GENETIC VARIABILITY, DEMOGRAPHY, AND HABITAT SELECTION IN A REINTRODUCED ELK (*CERVUS ELAPHUS*) POPULATION

by

JONATHAN MARK CONARD

B.S., Southwestern College, 2000
M.S., Kansas State University, 2003

AN ABSTRACT OF A DISSERTATION

submitted in partial fulfillment of the requirements for the degree

DOCTOR OF PHILOSOPHY

Division of Biology
College of Arts and Sciences

KANSAS STATE UNIVERSITY
Manhattan, Kansas

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Abstract

Understanding factors that influence genetic variability, demographic vital rates, and resource selection is important for conservation and management of wildlife populations. I examined factors influencing microsatellite variability, demographic vital rates, and habitat use for a reintroduced elk (*Cervus elaphus*) population at Fort Riley, Kansas based on data collected from 2003 – 2007. Levels of allelic richness, observed heterozygosity, and expected heterozygosity for the Fort Riley population were intermediate to other North American elk populations. Genetic variability in restored North American elk populations was not well explained by founding population size, number of founding populations, or number of years since the last translocation. I examined the influence of demographic vital rates on the rate of population change (λ) to test the hypothesis that variability in calf survival has a greater influence on rates of population change than adult survival. Survival for prime-age adult elk had the highest stage-specific elasticity value, but life-stage simulation analysis indicated that variation in calf survival had the highest correlation with variation in λ. These results suggest that calf survival varies temporally and is the vital rate most directly related to variation in λ for this population. I assessed the relative influence of risk-related and resource-related factors on elk habitat selection by comparing predictor variables included in top resource selection function models at the landscape and home range scales. All predictor variables, with the exception of fall and spring prescribed burns, were included in top models across seasons at both spatial scales. Elk selected low elevation areas, gentle slopes, edge habitat, and areas close to streams at both spatial scales. At the landscape scale, elk generally avoided roads and preferred areas on or near Fort Riley. At both spatial scales, elk used riparian woodlands more frequently than grasslands and selected for agricultural crops when seasonally available. These findings do not support the idea that risk-related factors are the primary determinant of elk habitat use at the landscape scale as has been found for ungulates in areas with natural predators.

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CHAPTER 1 - INTRODUCTION

In Kansas, the distribution of elk (*Cervus elaphus*) from the post-settlement period until extirpation has been described by Hoffmeister (1947) and Choate (1987). However, the historical and current status of elk in Kansas has not been reported following the reintroduction of free-ranging elk to the state. Reviewing the historical status of elk in Kansas may assist in understanding the ecological role of elk in prairie systems and provide background information that may be useful for better interpreting observed distributions and characteristics of current elk populations.

Historical status of elk in Kansas

Elk remains dating back to the middle Holocene (4000-8000 years before present) have been recovered in Kansas, and archaeological evidence suggests that by the late Holocene elk were distributed throughout much of the United States including all of Kansas and the Great Plains (O'Gara and Dundas 2002). Elk were utilized by Native American tribes in Kansas for a variety of purposes. Elk bones were present in faunal remains recovered from village sites along the Big Blue River that were inhabited from approximately 1757-1825 by members of the Kansa tribe (Molloy 1993). Cementum annuli analysis of bones recovered from the village site indicated that cervid remains were mostly of 2-5 year old individuals and that hunting took place primarily from January to September (Molloy 1993). Some northern Plains tribes may have hunted elk during the winter as an important source of meat when bison (*Bos bison*) herds were not available (McCabe 2002). Elk were probably hunted primarily for meat by Native American tribes in Kansas, but other documented uses included using bones and antlers for tools, hides for clothing and shelter, and upper canines as decorative ornamentation (McCabe 2002). Hunting of elk by native tribes in the Great Plains may have been dictated in part by the availability of bison. Bison were hunted preferentially when available, with elk and other cervids providing an important secondary source of meat during times of the year when bison were not readily available (McCabe 2002). In addition to evidence provided by faunal remains associated with Native American villages, the presence of elk in Kansas was also documented by early expeditions passing through the state. One of the earliest expeditions to document the presence of elk in the state was that of Lewis and Clark. On 5 July 1804, the Lewis and Clark expedition crossed to the Kansas side of the Missouri River in present day Doniphan County, and journal entries note that “Elk are plenty about those Praries” along with observations of a “great deel of Elk Sign” (Moulton and Dunlay 1986, pp. 350-351). The expedition of Zebulon Pike also observed elk while passing through Kansas during 1806. Pike sighted elk throughout the state and specifically mentions elk at locations along the Solomon River in north central Kansas and along the Arkansas River in central and southwest Kansas (Jackson 1966). Lt. James B. Wilkinson departed the Pike expedition near present day Great Bend, Kansas during October 1806 and proceeded downstream along the Arkansas River where he noted that “the herds of buffalo, elk, goat [pronghorn antelope (*Antilocapra americana*)], and deer, surpassed credibility.” (Barry 1972, p. 57). The Pike expedition hunted elk for meat throughout Kansas and Lt. Wilkinson used elk hides for canoes (Jackson 1966).

