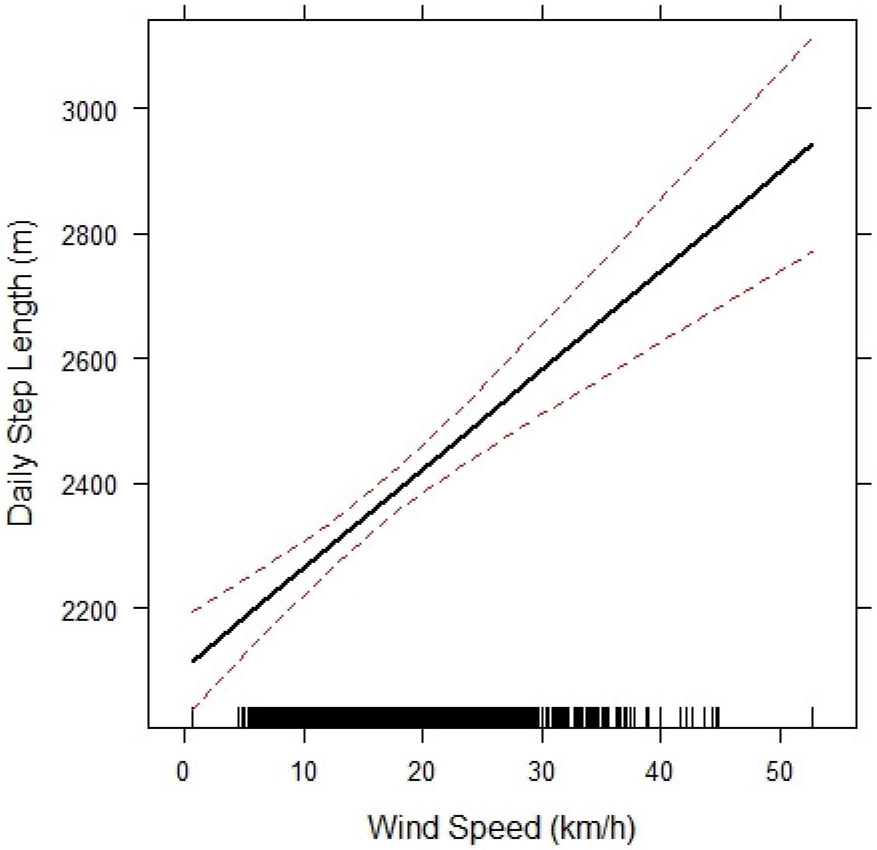

Figure 16. Model-predicted effects of wind speed on daily step lengths of tule elk at Point Reyes National Seashore, California, 2005 – 2008. Dashed lines indicate 95% confidence interval.

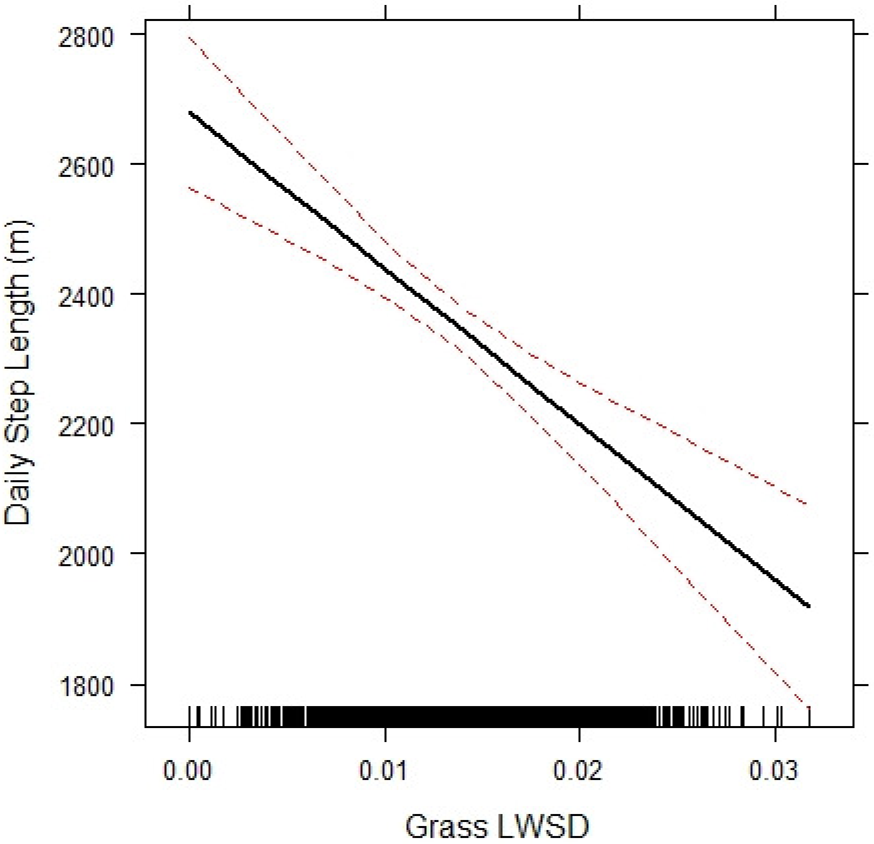

Figure 17. Model-predicted effect of variation in grass abundance along tule elk daily step length paths [length weighted standard deviation (LWSD)] on daily step length of tule elk at Point Reyes National Seashore, California, 2005-2008. Dashed lines indicate 95% confidence intervals.

CHAPTER 4

POPULATION DYNAMICS OF TULE ELK AT POINT REYES NATIONAL SEASHORE

INTRODUCTION

Locally-overabundant large herbivores in predator free, protected areas are an environmental problem in North America (Messmer 2009). High density populations of elk (*Cervus elaphus*) can have ecologically cascading effects (Ripple et al. 2001) on environmental processes (Wagner 2006), nitrogen cycling (Singer and Schoenecker 2003), small mammal abundance (Moser and Witmer 2000) and plant diversity (Stewart et al. 2009). Irruptive population growth patterns and subsequent population crashes typified by newly established large ungulate populations free of predation pressure (Caughley 1970) can lead to additional adverse population-level effects such as genetic bottlenecking or even local extinctions. Humans are directly affected by overabundant elk populations through economic losses (Hegel et al. 2009) and physical hazards (Conover et al. 1995), which can lead to changes in perceptions of wildlife. Because of these negative effects, managers of protected areas often commit to difficult and costly actions to actively regulate elk populations (e.g. elk in Rocky Mountain National Park) (Bradford and Hobbs 2008). Wildlife professionals challenged with managing potentially overabundant elk populations need accurate forecasts of population abundance to effectively address these issues.

Elk reintroductions are increasingly common in North America (Van Deelen 2000, Larkin et al. 2003, Telesco et al. 2007), and evaluating their success and impact requires long-term monitoring. Although reintroductions have increased, long-term datasets on the population dynamics of reintroduced populations are still rare (Fischer and Lindenmayer 2000, Seddon et al. 2007). Natural population regulation of elk can be facilitated through forage availability or quality (Stewart et al. 2006), climate (Langvatn et al. 1996) and predation (Garrott et al. 2009), which can work alone or in combination to drive annual pregnancy (Stewart et al. 2005), calf survival rates (Singer et al. 1997) and adult survival rates (Saether 1997). Accurate forecasts of population change and thorough understanding of environmental factors affecting population change are rare because they require detailed information on vital rates that is generally expensive or difficult to obtain.

Three distinct subpopulations of tule elk (*C. e. nannodes*) at different densities inhabit Point Reyes National Seashore (Pt. Reyes), California. Age-class and sex-specific counts of the elk have been conducted annually since their reintroduction in 1978, and early research has identified factors potentially affecting population growth (Gogan et al. 1989, Roberts 2000). Elk at Pt. Reyes initially exhibited severe copper deficiency stemming from naturally low soil copper levels that likely limited population growth rates (Gogan et al. 1989). Copper is an essential nutrient in large herbivore metabolism, and a deficiency in dietary copper can lead to reduced reproductive output (Bedwal and Bahuguna 1994) and even death (Grace and Wilson 2002). The role of copper deficiency in influencing the current population dynamics of elk at Pt. Reyes is not understood. In additional to low copper levels, selenium concentrations in forage at Pt. Reyes have shown seasonal fluctuations, indicating a potential for selenium deficiency in elk (Roberts 2000). Selenium deficiency can lead to reduced fecundity and juvenile survival rates in cervids (Stussy et al. 2000, Pourliotis et al. 2009), and therefore also has the potential to limit population growth of elk at Pt. Reyes. Johne's disease (*Mycobacterium avium paratuberculosis*), a potentially fatal wasting disease, may infect approximately half of Pt. Reyes elk (Manning et al. 2003), but its effect on elk population regulation is unknown. Fluctuations in annual precipitation from El Niño oscillations may regulate tule elk abundances at Pt. Reyes by facilitating plant productivity (Howell et al. 2002), but an updated assessment is needed to test this hypothesis. No large predators other than mountain lions and coyotes are present at Pt. Reyes. These species probably are not capable of regulating elk, but their effect on the Pt. Reyes elk is unknown.

In the absence of specific information on elk survival and reproduction at Pt. Reyes, the relationship between elk abundances and potential regulating factors remains unclear. My first goal in this study was to quantify annual elk cow and calf survival and fecundity rates. Specifically, I wanted to determine the primary sources of mortality for cow and calf elk. Given the low diversity and abundances of large predators at Pt. Reyes, I predicted that bottom-up (forage and nutrient deficiencies) would regulate elk survival, which would vary based on the previous year's precipitation. In addition, I wanted to quantify the prevalence and effects of Johne's disease and copper and selenium deficiencies on cow and calf elk survival rates. Finally, I wanted to compare survival and fecundity rates, and their regulating factors, between elk herds at different densities. My third goal was to quantify the relative effect that cow and calf survival and fecundity rates have on herd abundance. I expected that herd growth would be more strongly affected by cow survival than fecundity and calf survival, as observed in other ungulate populations (Saether 1997). My final goal was to forecast likely future herd abundances using stage-structured population models that incorporate estimated elk survival and fecundity rates and their observed variability.

METHODS

Population Abundance and Precipitation

Surveys of elk by age class and sex (cow, bull and calf) were conducted by NPS personnel annually from 1978 to 1983 and 1990 to 2008. Surveys from 1984 and 1989 were unclassified counts of elk abundance. Elk surveys from 1980 to 1998 were conducted on foot or horseback (Gogan 1986, Howell et al. 2002). Since 1999, elk surveys at Tomales have followed a standardized protocol of three simultaneously conducted transect surveys using horses and a boat observer each fall (October/ November) (Gates 2000). The highest count is considered the annual population estimate. The Limantour herd has been surveyed annually each fall by foot since their establishment in 1999. Although the D Ranch herd formed in 1999 from a small group (~2 to 3) of elk emigrating from the Limantour herd, distinct annual surveys for the D Ranch herd did not begin until 2004. Given the small population sizes of the Limantour (< 50 elk) and D Ranch (< 20 elk) herds, I considered surveys to be censuses of each herd.

Annual precipitation data were compiled from the Bodega Ocean Observing Node (Bodega Bay Marine Laboratory, Bodega, CA). I quantified the influence of annual precipitation (lagged one year) on annual rates of herd increase (λ) and annual calf: cow ratios using linear regression. I calculated annual rates of increase with the following formula:

$$\lambda = \ln\left(\frac{n_{t+1}}{n_t}\right),$$

where n_t is estimated elk abundance at time t, and n_{t+1} is estimated elk abundance at time $t + 1$.

Radio telemetry

Between January 10 and January 12, 2005, 32 adult female tule elk (cows) were immobilized using a net-gun fired from a helicopter (Leading Edge Aviation LLC, Lewiston, ID 83501). Elk were hobbled, blindfolded and given a low-dose nasal sedative of xylazine and an intragingival injection of lidocaine. Captured elk were fitted with a uniquely numbered ear tag (Nasco, Modesto, CA 95352) and with a mortality-sensing VHF radio telemetry collar (Telonics Inc., Mesa, AZ 85204). I chemically-immobilized 10 additional cows between 2005 and 2008 by ground darting (Arnemo et al. 1994), and fitted them with mortality-sensing, radio-telemetry collars and unique ear tags. I measured the chest girth, total length and hind leg length (distance from hock to hoof) of captured elk using a cloth tape measure. I used these measures to estimate cow body condition at capture with the following formula:

Cow Condition = Chest Girth / (Total Length + Hind Leg Length).

A single I-4 tooth was extracted from 36 captured elk and used to estimate age via cementum annuli analysis (Matson's Lab, Milltown, MT 59851). Cow pregnancy was determined using portable ultrasound equipment and by rectal palpitation of the helicopter-based captures (Greer and Hawkins 1967, Willard et al. 1994). Attempts were made to fit pregnant radio-telemetry collared elk with a radio telemetry vaginal implant transmitter (VITs, Advanced Telemetry Systems Inc., Isanti, MN) to determine calving success and to facilitate calf collaring. I attempted to monitor all instrumented elk 2 to 3-times per week until the end of the study, the animal died or the collar released (GPS collars).

In addition to fecal samples collected at capture, I collected fecal samples from radio-collared cows biannually to quantify Johne's disease prevalence (January-February and July – August). Pairs of researchers observed elk through binoculars and spotting scopes until the elk defecated and then marked fecal sample locations, aided by a laser rangefinder (Leica Rangemaster 1200, Leica, Solms, Germany). After the target elk group vacated the immediate area, a researcher was guided to locations of fecal samples using two-way radios and hand signals for communication. Three samples of approximately 5 ml of feces were transferred into three 50 ml tubes containing 20 ml of 0.75% hexadecylpyridinium chloride (HPC). Fecal samples were mailed overnight to the Johne's Testing Center (University of Wisconsin, Madison, WI 53706) for testing using radiometric cultures (Cook et al. 1997).

Between 2005 and 2008, I captured, collared and monitored 84 neonatal elk calves to determine calf survival rates and cause-specific mortality. I located calves on foot and horseback by closely monitoring and searching around solitary cows (Johnson 1951), by searching near expelled VITs (2005 only) and by intensively monitoring radio-collared cows on a daily basis during the parturition period. Calves were ear-tagged (Nasco, Modesto, CA 95352), weighed (Pesola, Baar, Switzerland) and fitted with expandable, drop-off, mortality-sensing radio-telemetry collars (Advanced Telemetry Systems Inc., Isanti, MN 55040). Latex gloves were worn by researchers during captures and capture equipment was washed with Scent Killer® (Wildlife Research Center, Ramsey, MN) to reduce researcher impacts and disease transfers between calves . Body measurements (total length, ear notch length, hock to hoof length, incisor length and girth) and observations (presence of canine, umbilical condition, hoof condition and wetness) were recorded and used to estimate age at capture (Johnson 1951, Sams et al. 1996). I estimated calf birth weight by regressing estimated age at capture on capture weight and sex (Zager et al. 2006), using Akaike's Information Criterion (AIC) to rank competing candidate models (Burnham and Anderson 2002). I compared birth weights and birth dates among herds and study years using Kruskal-Wallis chi square (KW χ^2) tests. I attempted to monitor radio-collared calves daily for the first 3 weeks post-capture, and then 2 to 3-times per week thereafter until the calf died, the collar dropped or until 31 March of the following year. I determined the status (live or dead) of radio-collared calves remotely via radio telemetry. I did not obtain visual locations on live, collared calves so as to not disturb them and influence their survival (Phillips and Alldredge 2000).

Radio-collared and opportunistically-discovered cow and calf mortalities were investigated the day that they were discovered, which was usually less than three days post-mortem. To determine the cause of death, I transported carcasses to the California Animal Heath and Food Safety laboratory (CAHFS, Davis, CA 95617) for histology-based necropsies when feasible. Necropsies included radiometric cultures of intestinal tissues for Johne's disease, and screening of the liver to quantify copper and selenium levels. When it was not possible to remove the carcass from the field, I conducted necropsies on site following established protocol (Roffe et al. 1996). I collected tissue samples during field necropsies, which were transported to CAHFS for Johne's disease, copper and selenium screening. I searched mortality sites for evidence of predation (tracks, scat and hair) and examined carcasses for evidence of pre-mortem trauma (puncture wounds and subcutaneous hemorrhaging). I quantified body condition using a femur marrow fat index (Cheatum 1949). This was done by sawing the femur bone in half, examining the fat content of the marrow and scoring it between on a scale of one to four. A single I-1 tooth was extracted and used to estimate age at death via cementum annuli analysis (Matson's Lab, Milltown, MT 59851).

Survival and Calf Production

I used known-fate models in Program MARK (White 1999) to estimate calf survival rates for all herds and cow survival rates for the Limantour and Tomales herds. Because of the small number of radio-collared cows (n = 3) and the small total number of elk at D Ranch (n = 20), I determined annual cow survival there by monitoring the herd biweekly. For all other herds, I quantified annual cow survival at monthly intervals, and annual calf survival at weekly intervals, using radio telemetry. Study years began 1 April and ended 31 March. I selected these dates as the beginning and end of study years because 1 April was earliest date that I observed new calves of the year.

I identified 7 *a priori* classes of predictor variables that could describe cow annual survival: time of year, study year, monthly rainfall, two age classes [cows (1 – 9 years old) and old cows (>9 years old)], herd membership, fixed kernel home range area (Chapter 1 for details) and body condition at capture. I identified 6 *a priori* classes of predictor variables that could describe calf survival: sex, birth date, birth weight, herd, study year and monthly rainfall. Monthly rainfall data were obtained from the Bodega Oceanographic Observing Node (National Oceanographic and Atmospheric Administration, www.srrb.noaa.gov/ highlights/sunrise/ sunrise.html). To allow numerical optimization algorithms in known-fate models to find the correct parameter estimates, I standardized (*z*-score) or scaled a subset of predictor variables prior to modeling (Table 1). I employed backward stepwise model selection and compared competing candidate models with Akaike's Information Criterion adjusted for small sample sizes

(AIC_c) (Burnham and Anderson 2002). My final estimates of monthly and annual survival were derived by modeling-averaging estimates, which allowed me to include model selection uncertainty in estimates of precision of the parameter and unconditional estimates of variances and standard errors (Buckland et al. 1997).

Annual calf production was defined as the proportion of radio-collared cows that gave birth each study year, by herd. In 2005 – 2006, I quantified calf production by monitoring VIT signals (Barbknecht et al. 2009) and by visually assessing the status and behavior of radio-collared cows on a daily basis during the parturition period (April 1 – July 1). VITs were not used in the remaining study years. I considered a cow to have produced a calf if I observed a calf with the cow or if the cow exhibited signs of having recently given birth (swollen labium, bleeding and unusual solitary behavior in known parturition habitat). I tested for differences in calf production among study years and herds using KW χ^2 tests.

Matrix Model and Population Projections

I quantified elk population dynamics for D Ranch, Limantour and Tomales herds with a female-based, post-breeding, stage-structured population matrix model in PopTools (Hood 2009). The model was composed of 6 age classes [stage 0 (newborn), stage 1 (1 year old), stage 2 (2 years old), stage 3 (3 – 9 years old), stage 4 (10 – 14 years old) and stage 5 (15 – 20 years old)] (Figure 1). I parameterized the model using cow and calf survival estimated from my known-fate models. I defined annual calf production for stages 3 and 4 as the proportion of radio-collared cows that produced a calf. I used estimates from the literature to quantify calf production for stages 2 and 5 because there were few radio-collared individuals in these age classes (Raithel et al. 2007, Murrow et al. 2009). I assumed that survival did not differ between stages 2 and 3, there was a 50:50 calf sex ratio and calf survival did not vary by sex (Singer et al. 1997).

I quantified the relative importance of individual vital rates to annual changes in the elk herd sizes with sensitivity and elasticity analyses (Caswell 2001). I used PopTools to calculate sensitivity and elasticity values (Hood 2009). Sensitivity values were quantified by determining the amount that dominant eigenvalues of the population matrices changed due to small changes in vital rate elements of the matrix. Elasticity values were sensitivity values scaled to 1, so that they could be compared more easily.

I forecasted elk abundances for 10 years for D Ranch, Limantour and Tomales herds with stochastic population projections (Hood 2009). I did not include density dependence in the models, which I believe was justified for the D Ranch and Limantour populations because Tomales herds had exhibited no signs of density dependence for the first ten years (Roberts 2000). Although this assumption is not likely for Tomales at this time, which has shown fluctuations in abundances and was approaching or even exceeded estimates of carrying capacity (90 – 1060 elk) (Gogan 1986, Bartolome 1993, Roberts 2000), I did not include density dependence in my population projection models for Tomales because it was not known how herd density may be affecting individual vital rates. Initial population sizes for each herd were defined as the number of cows quantified from the 2008 annual NPS elk survey. I assumed an equal sex ratio for calves, and I used the stable age distribution estimates from the matrix model to determine the starting number of elk in each stage class. Annual changes in abundance were quantified by stage class using estimates of survival and fecundity, which were allowed to vary stochastically at each time step around their estimated standard errors following a Beta distribution. The formula used to quantify expected herd sizes at the next time step (N_{t+1}) was:

$$N_{t+1} = \begin{bmatrix} S_0P_1 & S_1P_2 & S_2P_3 & S_wP_3 + S_xP_4 & S_yP_4 + S_zP_5 & S_5P_5 \\ S_0 & 0 & 0 & 0 & 0 & 0 \\ 0 & S_1 & 0 & 0 & 0 & 0 \\ 0 & 0 & S_2 & S_w & 0 & 0 \\ 0 & 0 & 0 & S_x & S_y & 0 \\ 0 & 0 & 0 & 0 & S_z & S_5 \end{bmatrix} \begin{bmatrix} n_0 \\ n_1 \\ n_2 \\ n_3 \\ n_4 \\ n_5 \end{bmatrix},$$

where S_0 is the estimated annual survival rate at stage class zero (newborn, 0 - 1 years), P_0 is estimated newborn production at stage class zero, and n_0 is the number in stage class zero. I quantified mean annual herd sizes and 95% confidence intervals with 10,000 Monte Carlo simulations of stochastic population projections. To get total herd estimates that included males, I multiplied model predictions by the average cow: bull ratio from 1978 to 2008 in the Tomales herds (1.55).

RESULTS

Population Abundance and Precipitation

Annual surveys indicated that the Tomales herds grew exponentially ($R^2 = 0.98$) from 10 elk in 1978 to approximately 549 elk in 1998 and then declined to 430 elk in 2005 (Figure 2). During my study, the Tomales herds increased 36% from 430 (2005) to 585 elk (2007) and then declined 22% to 459 elk (2008). The Limantour herd was relatively stable from 1999 (30 elk) to 2005 (29 elk), but increased 28% during my study from 29 elk (2005) to 37 elk (2008) (Figure 3). The D Ranch herd grew from 10 elk in 2004 to 15 elk in 2005, and then increased 106% from 15 (2005) to 31 elk (2008) during my study (Figure 4).

Annual precipitation averaged 87 cm (SE = 6.00) between 1978 and 2008 (Figure 5). One year lagged annual precipitation values were above average (108 cm) during the first two study years (2005 – 2007) and below average (60 cm) during the third year (2008). There was no relationship between annual rates of increase (λ) and lagged precipitation at any herd, or between calf- cow ratios and lagged precipitation for the D Ranch and Limantour herds (Table 2). Calf: cow ratios showed some correlation with lagged precipitation in the Tomales herds ($R^2 = 0.35$, $p = 0.07$) but only after herd sizes stabilized (post – 1998) (Figure 6).

Causes of Mortality

I captured and radio-marked 42 cows from 2005 – 2007 (32 in 2005, six in 2006, and four in 2007) (Table 3). The mean estimated age at capture was 6.3 years (range = 1 – 14 years). One cow died of capture-related injuries during the helicopter-based capture and was not included in this total. The live/dead status of radio-collared cows was visually assessed on average every 3.7 days (SE = 0.02). Ten of 42 (23%) radio-collared cows died during the study and I discovered an additional 45 adult mortalities (26 female, 19 male) (Table 4). The average age at death for adults was 10.2 years (SE = 0.56), and age at death did not differ between radio-collared cows and opportunistically-found elk (KW $\chi^2 = 1.49$, $p = 0.22$). Observed adult mortalities increased annually from eight in 2005 -2006 to 37 in 2007 – 2008 (Figure 7).

Starvation was the most common cause of death for radio-collared cows (six of ten, 60%). Although I was unable to determine the cause of death for the majority of unmarked elk (26 of 45, 60%), the most common known cause of death was also starvation (5 of 19, 26%), which was usually accompanied by copper and selenium deficiencies. Copper liver concentrations averaged 2.48 ppm (SE = 0.37) and selenium concentration averaged 0.04 ppm (SE = 0.003) for cow mortalities. Other sources of cow mortality included trauma (femur fractured in badger hole, caught in a vegetation exclosure), management action (escaped from the Tomales boundary and shot by the NPS), bronchopneumonia and predation (mountain lion).

I collected 368 fecal samples from radio-collared cows to quantify Johne's disease prevalence. Only one (3%) radio-collared cow in the Tomales herds tested positive for Johne's disease in a single fecal sample (0.3%) in February 2006. Johne's disease was not isolated from any cows (n = 14) or calves (n = 19) during laboratory necropsies. Elk from the D Ranch and Limantour herds showed no signs of Johne's disease through fecal or tissue sampling.

I captured and radio-collared 84 calves (41 male, 43 female) during the spring of 2005 (n = 21), 2006 (n = 34) and 2007 (n = 29) (Table 5). Four radio-collared calves (5%) dropped their collars within a month of capture and could not be subsequently monitored. Twenty of the remaining 80 (25%) radio-collared calves died, and I opportunistically discovered an additional 19 unmarked calf mortalities. Observed calf mortalities increased annually from three in 2005 – 2006 to 22 in 2007 – 2008 (Figure 8). I was unable to determine a cause of death for 21 of 39 (54%) calf mortalities due to warm conditions causing rapid decomposition. The most commonly identified cause of calf mortality was starvation (8 of 39, 44%), followed by septicemia (7 of 39, 39%) and selenium deficiency (6 of 39, 33%) (Table 6). Other sources of mortality included predation (unknown predator), stillborn, copper deficiency, bronchopneumonia and lungworm.

Calves averaged 3 days old at capture (range = 0 – 14 days). Estimated birth dates for calves ranged from 31 March to 14 August, but most were born between 31 March and 10 June (median = 24 April, Figure 9). Calves in the D Ranch and Limantour herds were born earlier than calves in the Tomales herds ($\bar{x}$ = 18 days earlier, KW $\chi^2 = 19.16$, $p < 0.001$). Calves born in 2006 – 2007 were born earlier than calves born in other study years (KW $\chi^2 = 9.54$, $p = 0.001$) (10).

The most parsimonious model for predicting calf birth weight included age and sex as predictors (Table 7). Calf daily weight gain was 0.88 kg / day (SE = 0.09) and male calves were estimated to weigh approximately one kg (SE = 0.48) more than females at birth, based on model output (Table 8). By applying the model to empirically-derived calf weights at capture and estimated calf ages at capture, I estimated the average calf birth weight was 10.97 kg (SE = 0.48) for female calves and 11.97 kg (SE = 0.89) for male calves. Calf birth weight varied somewhat among herds (KW $\chi^2 = 9.33$, $p = 0.10$) and less among years (KW $\chi^2 = 2.52$, $p = 0.28$) (Figure 10).

Survival and Calf Production

Annual cow survival averaged 0.96 (SE = 0.03). Estimates of annual cow survival showed some evidence of variation among herds, but the differences were not statistically significant (KW $\chi^2 = 3.82$, $p = 0.14$). There was no evidence of a statistically significant difference in annual variation in estimated annual cow survival (KW $\chi^2 = 1.05$, $p = 0.59$). However, estimated annual cow survival at Tomales declined from 1.00 (SE = 0) in 2005 – 2006 and 2006 – 2007 to 0.79 (SE = 0.08) in 2007 – 2008 (Table 9). All six cows at D Ranch survived the entire study, resulting in a survival estimate of 1.00. To be conservative, this estimate was adjusted to 0.98 (SE = 0.01) for matrix models and population projections.

Predictors of cow survival varied among herds. Because there were no observed cow mortalities at D Ranch during the study, I was not able to assess the predictors for cow survival for this herd. According to the most parsimonious known-fate model, cow survival for the Limantour herd varied by the time of year but was independent of all other predictors (Tables 10 and 11). Cow survival decreased over the study year from April (1.00, SE = 0.00) to March (0.97, SE = 0.03) in the Limantour herd. Cow survival in the Tomales herds was dependent upon the study year, time of year and age class, according to the most parsimonious known-fate model (Tables 12 and 13). This model was slightly favored ($w_i = 0.64$) over the next best model that excluded condition at capture ($\Delta AIC_c = 1.97$, $w_i = 0.24$). I found no evidence that cow survival in the Tomales herds varied according to home range size, monthly rainfall or by herd. Cow survival in the Tomales herds exhibited a large decline from 1.00 (SE = 0.00) from 2005 – 2007 to 2007 – 2008, especially for old cows (ß$_{\text{age class}}$ = 1.55, SE = 0.73) (Figure 11).

Annual calf survival averaged 0.81 (SE = 0.02) at Pt. Reyes. Calf survival estimates varied among herds (KW $\chi^2 = 6.54$, $p = 0.04$), but were consistent among years (KW $\chi^2 = 0.16$, $p = 0.92$) (Table 14). Average calf survival was highest at D Ranch (0.87, SE = 0.01) and lowest at the Limantour herd (0.75, SE = 0.01).

Predictors of calf survival varied among herds. According to the most parsimonious known-fate model for the D Ranch herd (Tables 15 and 16), calf survival increased from April to March (ß$_{\text{time}}$ = 21.01, SE = 0.01) but did not vary according to year, sex, monthly rainfall, birth date or birth weight. Annual survival of Limantour calves had no relationship to any of the candidate predictors (Tables 17 and 18), although small sample sizes precluded including sex as a predictor ($n_{\text{fermale}} = 2$). The most parsimonious known-fate model for calf survival in the Tomales herds included birth weight, time of year and birth date as predictor variables (Tables 19 and 20). There was no evidence that calf survival in the Tomales herds varied by sex, monthly rainfall or herd. The best model was only slightly favored ($w_i = 0.65$) over the next best model that included study year ($\Delta AIC_c = 1.50$, $w_i = 0.31$), providing some evidence for annual variation in calf survival. Estimated monthly calf survival in the Tomales herds was lowest after birth ($\hat{S}_{\text{april}} = 0.94$, SE = 0.03) and increased through study years ($\hat{S}_{\text{march}} = 1.00$, SE = 0.002) (Figure 12). In the Tomales herds, calves that were born heavier (ß$_{\text{birth weight}}$ = 5.32, SE = 1.36) and earlier in the season (ß$_{\text{time of year}}$ = 0.34, SE = 0.12) had higher estimated annual survival rates than lighter and late-born calves (Figures 13 and 14).

Calf production averaged 0.67 calves: cow (SE = 0.05) and varied among herds (KW $\chi^2 = 6.91$, $p = 0.03$) and years (KW $\chi^2 = 3.56$, $p = 0.17$), based on radio-collared cows (Table 21). The D Ranch herd consistently exhibited the highest annual calf production ($\bar{x} = 1.00$ calf: cow, SE = 0.00). Annual calf production for the Limantour herd ($\bar{x} = 0.81$ calves: cow, SE = 0.12) increased throughout the study. Calf production was lowest in the Tomales herds ($\bar{x} = 0.60$ calves: cow, SE = 0.09), and declined approximately 40% from 0.71 calves: cow in 2006 – 2007 to 0.42 calves: cow in 2007 – 2008.

Matrix Model and Population Projections

Matrix models were parameterized with survival and calf production estimates from known-fate models, and estimates from the literature for stage classes lacking empirical data (Table 22). Based on matrix model results, all herds at Pt. Reyes showed a positive rate of increase. These results were supported by concurrent annual NPS census results. The D Ranch herd exhibited the greatest rate of increase ($\lambda = 1.26$), and NPS annual censes recorded an increase of 15 to 31 elk from 2005 to 2008. Models for the Limantour herd quantified a lower rate of increase than D Ranch ($\lambda = 1.20$), and the herd increased from approximately 29 to 37 elk from 2005 to 2008 according to NPS censes. The Tomales herds exhibited the lowest rate of increase ($\lambda = 1.16$), and according to NPS surveys, these herds grew from approximately 430 to 585 elk from 2005 to 2007 and then decreased to 459 elk in 2008.

Sensitivity and elasticity analyses revealed that annual survival of cows from three to nine years old (S_w) was the most influential vital rate on herd growth for all herds, and was responsible for approximately 33% of the variability in annual rates of increase (Figure 15). Calf survival was the second most important contributor to annual rates of change, but contributed approximately half as much as survival of elk from 3 to 9 years. The survival and fecundity rates of older cows (10+ years) contributed the least to annual herd growth (< 1%).

Based on population projection models, the D Ranch herd is predicted to increase the fastest from 28 elk in 2008 to 393 elk (95% CI = 157 – 626) by 2018 (Figure 16). The Limantour herd is also predicted to increase from 39 in 2008 to 389 elk (95% CI = 171 – 685) by 2018 (Figure 17). When the population projection model was parameterized with the average annual vital rates for the entire study, the Tomales herds are predicted to increase from 387 elk in 2008 to 2,200 elk (95% CI = 794 – 4185) by 2018 (2005 – 2008) (Figure 18). However, the Tomales herds were predicted to only grew from 387 elk in 2008 to 420 elk (95% CI = 316 – 538) in 2018 when the population projection model was parameterized with the vital rates from 2007 – 2008, a year when precipitation from the previous year was below average (Figure 19).

DISCUSSION

The goals of this study were to quantify vital rates and causes of mortality of tule elk at Pt. Reyes, and use this information to model future population abundances. Sensitivity and elasticity results showed that cow survival had the largest effect on population growth of elk, followed by calf survival. Although cow survival was consistent among years in the lower density D Ranch and Limantour herds, cow survival declined at the higher density Tomales herds following a drier than average year (2007 – 2008). Unlike cow survival, annual variations in calf survival were not consistently associated with herd density. Starvation was the primary cause of death for cows and calves, and was often associated with copper and selenium deficiencies. Based on these vital rate estimates, simulation models indicated that the D Ranch and Limantour herds will exhibit exponential-like growth for at least 10 years, which could lead to future human-wildlife conflict with local ranchers. Forecasts of future elk abundances are less certain for the Tomales herds, although models indicate that elk abundances will likely fluctuate relative to the previous year's precipitation.

Cow survival estimates at Pt. Reyes were consistent with other nonhunted elk populations (Ballard et al. 2000, Garrott et al. 2003, Larkin et al. 2003, Murrow et al. 2009), and similar to previous estimates for the Tomales herds (Howell et al. 2002). Cows were generally in poor condition when they died and the primary cause of mortality was starvation, which was often accompanied by copper and selenium deficiencies. Liver copper levels for dead cows (2.5 ppm, SE = 0.66) were well below the suggested critical threshold (20 ppm) for deer species (Barlow 1978), and below levels in elk at Tomales shortly after their reintroduction (5.9 ppm) (Gogan et al. 1989). Copper deficiency can lead to weight loss, poor coat condition and lowered reproductive rates (Handeland et al. 2008), and may have been responsible for the slow initial population growth at Pt. Reyes (Gogan 1986). Copper deficiency at Pt. Reyes is caused by low forage copper levels resulting from naturally low levels of copper in the soil and bedrock material (Gogan et al. 1989). Plant copper content at Pt. Reyes varies by species and is an important factor in elk forage selection (Roberts 2000). As an essential dietary trace mineral, selenium is also critical to elk metabolism, specifically as a necessary component for glutathione peroxidase production, which limits oxidative damages to cellular tissue. Selenium deficiency can cause decreased fecundity from stillbirths, retained placenta, abortions, mastitis and delayed conception (Robbins 1993). Selenium deficiency has cause reduced survival through lowered feeding efficiency and wasting syndrome (Knox et al. 1987). At Pt. Reyes, 4 dystocia-related mortalities were discovered within a 2-week period that had selenium levels below optimal ranges established for domestic ruminant species (Imhof 1983). Selenium deficiency at Pt. Reyes is likely due to low forage selenium levels. Selenium levels for most forage species at Tomales were lower than the suggested minimum requirements for cattle, and were at their lowest during the partuition period (Roberts 2000). Pregnant and lactating cows have elevated selenium needs for during this time, which also corresponds to the partuition period and grass senescence, I did not observed higher cow mortality rates during that time. Even still, depressed selenium levels may have affected calf survival at Pt. Reyes, as observed with fawn survival of black-tailed deer in the Latour State Forest of northern California (Flueck 1994). I was not able to quantify mineral levels for elk that survived the study. My results provide lend support to the conclusion that trace mineral deficiencies have the ability to regulate native ungulate populations, contrary to earlier belief (Fielder 1986).

As expected, predation was not a primary source of mortality, and therefore did not likely regulate elk survival rates at Pt. Reyes. Wolves (*Canis lupis*) and grizzly bears (*Ursus arctos horribilis*) can regulate ungulate populations directly through predation (Messier 1991, Skogland 1991) and indirectly through behavioral responses to the threat of predation (Laundre et al. 2001), but these species have been absent from Pt. Reyes since at least the 1850s (Van Atta 1946, Schmidt 1991). Although not directly observed in this study, mountain lions have been seen at Tomales (Howell et al. 2002), but are likely at low abundances at Pt. Reyes. Coyote densities may be increasing (Gates, personal communication), but little is known of their abundances and spatial use patterns. High levels of human visitation, little cover and low black-tailed deer densities may discourage mountain lions from using Tomales. However, the Limantour herd range receives less visitor use, has shrubbier and more forested habitats, and thus has the potential for greater predation pressure. Elk predations were only recorded in the Limantour herd. My observation of a mountain lion preying on a healthy adult tule elk is rare, and may be the first on record. Although natural predation does not appear to be having a population-level effect on elk, illegal poaching is likely occurring on bulls at Tomales (N. Gates, NPS, personal communication). The effects of poaching on the population dynamics of elk at Pt. Reyes, while potentially significant, were beyond the scope of this paper.

My estimate of Johne's disease prevalence for the Tomales herds was much lower (3%) than the previous estimate (47%) (Manning et al. 2003). I found Johne's disease in only 1 cow and the disease was not associated with any mortalities, which was unexpected given that Johne's disease was recognized early in Tomales elk (Jessup et al. 1981). Johne's disease is difficult to detect, and infected elk at Pt. Reyes often appear healthy and show lower morbidity than captive cervids (Manning et al. 1998, Manning et al. 2003). I observed clinical signs of Johne's disease (wasting, fecal pasting of the hocks and perineum and rough, light brittle coats) for numerous unmarked elk in the Tomales herd, suggesting that infection rates may be higher than our sampling results indicated. Even though rates of detection using fecal sampling were lower than tissue sampling, because Johne's disease sheds erratically in feces, repeated fecal sampling remains the preferred method for testing Johne's disease in live, wild ruminants because it is non-invasive (tissue sampling can only be done post-mortem and serum sampling requires a blood sample) and has a higher rate of detection than serum sampling [(agar gel immunodiffusion assay (AGID)] (Manning et al. 2003). I tested radio-collared cows biannually as opposed to repeated monthly sampling by Manning et al., which may explain some of the discrepancies in our results. However, tissue samples from mortalities from this study showed no signs of Johne's disease, reaffirming my estimates of low Johne's disease prevalence. Although I did not isolate Johne's disease from the D Ranch or Limantour herds, these herds may acquire the disease through increased interactions with cattle especially if these herds continue to increase as expected. I recommend continued monitoring because prevalence and the disease's impacts on elk may increase with herd size increases.

Cow survival showed little inter-annual variation in low density D Ranch and Limantour herds, but was negatively correlated with previous year's precipitation in the high density Tomales herds at Pt. Reyes. Annual climate variability can influence ungulate population dynamics, but the relationship is not straightforward or consistent between populations (Post and Stenseth 1999). Although reduced fecundity rates have been associated with lagged annual precipitation (Howell et al. 2002), my results provide evidence that precipitation also affected cow survival rates at Pt. Reyes. In northern regions, ungulate survival often declines following warmer, wetter and windier winters due to increased movement and foraging costs in deep snow and reduced neonatal survival (Mech et al. 1987, Post and Stenseth 1999). However, in Mediterranean regions like Pt. Reyes, mild winter temperatures are probably not as energetically demanding. In addition, seasonal precipitation in the winter leads to increased plant productivity which may have cumulatively effected elk survival.

Calf annual survival estimates were similar to predator-free populations elsewhere (Linnell et al. 1995, Murrow et al. 2009), higher than populations experiencing predation (Raithel et al. 2007, Barber-Meyer et al. 2008) but lower than previously reported at Pt. Reyes (0.81 – 0.86) (Gogan and Barrett 1987). The primary cause of calf mortality was starvation, which was often accompanied by selenium deficiency and septicemia. These results, along with very little evidence of predation, provide evidence for forage limitations driving annual elk recruitment. Selenium deficiency likely was a contributor to poor physical condition at death. As noted earlier, selenium deficiency can lead to wasting and a general lack of thrift. Selenium can affect calves in particular, through fatal congenital nutritional myodegeneration (white muscle disease) (Pourliotis et al. 2009). Calf selenium deficiency was likely associated with low forage selenium levels available to dams during the parturition period (Pavlata et al. 2003). Another primary source of calf mortality was septicemia, usually via the naval passage. The cause of septicemia was unknown but unlikely to be associated with capture, given the precautions taken to reduce contamination between elk and researchers.

Heavier calves born earlier in the season were more likely to survive, as reported elsewhere (Guinness et al. 1978, Singer et al. 1997, Smith and Anderson 1998). The timing and birth weight of calves are affected by the summer-autumn nutritional health of dams. Even minor reductions in dietary digestible energy could have resulted in delayed cow conception, differences in weight gains and lower calf survival (Cook et al. 2004). In northern climates, late-born calves have lower survival rates because they have less time to mature before winter

(Clutton-Brock et al. 1982) and early born calves have reduced survival rates from increased predation pressure (Singer et al. 1997). These selective forces were relaxed at Pt. Reyes as in other regions with mild climates (Sinclair et al. 2000, Moe et al. 2007), which could explain the low synchrony in calf birth observed at Pt. Reyes compared to other regions (Toweill and Thomas 2002). Unlike northern regions, the parturition period was likely the most challenging time for calves at Pt. Reyes because high quality, annual grasses begin to senesce in May. Early born calves may have been more likely to survive at Pt. Reyes because dams of early born calves may have had more high quality grasses available while lactating than dams of late born calves. The relative availability of high quality forage during the parturition period and its effect on dam condition during the calving season may be driving calf mortality in mild climates, as opposed to calf predation and winter survival in northern climates.

Calf survival rates were consistent among herds and years at Pt. Reyes, which was unexpected. Survival of young is usually the most temporally variable vital rate for ungulates, and calf: cow ratios in the Tomales herds previously exhibited annual variations (Howell et al. 2002). Temporal variations in calf survival rates have been attributed to precipitation and density dependence (Clutton-Brock et al. 1985, Gaidet and Gaillard 2008, Bonenfant et al. 2009), but identifying the link between calf survival and these factors can be difficult because of potentially confounding environmental stochasticity (Saether 1997). Given the observed annual variations in calf production and lack of variation in calf survival at the higher density Tomales herds, I suspect that pregnancy rates or birthing success may be more responsive to herd density than calf survival. Unlike in northern regions, the rutting period at Pt. Reyes (September – November) occurs at the end of the dry season, when forage was most limited. Annual calf production, therefore, may be regulated by the relative condition of cows during this period and a function of the timing and amount of annual precipitation. More research is needed to clarify this relationship.

Annual changes in elk abundance were most sensitive to variations in cow survival and most resilient to variations in senescent cow survival and fecundity, as reported elsewhere (Nelson and Peek 1982, Eberhardt 2002, Murrow et al. 2009). Vital rate elasticity estimates did not vary among herds, suggesting that the relationships were independent of density. In addition to elasticity, the magnitude of annual variability of a vital rate is thought to contribute to its importance to population change (Raithel et al. 2007). For ungulate populations, especially in northern climates, juvenile survival often exhibits high annual variation and therefore also accounts for a large portion of annual population change (Coulson et al. 2005). This was not the case at Pt. Reyes, indicating that calf survival played a small role in the population dynamics of elk at Pt. Reyes. The observed difference may have been due to Pt. Reyes' mild Mediterranean climate minimizing exposure-related winter mortalities. Inter-annual variability in over-winter survival can be greater in areas that experience high predation pressure (Mech et al. 2001), which Pt. Reyes does not. Calf production did show high annual variability, and therefore was probably a more important driver of annual population change than elasticity results suggested.

The D Ranch and Limantour herds were predicted by matrix models to show an irruptive pattern of growth commonly observed in ungulate populations that experience little predation pressure and are at low densities (Caughley 1970, Kaji et al. 2004, White et al. 2007). A similar pattern of irruptive growth was exhibited by the Tomales herds for 20 years after their reintroduction (Howell et al. 2002). The Tomales herds showed little evidence of density dependence during this period, so I believe that my density-independent predictions are valid for the D Ranch and Limantour herds. Unlike elk in the Tomales herds, elk in the D Ranch and

Limantour herds are not constrained by fences, and thus have much more available high quality habitat surrounding their current ranges. According to resource selection function analyses (Chapter 3), elk at Pt. Reyes prefer flat grasslands and ranchland. Given the predicted future abundances of elk and the close proximity of current elk range with ranches, conflicts between elk and local ranchers are likely to occur within the next ten years at Pt. Reyes as the growing elk population expands onto preferred habitat (Fretwell and Lucas 1969). Abundant elk on agricultural lands can cause economic losses, which lead to tension between ranchers and managing government agencies (Edge and Marcum 1990, Van Tassell et al. 1999, Brook 2009, Hegel et al. 2009). NPS managers at Pt. Reyes are strongly encouraged to develop a proactive plan to address this issue.

Projections of future elk abundances in the high density Tomales herds were less certain than the other herds because of large annual variations in estimated cow survival and calf production rates. Parameterizing the population projection model with average vital rate estimates for the Tomales herds may have led to biased projections because two of the three study years followed above-average precipitation. Using vital rate estimates following a drier than average year (2008), the population projection models predicted that the Tomales herds would show only slight growth. Carrying capacity estimates for the Tomales herds ranged from 91 to 1042 elk (Gogan 1986, Bartolome 1993, Roberts 2000) but after growing exponentially between 1978 and 1998 ($\overline{\lambda} = 0.2$), the Tomales herds fluctuated around a mean of 448 elk for ten years ($\overline{\lambda}_{1998\text{-}2008} = -0.004$), suggesting that the herd may have been at carrying capacity during the my study. Therefore, although density dependence was not added into population projection models for the Tomales herds, estimates of elk vital rates and their variability should have inherently incorporated some density dependence effects. Given the limited duration of this study, I was not able to estimate the effect that density dependence had on individual vital rates but with additional research this would be possible and would result in more realistic models and more accurate population projections.

CONCLUSIONS

Vital rates of tule elk at the low density D Ranch and Limantour herds at Pt. Reyes were consistent among years. Alternatively, cow survival and calf production at the high density Tomales herds were negatively correlated with precipitation the previous year. Both cow mortality, which had the largest impact on annual population change, and calf survival were caused primarily by malnutrition and related copper and selenium deficiencies. Predation on cows and calves by mountain lions and other predators was rare. Johne's disease was also much less prevalent than previously estimated, indicating that predation and disease played a small role in the current regulation of herds at Pt. Reyes. Combined with observations of significant population increases during El Nino events (Gogan and Barrett 1987, Howell et al. 2002), my results indicated that elk population regulation at Pt. Reyes was likely driven by cow survival and calf production rates, which were controlled by forage availability and varied as a function of cyclic precipitation levels. Population projections for the Tomales herds varied widely from stable to increasing because of large annual variation in observed cow survival and calf production rates during the study. However, abundances in the Tomales herds have been stable overall for 10 years after exhibiting 20 years of exponential growth, suggesting that these herds are at or near carrying capacity. Population projection models for the D Ranch and Limantour herds forecast irruptive population growth over the next 10 years. Herd sizes were likely to increase to approximately 400 elk in each herd by 2018. Given the initial pattern of growth in the Tomales herds, density dependence is not likely to slow growth for these herds during this period. Increased elk abundance is expected to lead to future conflicts between ranch owners and Pt. Reyes management. A proactive elk management plan is recommended.

LITERATURE CITED

Arnemo, J. M., T. Negard, and N. E. Soli. 1994. Chemical capture of free-ranging red deer (*Cervus elaphus*) with medetomidine-ketamine. Rangifer 14:123-127.

Ballard, W. B., H. A. Whitlaw, B. F. Wakeling, R. L. Brown, J. C. deVos, and M. C. Wallace. 2000. Survival of female elk in northern Arizona. Journal of Wildlife Management 64:500-504.

Barber-Meyer, S. M., L. D. Mech, and P. J. White. 2008. Elk calf survival and mortality following wolf restoration to Yellowstone National Park. Wildlife Monographs 169:1-30.

Barbknecht, A. E., W. S. Fairbanks, J. D. Rogerson, E. J. Maichak, and L. L. Meadows. 2009. Effectiveness of vaginal-implant transmitters for locating elk parturition sites. Journal of Wildlife Management 73:144-148.

Barlow, R. M. 1978. Enzootic ataxia of deer. Pages 68 - 71 *in* R. S. Montali, and G. Gimaki, editors. Symposia on the Comparative Pathology of Zoo Animals. Smithsonian Institute Press, Washington, D.C.

Bartolome, J. W. 1993. Range analysis of the Tomales Point Elk Range. Department of Environmental Science, Policy and Management. Project 1443. PX8530-93-206. Berkeley, CA.

Bedwal, R. S., and A. Bahuguna. 1994. Zinc, copper, and selenium in reproduction. Experientia 50:626-640.

Bonenfant, C., J. M. Gaillard, T. Coulson, M. Festa-Bianchet, A. Loison, M. Garel, L. E. Loe, P. Blanchard, N. Pettorelli, N. Owen-Smith, J. Du Toit, and P. Duncan. 2009. Empirical evidence of density dependence in populations of large herbivores. Pages 313-357 *in* Advances in Ecological Research.

Bradford, J. B., and N. T. Hobbs. 2008. Regulating overabundant ungulate populations: an example for elk in Rocky Mountain National Park, Colorado. Journal of Environmental Management 86:520-528.

Brook, R. K. 2009. Historical review of elk-agriculture conflicts in and around Riding Mountain National Park, Manitoba, Canada. Human-Wildlife Conflicts 3:72-87.

Buckland, S. T., K. P. Burnham, and N. H. Augustin. 1997. Model selection: An integral part of inference. Biometrics 53:603-618.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference. 2nd edition. Springer, New York, NY.

Caswell, H. 2001. Matrix population models: construction, analysis and interpretation. 2nd edition. Sinauer Associates, Inc., Sunderland, MA.

Caughley, G. 1970. Eruption of ungulate populations, with emphasis on himalayan thar in New Zealand. Ecology 51:53-72.

Cheatum, E. L. 1949. Bone marrow as an index of malnutrition in deer. New York State Conservation 3:19-22.

Clutton-Brock, T., F. Guinness, and S. Albon. 1982. Red Deer: behavior and ecology of two sexes. Edinburgh University Press, Edinburgh, UK.

Clutton-Brock, T. H., M. Major, and F. E. Guinness. 1985. Population regulation in male and female red deer. Journal of Animal Ecology 54:831-846.

Conover, M. R., W. C. Pitt, K. K. Kessler, T. J. Dubow, and W. A. Sanborn. 1995. Review of human injuries, illnesses, and economic losses caused by wildlife in the United States. Wildlife Society Bulletin 23:407-414.

Cook, J. G., B. K. Johnson, R. C. Cook, R. A. Riggs, T. Delcurto, L. D. Bryant, and L. L. Irwin. 2004. Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. Wildlife Monographs:1-61.

Cook, W. E., T. E. Cornish, S. Shideler, B. Lasley, and M. T. Collins. 1997. Radiometric culture of *Mycobacterium avium paratuberculosis* from the feces of tule elk. Journal of Wildlife Diseases 33:635-637.

Coulson, T., J. M. Gaillard, and M. Festa-Bianchet. 2005. Decomposing the variation in population growth into contributions from multiple demographic rates. Journal of Animal Ecology 74:789-801.

Eberhardt, L. L. 2002. A paradigm for population analysis of long-lived vertebrates. Ecology 83:2841-2854.

Edge, W. D., and C. L. Marcum. 1990. Elk and cattle on public lands: a new look at an old conflict. Western Wildlands 16:12-15.

Fielder, P. C. 1986. Implications of selenium levels in Washington mountain goats, mule deer and Rocky Mountain elk. Northwest Science 60:15-20.

Fischer, J., and D. B. Lindenmayer. 2000. An assessment of the published results of animal relocations. Biological Conservation 96:1-11.

Flueck, W. T. 1994. Effect of trace-elements on population dynamics: selenium deficiency in free-ranging black-tailed deer. Ecology 75:807-812.

Fretwell, S. D., and H. L. J. Lucas. 1969. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheoretica 19:16-52.

Gaidet, N., and J. M. Gaillard. 2008. Density-dependent body condition and recruitment in a tropical ungulate. Canadian Journal of Zoology 86:24-32.

Garrott, R. A., L. L. Eberhardt, P. J. White, and J. Rotella. 2003. Climate-induced variation in vital rates of an unharvested large-herbivore population. Canadian Journal of Zoology 81:33-45.

Garrott, R. A., P. J. White, J. J. Rotella, and F. G. R. Watson. 2009. The Madison headwaters elk herd: transitioning from bottom-up regulation to top-down limitation. Pages 489-517 *in* R. A. Garrott, P. J. White, and F. G. R. Watson, editors. The Ecology of Large Mammals in Central Yellowstone: Sixteen Years of Integrated Field Studies. Elsevier Academic Press, Oxford, UK.

Gates, N. B. 2000. Tomales Point elk census report, Fall 2000. National Park Service, unpublished report. Point Reyes National Seashore, California.

Gogan, P. 1986. Ecology of the tule elk range, Point Reyes National Seashore, California. Ph.D. dissertation, University of California, Berkeley.

Gogan, P. J. P., and R. H. Barrett. 1987. Comparative dynamics of introduced tule elk populations. Journal of Wildlife Management 51:20-27.

Gogan, P. J. P., D. A. Jessup, and M. Akeson. 1989. Copper deficiency in tule elk at Point Reyes, California. Journal of Range Management 42:233-238.

Grace, N. D., and P. R. Wilson. 2002. Trace element metabolism, dietary requirements, diagnosis and prevention of deficiencies in deer. New Zealand Veterinary Journal 50:252-259.

Greer, K. R., and W. W. Hawkins. 1967. Determining pregnancy in elk by rectal palpation. Journal of Wildlife Management 31:145-&.

Guinness, F. E., T. H. Clutton-Brock, and S. D. Albon. 1978. Factors affecting calf mortality in red deer (*Cervus elaphus*). Journal of Animal Ecology 47:817-832.

Handeland, K., A. Bernhoft, and M. S. Aartun. 2008. Copper deficiency and effects of copper supplementation in a herd of red deer (*Cervus elaphus*). Acta Veterinaria Scandinavica 50.

Hegel, T. M., C. C. Gates, and D. Eslinger. 2009. The geography of conflict between elk and agricultural values in the Cypress Hills, Canada. Journal of Environmental Management 90:222-235.

Hood, G. 2009. PopTools version 3.1.1. Available on the internet URL: http://www.cse.csiro.au/poptools.

Howell, J. A., G. C. Brooks, M. Semenoff-Irving, and C. Greene. 2002. Population dynamics of tule elk at Point Reyes National Seashore, California. Journal of Wildlife Management 66:478-490.

Imhof, N. 1983. Selenium deficiencies in lifestock. Animal Nutrition and Health June / July:22-25.

Jessup, D. A., B. Abbas, D. Behymer, and P. Gogan. 1981. Para-tuberculosis in tule elk in California. Journal of the American Veterinary Medical Association 179:1252-1254.

Johnson, D. E. 1951. Biology of the elk calf, *Cervus canadensis nelsoni*. Journal of Wildlife Management 15:396-410.

Kaji, K., H. Okada, M. Yamanaka, H. Matsuda, and T. Yabe. 2004. Irruption of a colonizing sika deer population. Journal of Wildlife Management 68:889.

Knox, D. P., H. W. Reid, and J. G. Peters. 1987. An outbreak of selenium responsive unthriftiness in farmed red deer (*Cervus elaphus*). Veterinary Record 120:91-92.

Langvatn, R., S. D. Albon, T. Burkey, and T. H. Clutton-Brock. 1996. Climate, plant phenology and variation in age of first reproduction in a temperate herbivore. Journal of Animal Ecology 65:653-670.

Larkin, J. L., D. S. Maehr, J. J. Cox, D. C. Bolin, and M. W. Wichrowski. 2003. Demographic characteristics of a reintroduced elk population in Kentucky. Journal of Wildlife Management 67:467-476.

Laundre, J. W., L. Hernandez, and K. B. Altendorf. 2001. Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, USA. Canadian Journal of Zoology 79:1401-1409.

Linnell, J. D. C., R. Aanes, and R. Andersen. 1995. Who killed Bambi? The role of predation in the neonatal mortality of temperate ungulates. Wildlife Biology 1:209-223.

Manning, E. J. B., T. E. Kucera, N. B. Gates, L. M. Woods, and M. Fallon-McKnight. 2003. Testing for *Mycobacterium avium* paratuberculosis infection in asymptomatic free-ranging tule elk from an infected herd. Journal of Wildlife Diseases 39:323-328.

Manning, E. J. B., H. Steinberg, K. Rossow, G. R. Ruth, and M. T. Collins. 1998. Epizootic of paratuberculosis in farmed elk. Journal of the American Veterinary Medical Association 213:1320-+.

Mech, L. D., R. E. McRoberts, R. O. Peterson, and R. E. Page. 1987. Relationship of deer and moose populations to previous winters snow. Journal of Animal Ecology 56:615-627.

Mech, L. D., D. W. Smith, K. M. Murphy, and D. R. MacNulty. 2001. Winter severity and wolf predation on a formerly wolf-free elk herd. Journal of Wildlife Management 65:998-1003.

Messier, F. 1991. The significance of limiting and regulating factors on the demography of moose and white-tailed deer. Journal of Animal Ecology 60:377-393.

Messmer, T. A. 2009. Human-wildlife conflicts: emerging challenges and opportunities. Human-Wildlife Conflicts 3:10-17.

Moe, S. R., L. P. Rutina, and J. T. du Toit. 2007. Trade-off between resource seasonality and predation risk explains reproductive chronology in impala. Journal of Zoology 273:237-243.

Moser, B. W., and G. W. Witmer. 2000. The effects of elk and cattle foraging on the vegetation, birds, and small mammals of the Bridge Creek Wildlife Area, Oregon. International Biodeterioration & Biodegradation 45:151-157.

Murrow, J. L., J. D. Clark, and E. K. Delozier. 2009. Demographics of an experimentally released population of elk in Great Smoky Mountains National Park. Journal of Wildlife Management 73:1261-1268.

Nelson, L. J., and J. M. Peek. 1982. Effect of survival and fecundity on rate of increase of elk. Journal of Wildlife Management 46:535-540.

Pavlata, L., J. Prasek, A. Podhorsky, A. Pechova, and T. Haloun. 2003. Selenium metabolism in cattle: Maternal transfer of selenium to newborn calves at different selenium concentrations in dams. Acta Veterinaria Brno 72:639-646.

Phillips, G. E., and A. W. Alldredge. 2000. Reproductive success of elk following disturbance by humans during calving season. Journal of Wildlife Management 64:521-530.

Post, E., and N. C. Stenseth. 1999. Climatic variability, plant phenology, and northern ungulates. Ecology 80:1322-1339.

Pourliotis, K., N. D. Giadinis, G. Sofianidis, G. D. Brellou, V. Psychas, N. Roubies, and H. Karatzias. 2009. Congenital nutritional myodegeneration (white muscle disease) in a red deer (*Cervus elaphus*) calf. New Zealand Veterinary Journal 57:244-247.

Raithel, J. D., M. J. Kauffman, and D. H. Pletscher. 2007. Impact of spatial and temporal variation in calf survival on the growth of elk populations. Journal of Wildlife Management 71:795-803.

Ripple, W. J., E. J. Larsen, R. A. Renkin, and D. W. Smith. 2001. Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. Biological Conservation 102:227-234.

Robbins, C. T. 1993. Wildlife feeding and nutrition. 2nd edition. Academic Press, New York, NY.

Roberts, S. L. 2000. Foraging ecology of tule elk at Tomales Point, Point Reyes National Seashore, California. MS thesis, University of Idaho, Boise, ID.

Roffe, T. J., M. Friend, and L. N. Locke. 1996. Evaluation of causes of wildlife mortality. Pages 324-348 *in* T. A. Bookhout, editor. Research and management techniques for wildlife and habitats. The Wildlife Society, Bethesda, MD.

Saether, B. E. 1997. Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. Trends in Ecology and Evolution 12:143-149.

Sams, M. G., R. L. Lochmiller, E. C. Hellgren, W. D. Warde, and L. W. Varner. 1996. Morphometric predictors of neonatal age for white tailed deer. Wildlife Society Bulletin 24:53-57.

Schmidt, R. H. 1991. Gray wolves in California - their presence and absence. California Fish and Game 77:79-85.

Seddon, P. J., D. P. Armstrong, and R. F. Maloney. 2007. Developing the science of reintroduction biology. Conservation Biology 21:303-312.

Sinclair, A. R. E., S. A. R. Mduma, and P. Arcese. 2000. What determines phenology and synchrony of ungulate breeding in Serengeti? Ecology 81:2100-2111.

Singer, F. J., A. Harting, K. K. Symonds, and M. B. Coughenour. 1997. Density dependence, compensation, and environmental effects on elk calf mortality in Yellowstone National Park. Journal of Wildlife Management 61:12-25.

Singer, F. J., and K. A. Schoenecker. 2003. Do ungulates accelerate or decelerate nitrogen cycling? Forest Ecology And Management 181:189-204.

Skogland, T. 1991. What are the effects of predations on large ungulate populations? Oikos 61:401-411.

Smith, B. L., and S. H. Anderson. 1998. Juvenile survival and population regulation of the Jackson Elk Herd. Journal of Wildlife Management 62:1036-1045.

Stewart, K. M., R. T. Bowyer, B. L. Dick, B. K. Johnson, and J. G. Kie. 2005. Density-dependent effects on physical condition and reproduction in North American elk: an experimental test. Oecologia 143:85.

Stewart, K. M., R. T. Bowyer, J. G. Kie, B. L. Dick, and R. W. Ruess. 2009. Population density of North American elk: effects on plant diversity. Oecologia 161:303-312.

Stewart, K. M., R. T. Bowyer, R. W. Ruess, B. L. Dick, and J. G. Kie. 2006. Herbivore optimization by North American elk: consequences for theory and management. Wildlife Monographs 167:1-24.

Stussy, R. J., S. L. Findholt, B. K. Johnson, J. H. Noyes, and B. L. Dick. 2000. Selenium levels and productivity in three Oregon elk herds. Northwest Science 74:97-101.

Telesco, R. L., F. T. Van Manen, J. D. Clark, and M. E. Cartwright. 2007. Identifying sites for elk restoration in Arkansas. Journal of Wildlife Management 71:1393-1403.

Toweill, D. E., and J. W. Thomas. 2002. North American elk: ecology and management. Smithsonian Institution Press, Washington, D.C.

Van Atta, C. E. 1946. Notes on the former presence of grizzly and black bears in Marin County, California. California Fish and Game 32:27-29.

Van Deelen, T. R. 2000. Simulation modeling to evaluate the restoration of an elk population to southern Illinois. Transactions of the Illinois State Academy of Science 93:47-61.

Van Tassell, L. W., C. Phillips, and B. Z. Yang. 1999. Depredation claim settlements in Wyoming. Wildlife Society Bulletin 27:479-487.

Wagner, F. H. 2006. Yellowstone's destabilized ecosystem: elk effects, science, and policy conflict. Yellowstone's destabilized ecosystem: elk effects, science, and policy conflict.:i-xiv, 1-371.

White, G. C. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study 46:120-138.

White, P. J., J. E. Bruggeman, and R. A. Garrott. 2007. Irruptive population dynamics in yellowstone pronghorn. Ecological Applications 17:1598-1606.

Willard, S. T., R. G. Sasser, J. C. Gillespie, J. T. Jaques, T. H. Welsh, and R. D. Randel. 1994. Methods for pregnancy determination and the effects of body condition on pregnancy status in Rocky Mountain elk (*Cervus elaphus nelsoni*). Theriogenology 42:1095-1102.

Zager, P., C. White, and G. Pauley. 2006. Elk ecology study IV: factors influencing elk calf recruitment. Project W-160-R-33. Idaho Department of Fish and Game. Boise, Idaho.

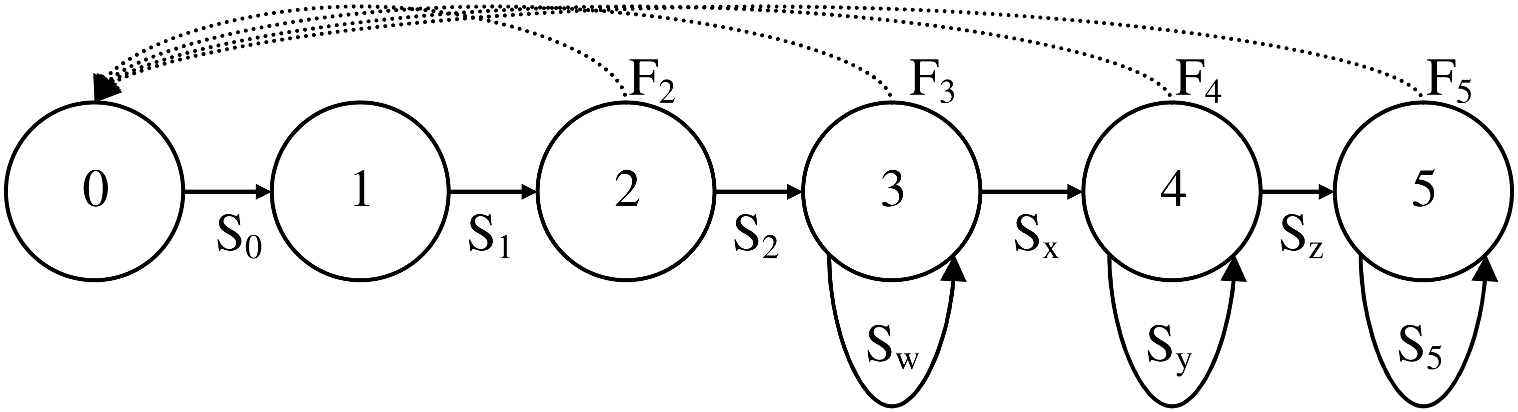

Figure 1. Life cycle of tule elk for stage-based matrix models, Point Reyes National Seashore, California. The model was female-based and post-breeding. Circles indicate stage classes [0 = newborn, 1 = calf (one year old), 2 = yearling (two years old), 3 = cow (three to nine years old), 4 = old cow (ten to 14 years old) and 5 = senescent cow (15 to 20 years old)]. Dashed arrows (F) indicate fecundity and solid arrows (S) indicate survival probabilities. Annual time periods began 1 April and ended 31 March.

Table 1. Predictor variables in candidate known-fate models quantifying tule elk cow or calf monthly and annual survival at Point Reyes National Seashore, California, 2005 – 2008.

Predictor variable	Value	Standardized / scaled	Cow models	Calf models
Age class	prime age (1-10 yrs.), senescent (>10 yrs.)	No	√	
Home range	ha	divided by 100	√	
Body condition at capture	chest girth / (total length + hind leg length)	No	√	
Time of year	1 - 12 (months)	No	√	√
Study year	2005-2006, 2006-2007 or 2007-2008	No	√	√
Rainfall, monthly	m	No	√	√
Herd*	North, Plateau, White Gulch and South	No	√	√
Sex	male, female	No		√
Birth date	day of year (1 - 365)	z-score		√
Birth weight	kg	divided by 10		√

*only considered for the Tomales herd models

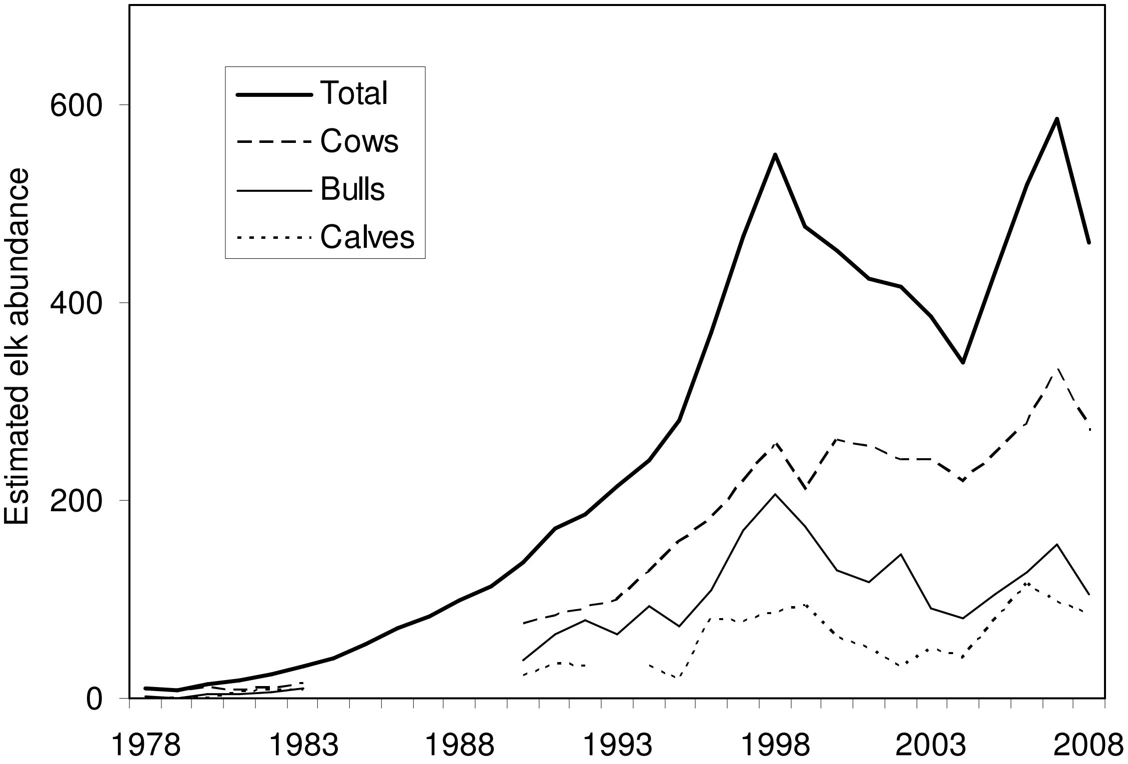

Figure 2. Estimated annual tule elk abundance in the Tomales Point Elk Reserve herds, Point Reyes National Seashore, California, 1978 – 2008. Data were from annual NPS surveys conducted each fall.

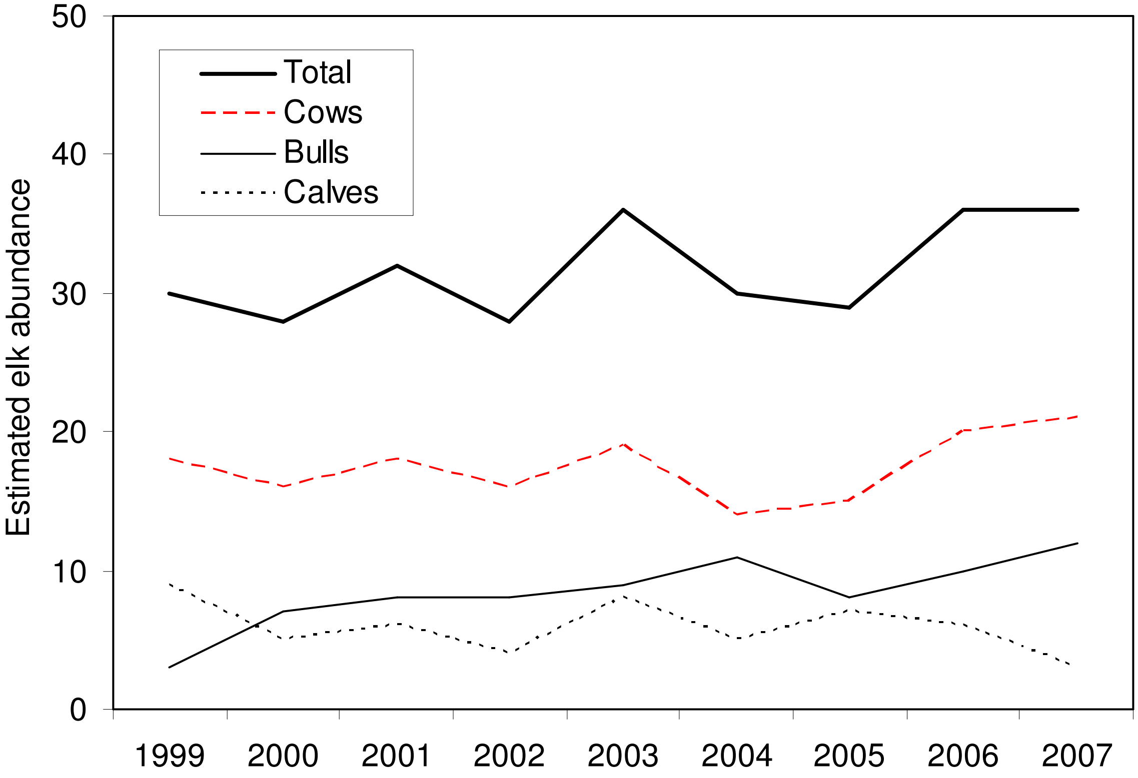

Figure 3. Estimated annual tule elk abundance in the Limantour herd, Point Reyes National Seashore, California, 1999 – 2008. Data were from annual NPS surveys conducted each fall.

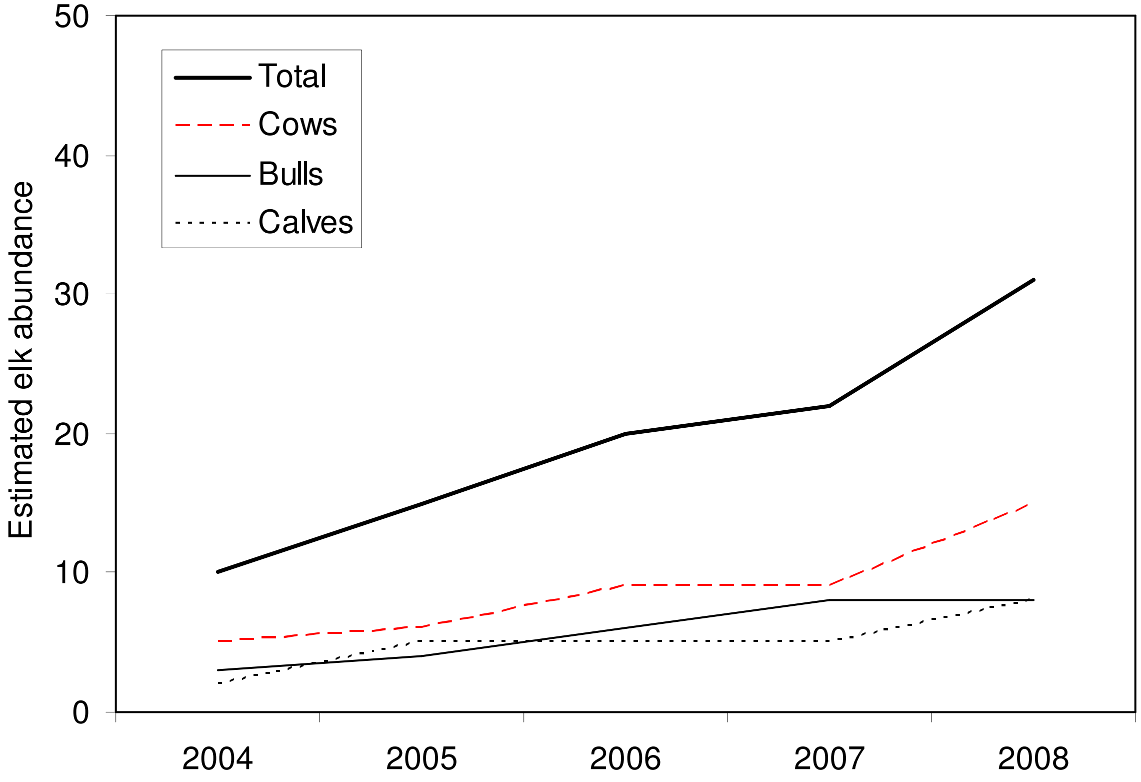

Figure 4. Estimated annual tule elk abundance in the D Ranch herd, Point Reyes National Seashore, California, 2004 – 2008. Data were from annual NPS surveys conducted each fall.

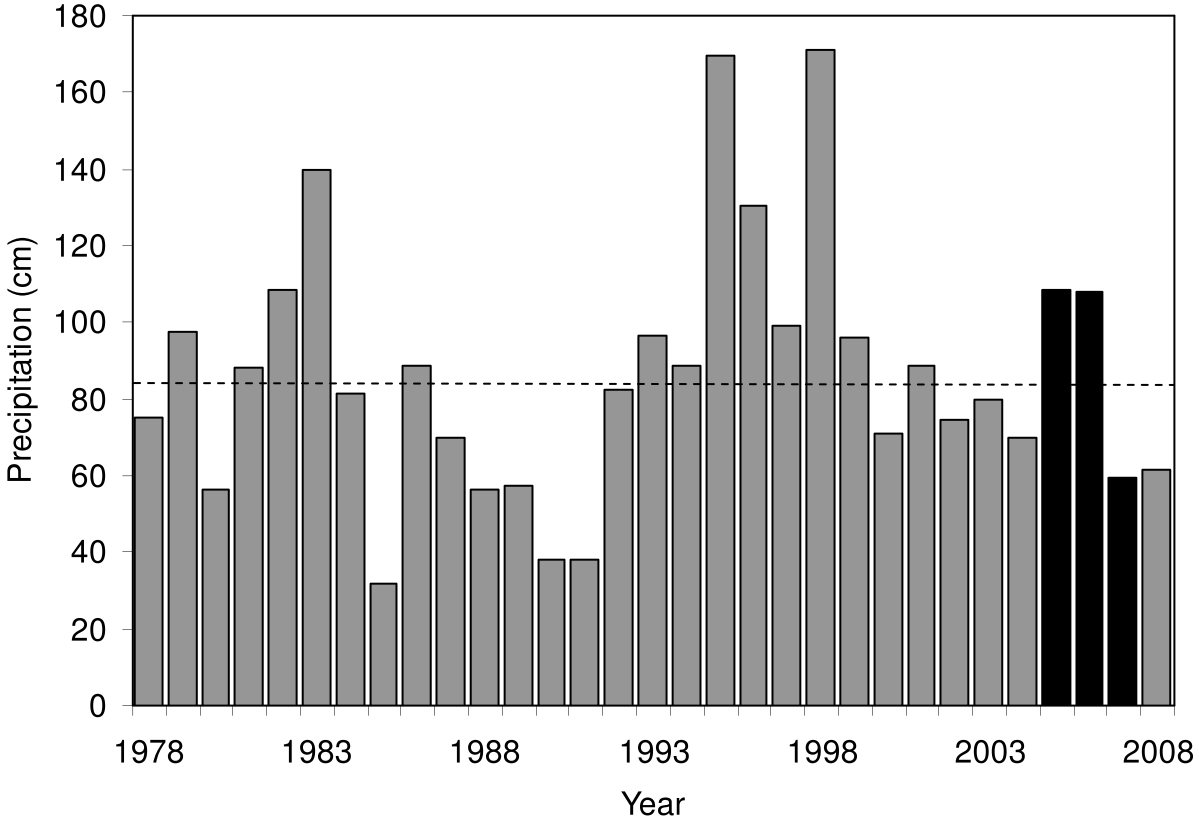

Figure 5. Annual precipitation (cm) at Bodega, California, 1978 – 2008. Data were compiled from the Bodega Ocean Observing Node. The dashed line indicates the average annual precipitation during this period (87 cm). The black bars indicate one year lagged annual precipitation values during the study.

Table 2. Results of linear regression analyses examining the relationship between the response variable, annual precipitation (lagged one year), and the predictor variables, annual calf: cow ratios and annual rate of population change (λ). Lagged precipitation and annual calf: cow ratios were statistically correlated (α = 0.10) in the Tomales Point Elk Reserve herds after the elk stopped exhibiting exponential growth (post-1998).

		p-value	
Herd	Years	Calf: cow ratio	λ
D Ranch	2004-2008	0.74	0.75
Limantour	1999-2008	0.46	0.53
Tomales	1978-2008	0.79	0.55
Tomales	1999-2008	*0.07*	0.49

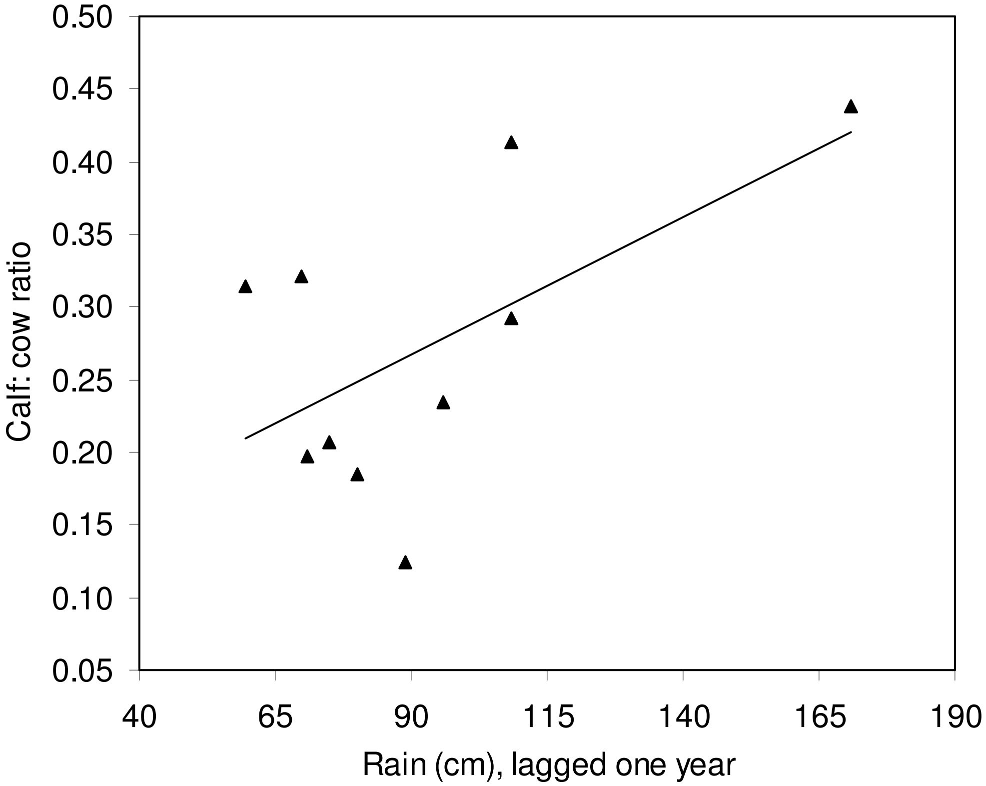

Figure 6. Scatter plot of precipitation (lagged one year) and tule elk calf: cow ratios at the Tomales Point Elk Reserve, Point Reyes National Seashore, California, 1999 – 2008. Solid line depicts the linear regression analysis result.

Table 3. Average age at capture (years) and fate of radio-collared tule elk cows by herd, Point Reyes National Seashore, California, 2005 – 2008. Age was quantified by cementum annuli analysis of the I-4 or I-1 tooth.

			Fate	
Herd	n	Average age	Survived	Died
D Ranch	3	2.0	100% (3)	0
Limantour	7	6.4	86% (6)	14% (1)
North (Tomales)	10	7.6	70% (7)	30% (3)
Plateau (Tomales)	4	7.8	50% (2)	50% (2)
White Gulch (Tomales)	11	5.6	73% (8)	27% (3)
South (Tomales)	7	5.8	86% (6)	14% (1)
Total	42	6.3	77% (32)	23% (10)

Table 4. Causes of mortalities for radio-collared tule elk cows and unmarked tule elk cows and bulls found opportunistically, Point Reyes National Seashore, CA, 2005-2008. Study years ran from 1 April to 31 March.

		2005-2006			2006-2007			2007-2008			Total		
Cause of death*	n	Collared ♀	♀	♂	Collared ♀	♀	♂	Collared ♀	♀	♂	Collared ♀	♀	♂
Starvation	11	0	0	0	0	0	0	6	3	2	6	3	2
Copper deficiency	7	0	0	0	0	0	0	0	6	1	0	6	1
Selenium deficiency	7	0	0	0	0	0	0	0	6	1	0	6	1
Dystocia	5	0	0	0	0	5	0	0	0	0	0	5	0
Trauma	3	0	0	1	0	0	0	1	0	1	1	0	2
Management action	2	0	0	0	0	0	0	0	1	1	0	1	1
Bronchopneumonia	1	0	0	0	0	0	0	1	0	0	1	0	0
Predation	1	0	0	0	1	0	0	0	0	0	1	0	0
Unknown	28	0	3	4	0	3	1	1	7	9	1	13	14
Total**	55	0	3	5	1	8	1	9	15	13	10	26	19

*Multiple causes of death possible for individual elk

** Total number of mortalites

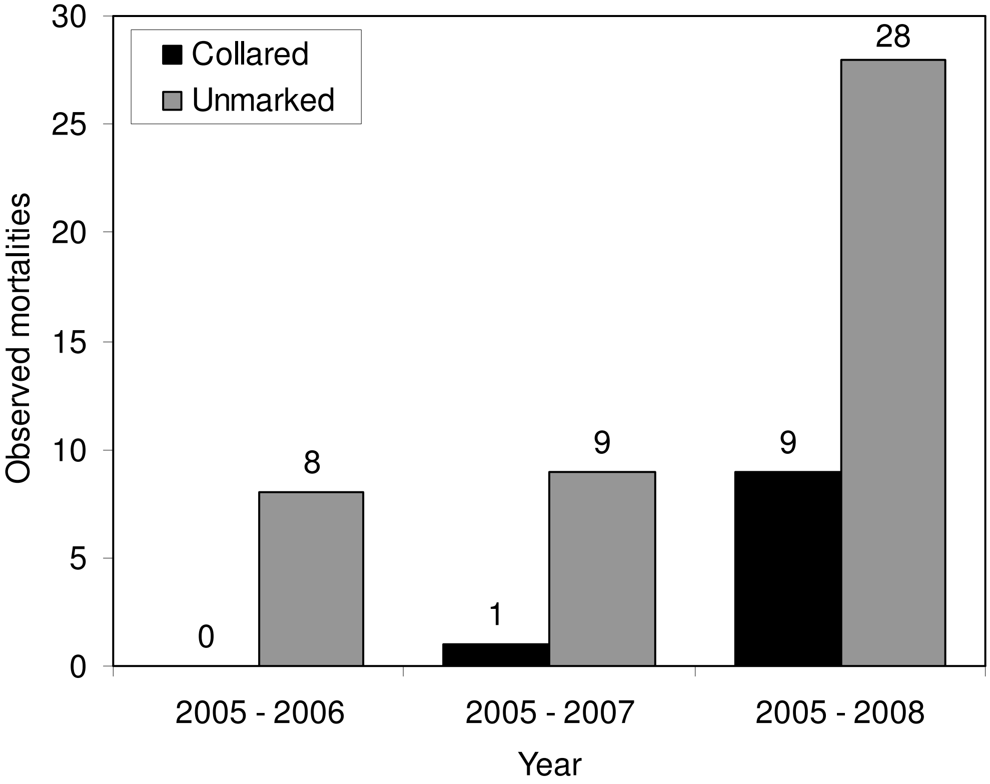

Figure 7. Bar graph of radio-collared tule elk cow and unmarked adult (cow and bull) mortalities discovered opportunistically by study year, Point Reyes National Seashore, California, 2005 – 2008. Study years ran from 1 April to 31 March.

Table 5. Sex and fate of radio-collared tule elk calves by herd, Point Reyes National Seashore, California, 2005-2008.

		Sex		Fate		
Herd	*n*	Male	Female	Survived	Died	Collar Drop
D Ranch	9	7	2	89% (8)	11% (1)	0
Limantour	8	3	5	63% (5)	37% (3)	0
North (Tomales)	13	4	9	62% (8)	39% (5)	0
Plateau (Tomales)	8	4	4	63% (5)	25% (2)	13% (1)
White Gulch (Tomales)	30	15	15	70% (21)	20% (6)	10% (3)
South (Tomales)	16	8	8	81% (13)	19% (3)	0
Total	84	49% (41)	51% (43)	71 % (60)	24% (20)	5% (4)

Table 6. Causes of mortalities for radio-collared tule elk calves and unmarked calves found opportunistically, Point Reyes National Seashore, CA, 2005-2008. Study years ran from 1 April to 31 March.

		2005-2006		2006-2007		2007-2008		Total	
Cause of Death*	n	Collared	Unmarked	Collared	Unmarked	Collared	Unmarked	Collared	Unmarked
Starvation	8	1	0	3	1	2	1	6	2
Septicimia	7	0	0	1	2	3	1	4	3
Selenium deficiency	6	0	0	2	3	0	1	2	4
Predation	2	1	0	1	0	0	0	2	0
Stillborn	2	0	0	0	1	0	1	0	2
Copper deficiency	1	0	0	0	0	0	1	0	1
Bronchopneumonia	1	0	0	1	0	0	0	1	0
Lungworm	1	0	0	0	0	0	1	0	1
Unknown	21	1	0	2	3	7	8	10	11
Total**	39	3	0	6	8	11	11	20	19

*Multiple causes of death possible for individual elk

** Total number of mortalities

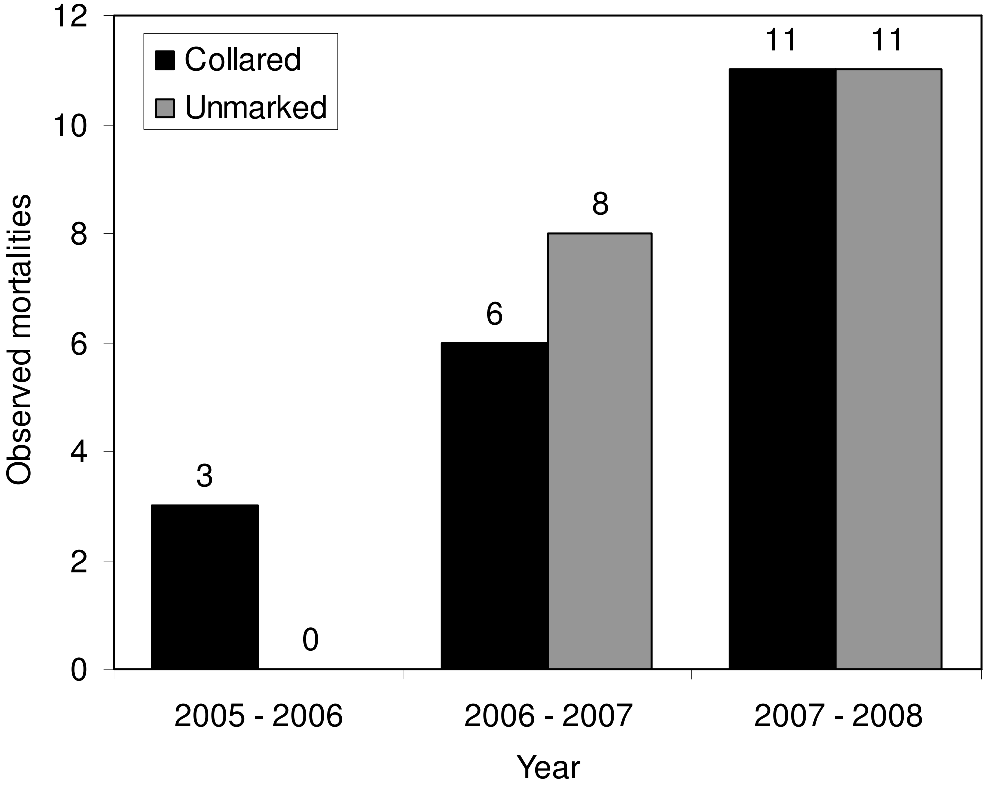

Figure 8. Bar graph of radio-collared tule elk calf and opportunistically-discovered calf mortalities by study year, Point Reyes National Seashore, California. Study years ran from 1 April to 31 March.

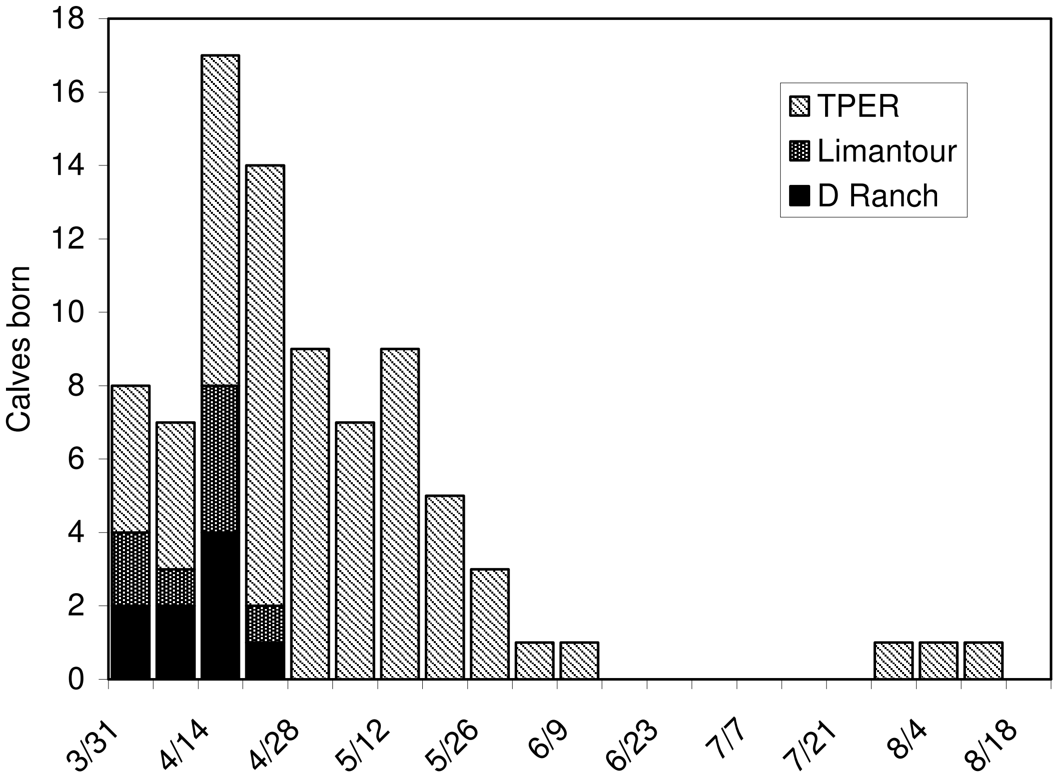

Figure 9. Stacked bar graph of the timing of birth, by week of the year, for radio-collared tule elk calves at Point Reyes National Seashore, California, 2005-2008. Dates indicate the first day of the week. The median birth date is 24 April.

Table 7. Candidate linear regression models quantifying birth weight of radio-collared tule elk calves, Point Reyes National Seashore, California, 2005 – 2008. Models are ranked in ascending order based on Akaike Information Criteria (AIC) and Akaike's weights (w_i). The most parsimonious model contains age at capture and sex as predictor variables. I estimated radio-collared calf birth weights by applying empirically-derived values of capture weight and estimated values of calf age at capture to the most parsimonious model, and quantifying intercept values.

Model	AIC	ΔAIC	w_i
Age at capture + Sex	351.33	0.00	0.77
Age at capture	353.76	2.43	0.23
Sex	413.61	62.28	0.00

Table 8. Results of the most parsimonious linear regression model quantifying birth weight of radio-collared tule elk calves, Point Reyes National Seashore, California, 2005 – 2008. Age at capture was the most influential predictor, followed by the sex of the calf. Empirically-derived values of capture weight and estimated values of calf age at capture were applied to the best model to estimate individual radio-collared birth weights. The intercept is an estimate of mean calf weight at birth for a female calf. Males were on average 1.0 kg (intercept Sex[Male]) heavier than female calves at capture. Estimated average daily weight gain was 0.89 kg/day.

Predictor	Estimate	SE	*p*-value
(Intercept)	10.97	0.41	< 0.001
Age at capture	0.89	0.09	< 0.001
Sex [male]	1.00	0.48	0.04

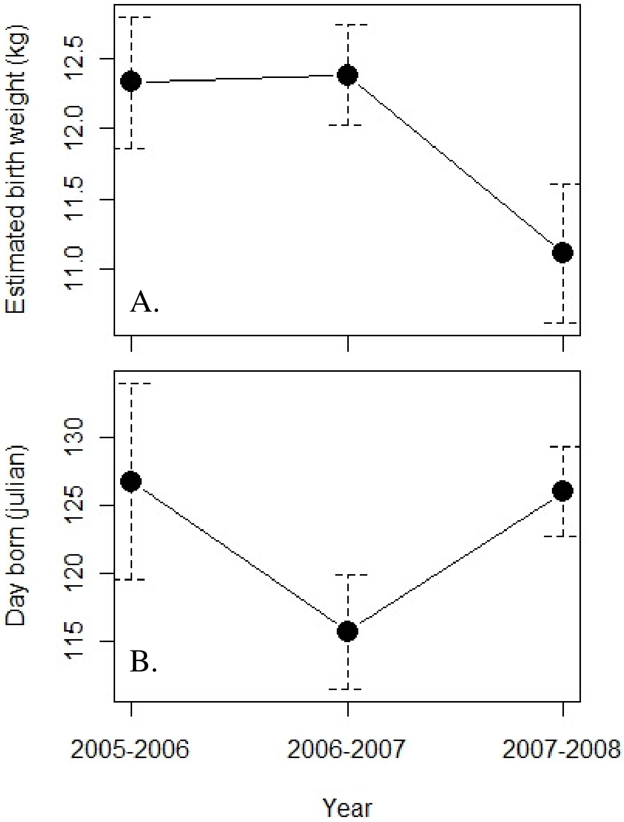

Figure 10. Estimated radio-collared tule elk calf birth weights (A) and birth dates (B) by study year, Point Reyes National Seashore, California, 2005 – 2008. Dashed lines indicate ± one SE from the mean. Birth weights were estimated by regressing estimated age at capture on capture weight and sex. Birth date was estimated using morphological characteristics (Johnson 1951, Sams et al. 1996). Study years ran from 1 April to 31 March.

Table 9. Estimated annual survival of tule elk cows by herd and year, Point Reyes National Seashore, California, 2005 – 2008. Annual survival estimates for tule elk cows in the D Ranch herd were based on biweekly visual observations of the elk herd (n = 8). Annual survival estimates for tule elk cows in the Limantour and D Ranch herds were quantified by model-averaging known-fate model results.

	Estimated annual survival of tule elk cows							
Herd	2005-2006	SE	2006-2007	SE	2007-2008	SE	Average	SE
D Ranch	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00
Limantour	0.96	0.04	0.94	0.06	0.96	0.04	0.96	0.05
TPER	1.00	0.00	1.00	0.00	0.79	0.08	0.93	0.07

Table 10. Candidate known-fate models for estimating annual survival of tule elk cows in the Limantour herd, Point Reyes National Seashore, California, 2005 – 2008. Models are listed in order of likelihood, based on AIC$_c$ values and Akaike's weights (w_i). The final annual survival estimate for tule elk cows ($\hat{S}_{cow}$) was quantified by model-averaging the derived parameters from the top models.

Model	AIC$_c$	ΔAIC$_c$	w_i	Model Likelihood	Parameters	Deviance
S(t)	14.51	0.00	0.24	1.00	2	10.45
S(.)	14.62	0.11	0.23	0.95	1	12.60
S(condition)	15.58	1.07	0.14	0.59	2	11.51
S(age class)	16.09	1.58	0.11	0.45	2	12.03
S(hr)	16.17	1.66	0.11	0.44	2	12.11
S(monthly rain)	16.54	2.03	0.09	0.36	2	12.48
S(year)	16.63	2.12	0.08	0.35	3	10.51

Table 11. Results of the most parsimonious known-fate model for estimating annual survival of tule elk cows in the Limantour herd, Point Reyes National Seashore, Calfornia, 2005 – 2008.

Predictor	Estimate	SE
(Intercept)	11.89	8.03
Time of year	-0.70	0.72

Table 12. Candidate known-fate models for estimating annual survival of tule elk cows at the Tomales Point Elk Reserve, Point Reyes National Seashore, Calfornia, 2005 – 2008. Models are listed in order of likelihood, based on AIC_c values and Akaike's weights (w_i). The final annual survival estimate for tule elk cows ($\hat{S}_{cow}$) was quantified by model-averaging the derived parameters from the top models.

Model	AIC_c	ΔAIC_c	w_i	Model Likelihood	Parameters	Deviance
S(year+t+age class+condition)	80.63	0.00	0.64	1.00	6	68.55
S(year+t+age class)	82.60	1.97	0.24	0.37	5	72.54
{S(year+t)}	85.84	5.21	0.05	0.07	4	77.80
S(year+age class+condition)	86.02	5.39	0.04	0.07	5	75.96
S(year+age class)	86.87	6.23	0.03	0.04	4	78.83
{S(year)}	89.42	8.79	0.01	0.01	3	83.40
S(age class+t)	97.89	17.26	0.00	0.00	3	91.87
S(t+condition)	99.38	18.75	0.00	0.00	3	93.36
S(age class)	100.85	20.21	0.00	0.00	2	96.83
S(t)	101.93	21.29	0.00	0.00	2	97.91
S(condition	101.98	21.35	0.00	0.00	2	97.97
S(.)	104.49	23.86	0.00	0.00	1	102.49
S(hr)	106.28	25.65	0.00	0.00	2	102.27
S(herd)	109.18	28.55	0.00	0.00	4	101.14

Table 13. Results of the most parsimonious known-fate model for estimating annual survival of tule elk cows at the Tomales Point Elk Reserve, Point Reyes National Seashore, Calfornia, 2005 – 2008. Predictor variables (in order of importance) were study year, time of year, age class [prime age (2 – 10 years old) = 0 and old (>10 years old) = 1] and condition at capture.

Predictor	Estimate	SE
(Intercept)	5.10	0.01
2006-2007	6.50	0.01
2007-2008	-13.61	10.47
Time of year	-0.30	0.12
Age class	1.55	0.73
Condition	35.14	20.35

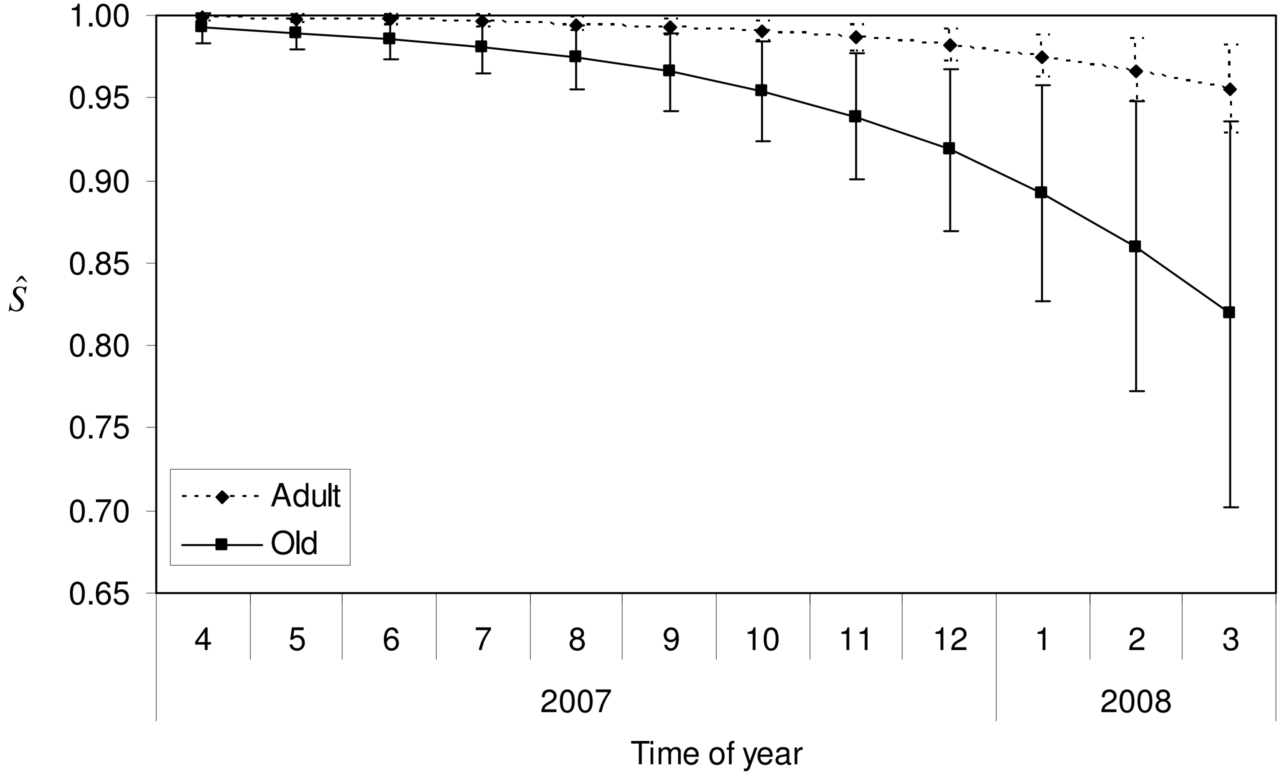

Figure 11. Estimated monthly survival ($\hat{s}$) of prime age (2 – 10 years old) and old (>10 years old) tule elk cows at the Tomales Point Elk Reserve, Point Reyes National Seashore, California, 2007 – 2008. Error bars indicate ± 1 SE from the mean.

Table 14. Estimated annual survival of tule elk calves by herd and year, Point Reyes National Seashore, California, 2005 – 2008. Annual survival estimates for tule elk calves were quantified by model-averaging known-fate model results.

	Estimated annual survival of calves							
Herd	2005-2006	SE	2006-2007	SE	2007-2008	SE	Average	SE
D Ranch	0.88	0.12	0.88	0.12	0.86	0.13	0.87	0.01
Limantour	0.73	0.18	0.74	0.18	0.79	0.14	0.75	0.01
TPER	0.84	0.07	0.76	0.09	0.80	0.08	0.80	0.01

Table 15. Candidate known-fate models for estimating annual survival of tule elk calves in the D Ranch herd, Point Reyes National Seashore, California, 2005 – 2008. Models are listed in order of likelihood, based on AIC_c values and Akaike's weights (w_i). The final annual survival estimate of tule elk calves ($\hat{S}_{calf}$) was quantified by model-averaging the derived parameters from the top models.

Model	AIC_c	ΔAIC_c	w_i	Model Likelihood	Parameters	Deviance
S(t)	9.91	0.00	0.55	1.00	2	5.74
S(.)	12.68	2.77	0.14	0.25	1	10.62
S(birth date)	13.58	3.67	0.09	0.16	2	9.41
S(sex)	14.05	4.14	0.07	0.13	2	9.88
S(weight)	14.43	4.52	0.06	0.10	2	10.26
S(year)	14.65	4.74	0.05	0.09	3	8.31
S(monthly rain)	14.77	4.86	0.05	0.09	2	10.60

Table 16. Results of the most parsimonious known-fate model for estimating annual survival of tule elk calves in the D Ranch herd, Point Reyes National Seashore, California, 2005 – 2008.

Predictor	Estimate	SE
(Intercept)	-19.22	1.07
Time of year	21.01	0.01

Table 17. Candidate known-fate models for estimating annual survival of tule elk calves in the Limantour herd, Point Reyes National Seashore, California, 2005 – 2008. Models are listed in order of likelihood, based on AIC_c values and Akaike's weights (w_i). The final annual survival estimate for tule elk calves ($\hat{S}_{calf}$) was quantified by model-averaging the derived parameters from the top models.

Model	AIC_c	ΔAIC_c	w_i	Model Likelihood	Parameters	Deviance
S(.)	20.76	0.00	0.31	1.00	1	18.71
S(birth date)	21.15	0.39	0.26	0.82	2	16.99
S(weight)	21.80	1.04	0.18	0.59	2	17.64
S(t)	22.50	1.74	0.13	0.42	2	18.34
S(year)	22.67	1.91	0.12	0.38	3	16.35

Table 18. Results of the most parsimonious known-fate model for estimating annual survival of tule elk calves in the Limantour herd, Point Reyes National Seashore, California, 2005 – 2008.

Predictor	Estimate	SE
(Intercept)	1.25	0.11

Table 19. Candidate known-fate models for estimating annual survival of tule elk calves at the Tomales Point Elk Reserve, Point Reyes National Seashore, California, 2005 - 2008. Models are listed in order of likelihood, based on AIC_c values and Akaike's weights (w_i). The final annual survival estimate for tule elk calves ($\hat{S}_{calf}$) was quantified by model-averaging the derived parameters from the top models.

Model	AIC_c	ΔAIC_c	w_i	Model Likelihood	Parameters	Deviance
S(weight+t+birth day)	118.39	0.00	0.65	1.00	4	110.32
S(weight+t+birth day+year)	119.88	1.50	0.31	0.47	6	107.73
S(weight+t)	124.23	5.85	0.04	0.05	3	118.19
S(weight)	129.97	11.58	0.00	0.00	2	125.95
S(t+birth day)	135.28	16.89	0.00	0.00	3	129.23
S(t+year)	143.93	25.54	0.00	0.00	4	135.86
S(t)	145.83	27.44	0.00	0.00	2	141.81
S(birth day+year)	146.52	28.13	0.00	0.00	4	138.45
S(birth day)	149.33	30.94	0.00	0.00	2	145.30
S(year)	153.51	35.12	0.00	0.00	3	147.46
S(.)	154.80	36.41	0.00	0.00	1	152.79
S(sex)	155.83	37.44	0.00	0.00	2	151.81
S(herd)	156.28	37.89	0.00	0.00	4	148.21

Table 20. Results of the most parsimonious known-fate model for estimating annual survival of tule elk calves at the Tomales Point Elk Reserve, Point Reyes National Seashore, California, 2005 – 2008. The predictor variables of annual survival of tule elk calves (in order of importance) were: estimated calf birth weight (kg x 10), time of year and calf birth date (z-score of day of year). Study year showed some correlation with survival of tule elk calves at Tomales, but was excluded from the best model.

Predictor	Estimate	SE
(Intercept)	-3.77	1.39
Weight	5.32	1.36
Time of year	0.34	0.12
Birth date	-0.76	0.24

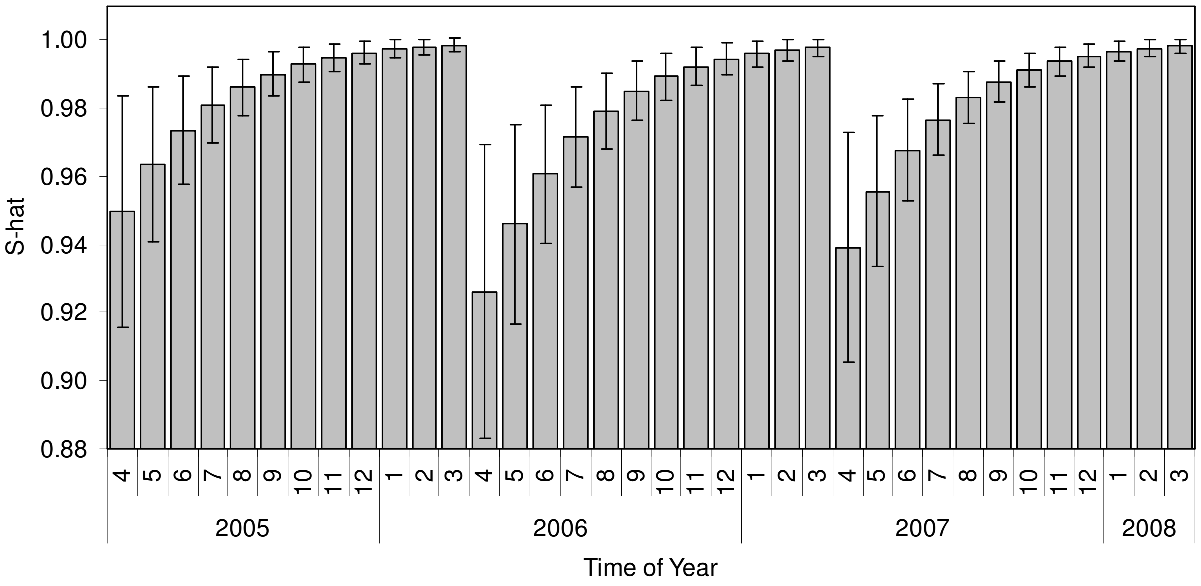

Figure 12. Estimated monthly survival of tule elk calves at the Tomales Point Elk Reserve, Point Reyes National Seashore, 2005 – 2008, based on model-averaged results from known-fate models. Dashed lines indicate ± 1 SE from the mean.

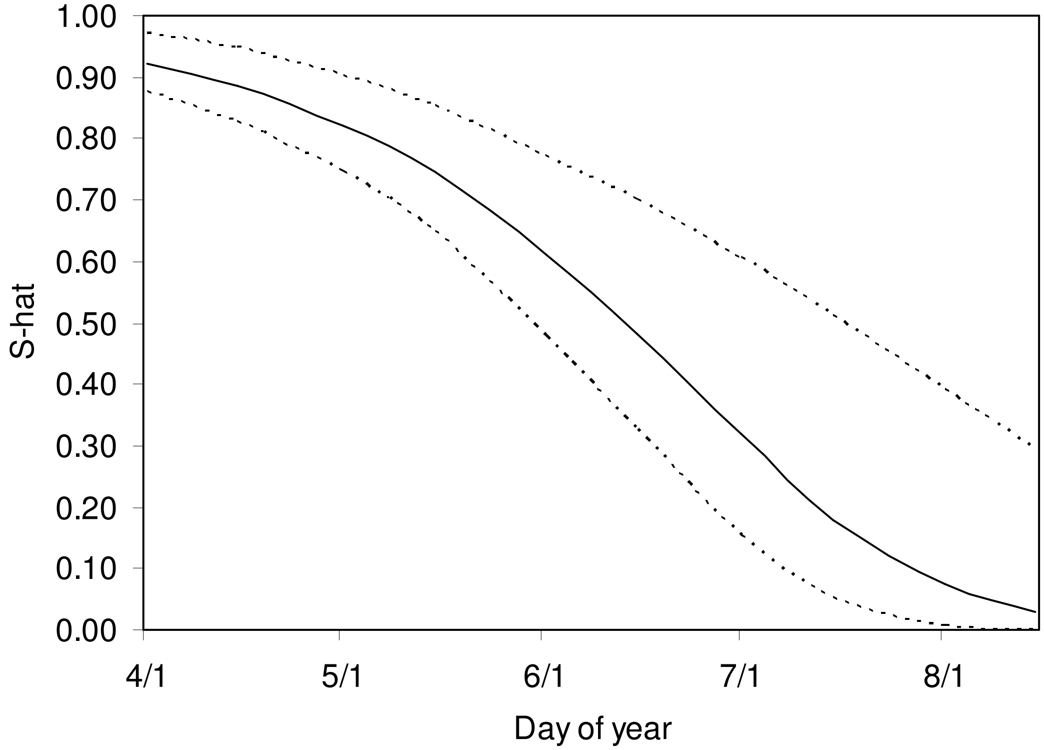

Figure 13. Effect of birth date (day of year) on estimated annual survival of tule elk calves at the Tomales Point Elk Reserve, Point Reyes National Seashore, 2005 – 2008, based on known-fate model results. Original z-score values used in the known-fate model were back-translated to date of the year for clarity. Dashed lines indicate ± 1 SE from the mean.

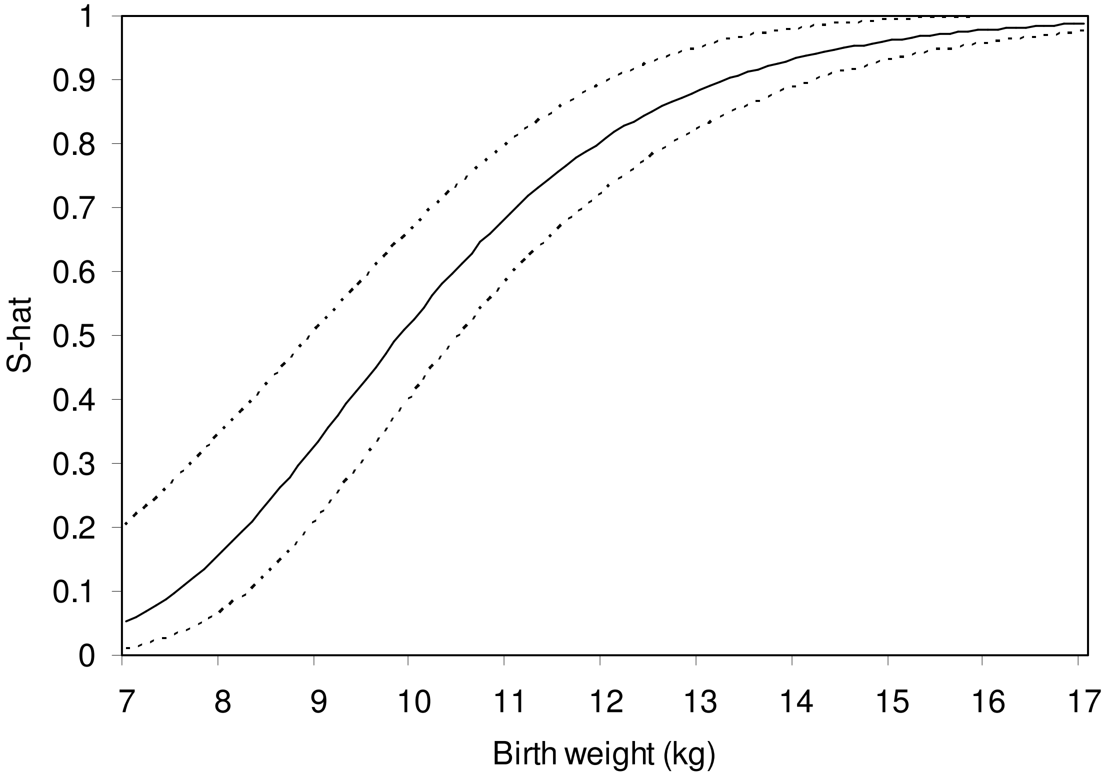

Figure 14. Effect of birth weight (kg) on estimated annual survival of tule elk calves at the Tomales Point Elk Reserve, Point Reyes National Seashore, 2005 – 2008, based on known-fate model results. Dashed lines indicate ± 1 SE from the mean.

Table 21. Tule elk calf production (calves: cow) by herd and year based on observations of radio-collared cow elk, Point Reyes National Seashore, 2005 – 2008.

	Calves:cow			
Herd	05-06	06-07	07-08	Average (SE)
D Ranch	1.00	1.00	1.00	1.00 (0.00)
Limantour	0.60	0.83	1.00	0.81 (0.12)
TPER	0.67	0.71	0.42	0.60 (0.09)
Overall	0.69	0.76	0.55	0.67 (0.05)

Table 22. Tule elk vital rate estimates and standard errors used in matrix and population projection models, Point Reyes National Seashore, California, 2005 – 2008. Vital rates for quantified separately for the D Ranch, Limantour and Tomales Point Elk Reserve herds.

Parameter	D Ranch	SE	Limantour	SE	TPER	SE
Stage 0 survival	0.86	0.13	0.74	0.16	0.80	0.07
Stage 0 calf production	0.00	0.00	0.00	0.00	0.00	0.00
Stage 1 survival	0.98	0.05	0.96	0.05	0.93	0.07
Stage 1 calf production	0.00	0.00	0.00	0.00	0.00	0.00
Stage 2 survival	0.98	0.05	0.96	0.05	0.93	0.07
Stage 2 calf production*	0.25	0.16	0.25	0.16	0.25	0.16
Stage 3 survival	0.98	0.05	0.96	0.05	0.93	0.07
Stage 3 calf production	0.95	0.46	0.81	0.12	0.60	0.09
Stage 4 survival	0.80**	0.02	0.80	0.02	0.80	0.20
Stage 4 calf production	0.67	0.15	0.67	0.15	0.60	0.09
Stage 5 survival*	0.72	0.02	0.72	0.02	0.72	0.08
Stage 5 calf production*	0.27	0.15	0.67	0.15	0.27	0.05
Calf sex ratio	0.50		0.50		0.50	
Initial population size (females, 2008)	18		26		250	

*data from Raithel et al. (2007)

*no old adults, Limantour data used

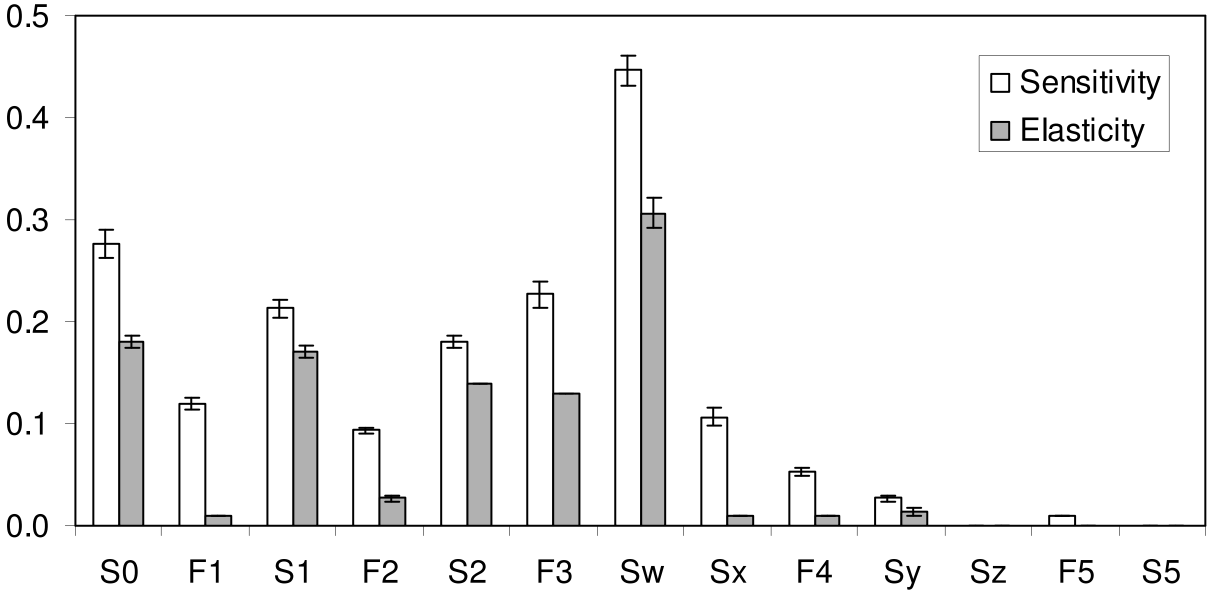

Figure 15. Estimates of sensitivity and elasticity of tule elk population growth to changes in individual vital rates, Point Reyes National Seashore, California, 2005 – 2008. Population growth was most sensitive to changes in the survival rate of cows from three to nine ages old (Sw). Error bars indicate ± 1 SE from the mean.

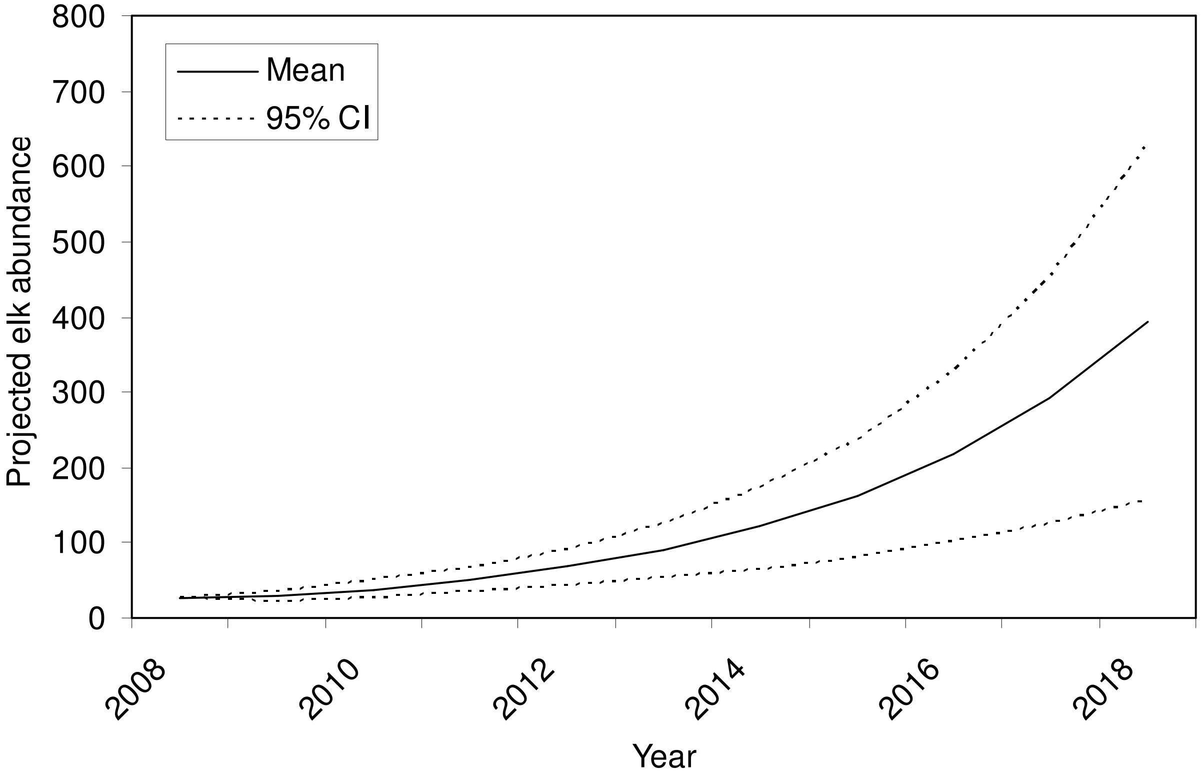

Figure 16. Projected tule elk abundance in the D Ranch herd, Point Reyes National Seashore, California, 2008 – 2018. Predictions are based on 10,000 Monte Carlo simulations of stochastic, density-independent population projections that were parameterized with estimated tule elk vital rates from 2005 – 2008.

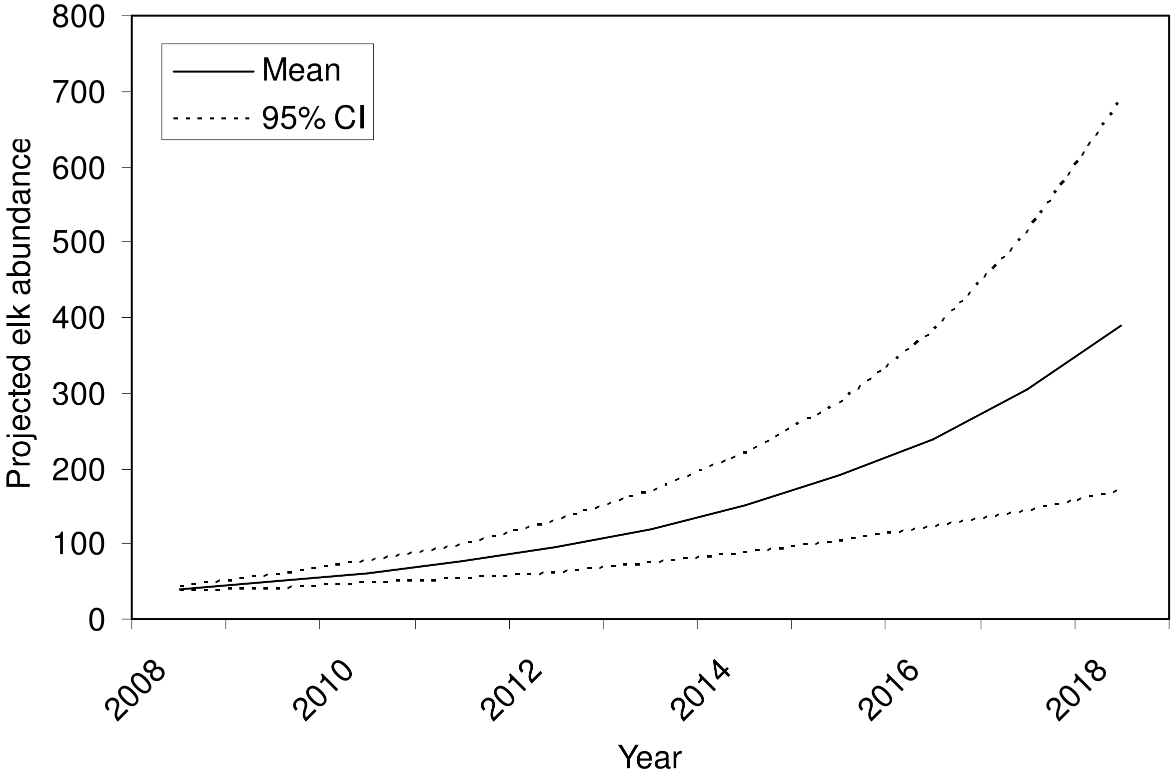

Figure 17. Projected tule elk abundance in the Limantour herd, Point Reyes National Seashore, California, 2008 – 2018. Predictions are based on 10,000 Monte Carlo simulations of stochastic, density-independent population projections that were parameterized with estimated tule elk vital rates from 2005 – 2008.

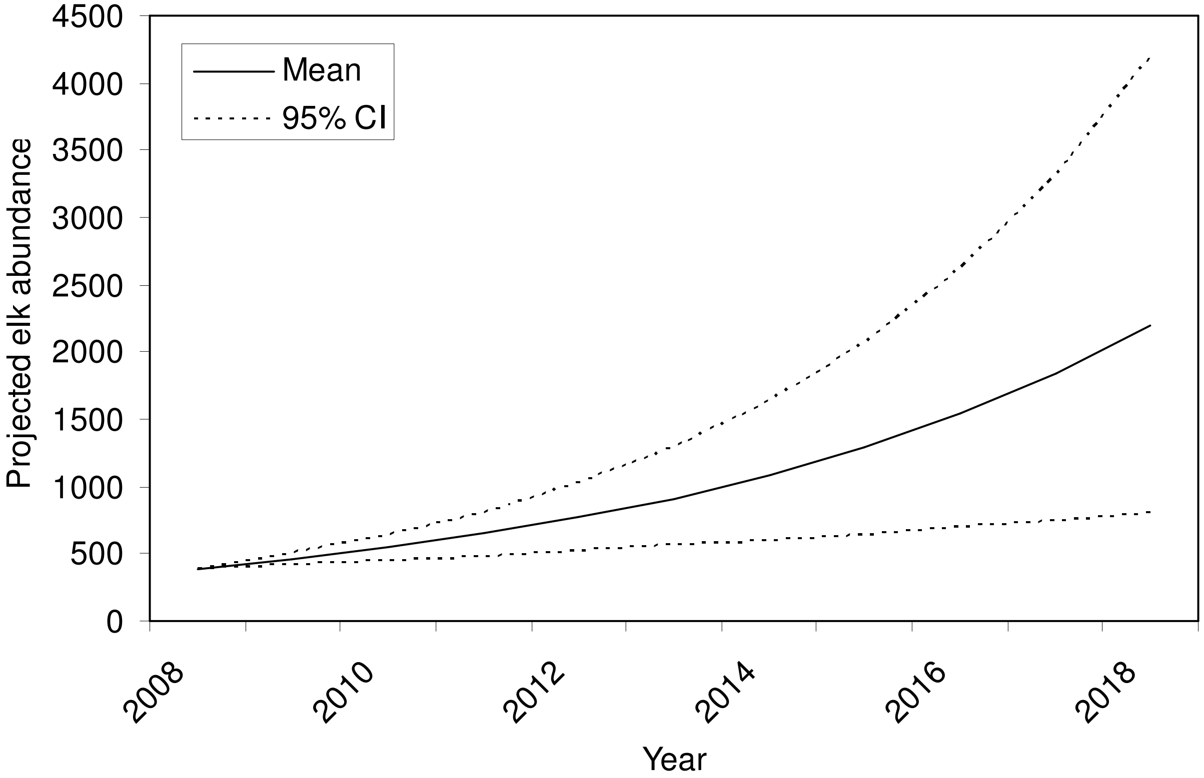

Figure 18. Projected tule elk abundance in the Tomales Point Elk Reserve herds, Point Reyes National Seashore, California, 2008 – 2018. Predictions are based on 10,000 Monte Carlo simulations of stochastic, density-independent population projections that were parameterized with estimated tule elk vital rates from 2005 – 2008.

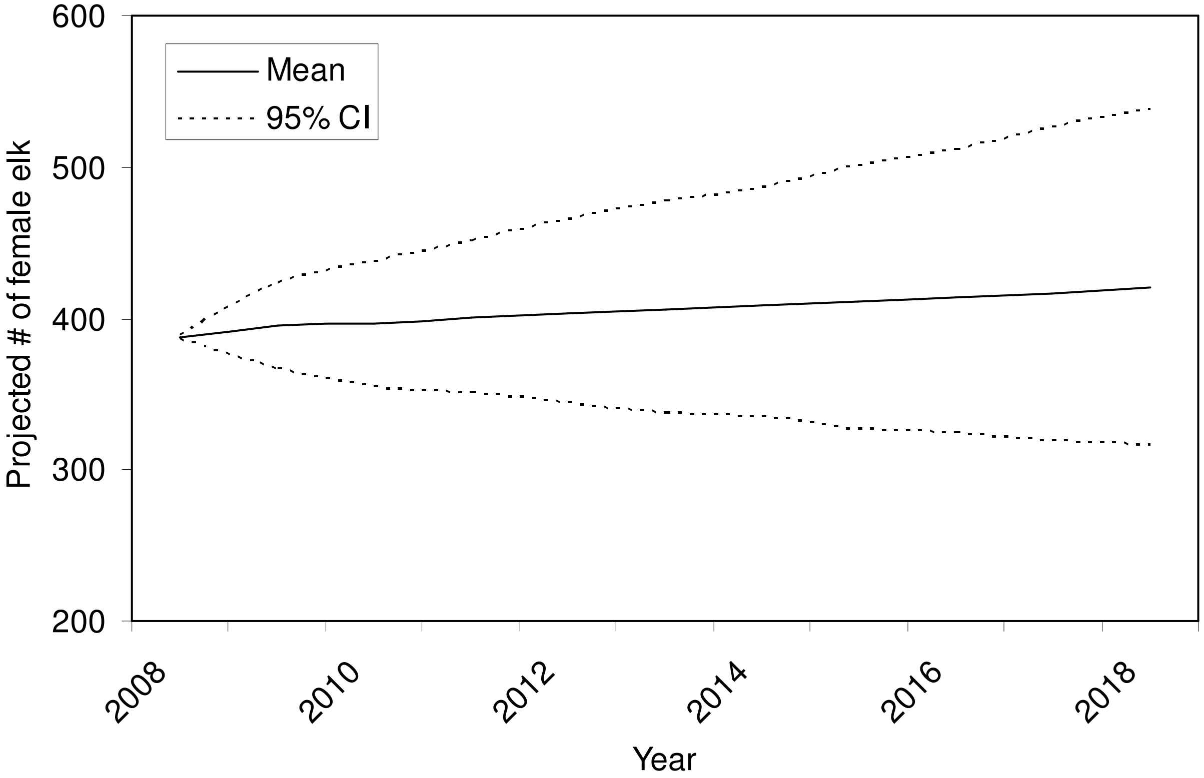

Figure 19. Projected tule elk abundance in the Tomales Point Elk Reserve herds, Point Reyes National Seashore, California, 2008 – 2018. Predictions are based on 10,000 Monte Carlo simulations of stochastic, density-independent population projections that were parameterized with estimated vital rate following a dry year (2007 – 2008).

APPENDIX

Resource selection function (RSF) coefficient estimates for the D Ranch herd of tule elk, Point Reyes National Seashore, California, 2005-2008.

Coefficient	Estimate	SE	*p*-value
(Intercept)	-2.898	0.144	< 0.001
SE aspect	0.531	0.356	0.136
Road	0.001	< 0.001	< 0.001

Resource selection function (RSF) coefficient estimates from the best model for Limantour herd of tule elk, Point Reyes National Seashore, California, 2005-2008.

Coefficient	Estimate	SE	*p*-value
(Intercept)	-4.988	0.487	< 0.001
Grass	2.671	0.443	< 0.001
Scrub	2.024	0.528	< 0.001
NW aspect	0.566	0.186	0.002
Slope	-0.036	0.011	0.002
Road	0.001	< 0.001	< 0.001
Grass * Scrub	-2.455	0.771	0.001
Scrub * Road	0.001	< 0.001	0.004

Resource selection function (RSF) coefficient estimates for the North herd of tule elk, Point Reyes National Seashore, California, 2005-2008.

Coefficient	Estimate	SE	*p*-value
(Intercept)	-1.488	0.182	< 0.001
Grass	0.386	0.181	0.033
Slope	-0.110	0.012	< 0 .001

Resource selection function (RSF) coefficient estimates for the Plateau herd of tule elk, Point Reyes National Seashore, California, 2005-2008.

Coefficient	Estimate	SE	*p*-value
(Intercept)	-1.406	0.165	< 0.001
NW aspect	-3.091	0.827	< 0.001
Slope	-0.063	0.010	< 0.001
Trail	0.001	< 0.001	< 0.001
NW aspect * Slope	0.142	0.046	0.002

Resource selection function (RSF) coefficient estimates for the White Gulch herd of tule elk, Point Reyes National Seashore, California, 2005-2008.

Coefficient	Estimate	SE	*p*-value
(Intercept)	-5.218	0.990	< 0.001
Grass	3.414	1.051	0.001
Scrub	3.429	1.008	0.001
NE aspect	1.618	0.200	< 0.001
SE aspect	2.315	0.307	< 0.001
SW aspect	-0.989	0.280	< 0.001
Slope	-0.069	0.019	< 0.001
Trail	0.002	< 0.001	< 0.001
SE aspect * Scrub	-2.303	0.569	< 0.001
Grass * Slope	0.068	0.032	0.032

Resource selection function (RSF) coefficient estimates for the South herd of tule elk, Point Reyes National Seashore, California, 2005-2008.

Coefficient	Estimate	SE	*p*-value
(Intercept)	-7.049	1.656	< 0.001
Grass	6.069	1.670	< 0.001
Scrub	5.430	1.664	0.001
NW aspect	1.255	0.239	< 0.001
SE aspect	-0.624	0.310	0.044
Slope	-0.058	0.013	< 0.001
Road	-0.002	< 0.001	< 0.001
NW aspect * Grass	-0.805	0.353	0.022
Grass * Scrub	-2.177	0.604	< 0.001

Resource selection function (RSF) candidate model list for the D Ranch herd of tule elk, Point Reyes National Seashore, California, 2005-2008.

Model	AIC	dAIC	*w*
SE aspect + road	1427.60	0.00	0.34
Road	1427.70	0.10	0.32
NE aspect + SW aspect + road	1428.60	1.00	0.20
Grass + NE aspect + SW axpect + Road	1430.00	2.40	0.10
Grass + NE aspect + SW aspect + Road + Trail	1431.90	4.30	0.04

Resource selection function (RSF) candidate model list for the Limantour herd of tule elk, Point Reyes National Seashore, California, 2005-2008.

Model	AIC	dAIC	*w*
Grass + Scrub + NW aspect + Slope + Road + (Grass*Scrub) + (Scrub*Road)	2171.50	0.00	0.95
Grass + Scrub + NW aspect + Slope + Road + (Grass*Scrub)	2177.70	6.20	0.04
Grass + Scrub + NW aspect + Slope + Road	2183.90	12.40	0.00
Grass + Scrub + NW aspect + Slope + Road + Trail	2185.10	13.60	0.00

Resource selection function (RSF) candidate model list for the North herd of tule elk, Point Reyes National Seashore, California, 2005-2008.

Model	AIC	dAIC	*w*
Grass + Slope	2351.00	0.00	0.71
Grass + Scrub + Slope + SRI + Trail	2352.80	1.80	0.29

Resource selection function (RSF) candidate model list for the Plateau herd of tule elk, Point Reyes National Seashore, California, 2005-2008.

Model	AIC	dAIC	*w*
NW aspect + Slope + Trail + (NW aspect * slope)	2130.40	0.00	0.96
Grass + Scrub + NW aspect + Slope + Trail	2138.00	7.60	0.02
NW aspect + Slope + Trail	2138.20	7.80	0.02

Resource selection function (RSF) candidate model list for the White Gulch herd of tule elk, Point Reyes National Seashore, California, 2005-2008.

Model	AIC	dAIC	*w*
Grass + Scrub + NE aspect + SE aspect + SW aspect + Slope + Trail + (Grass * Slope) + (SE aspect * Scrub)	2680.80	0.00	0.79
Grass + Scrub + NE aspect + SE aspect + SW aspect + Slope + Trail + (SE aspect * Scrub)	2683.50	2.70	0.21
Grass + Scrub + NE aspect + SE aspect + SW aspect + Slope + Trail + (Grass * Slope)	2696.10	15.30	0.00
Grass + Scrub + NE aspect + SE aspect + SW aspect + Slope + Trail	2703.40	22.60	0.00
Grass + Scrub + Forest + NE aspect + SE aspect + SW aspect + Slope + Trail	2703.60	22.80	0.00
Grass + Scrub + Forest + NE aspect + NW aspect + SE aspect + SW aspect + Slope + Trail	2705.10	24.30	0.00

Resource selection function (RSF) candidate model list for the South herd of tule elk, Point Reyes National Seashore, California, 2005-2008.

Model	AIC	dAIC	*w*
Grass + Scrub + NW aspect + SE aspect + Slope + Road + (Grass * Scrub) + (NW aspect * Grass)	2357.60	0.00	0.83
Grass + Scrub + NW aspect + SE aspect + Slope + Road + (Grass * Scrub)	2360.80	3.20	0.17
Grass + Scrub + NW aspect + SE aspect + Slope + Road + (NW aspect * Grass)	2368.90	11.30	0.00
Grass + Scrub + NW aspect + SE aspect + Slope + Road	2373.20	15.60	0.00
Grass + Scrub + NE aspect + NW aspect + SE aspect + Slope + Road	2374.60	17.00	0.00
Grass + Scrub + NE aspect + NW aspect + SE aspect + Slope + SRI + Road	2375.60	18.00	0.00
Grass + Scrub + Forest + NE aspect + NW aspect + SE aspect + Slope + SRI + Road	2376.60	19.00	0.00
Grass + Scrub + Forest + NE aspect + NW aspect + SE aspect + Slope + SRI + Road + Trail	2378.40	20.80	0.00