Written accounts compiled from other expeditions in the Great Plains during the time period from 1806-1857 indicated that elk were originally sighted most frequently in tallgrass prairie, but were not documented in this habitat later than 1832 (Shaw and Lee 1997). Elk were seen by expeditions in mixed grass prairie regions through 1857, although they may have been sighted less frequently than sightings reported earlier from tallgrass prairie regions (Shaw and Lee 1997). It appears that elk populations in Kansas were first extirpated from the eastern part of the state. This pattern of extirpation may have been caused by increased hunting pressure and habitat modification in this area of the state due to higher human population densities present in eastern Kansas during the early 1800s.

In addition to expeditions passing through the state, records from settlers, hunters, and newspaper accounts provide additional evidence of the distribution and economic importance of elk in the state from 1850-1900. J. R. Mead, a naturalist and hunter, saw no elk while traveling through eastern Kansas but noted that his first elk sighting occurred in 1859 along the Saline River, northwest of present day Salina, Kansas (Mead 1986). According to Mead, the eastern edge of elk distribution in Kansas from 1859-1864 was “a line drawn north and south through El Dorado, Butler County. All country west of that in Kansas was presumably ranged over by them. . .” (Hoffmeister 1947, p. 75). Mead also hunted elk and bison as late as 1863 in present day Sedgwick County along the Arkansas River (Mead 1986). Mead noted that elk were most abundant in the state north of the Smoky Hill River, and he saw herds of over 1,000 individuals crossing the Saline River near present day Lincoln, Kansas (Hoffmeister 1947). Elk herds of similarly large numbers were reported in the area up to 1866 (Cockrum 1952). As late as 1874, an article published in the Smith County Pioneer reported that "herds of elk feed in the sparsely settled portions during the winter time" (Fleharty 1995, pp. 26-27). Similarly, in 1875 the Ellsworth Reporter published a note indicating that "Antelope and Elk range over the hills in large numbers" (Fleharty 1995, p. 34). The drainages of the Smoky Hill, Solomon, and Saline rivers may indeed have been one of the last strongholds of elk in Kansas. Elk persisted in this region as long as any area of the state, with settlers reporting elk to be present in Ellsworth County as late as 1890 (Choate 1987). In 1875, Knox compiled a list of mammals in Kansas and reported that elk were "Quite common in the west parts of the state" (Knox 1875, p. 20). However, it is important to note that declines in elk populations had probably already begun even in western Kansas during this time period. Settlers arriving in western counties during the 1800s often reported that elk were already extirpated in these areas although bones were frequently encountered on the prairie (Choate 1987). Settlers in western Kansas last reported elk to be present in the state in 1890 (Choate 1987). Presumably, elk were indeed absent from the state after this time, and by 1905 reports were first published that formally indicated that the species had been extirpated from the state (Cockrum 1952).

Reintroduction of elk to Kansas

Following extirpation between 1890-1905, free-ranging elk were absent from the state for over 75 years. A small captive elk herd was reintroduced to state lands on the Maxwell Wildlife Refuge in central Kansas in 1951 from the Wichita Mountains National Wildlife Refuge, Oklahoma. This captive herd served as a source for subsequent reintroductions to other areas of the state. In 1981, the Kansas Department of Wildlife and Parks reintroduced 12 elk from Maxwell Wildlife Refuge to the Cimarron National Grassland in Morton County in southwestern Kansas. The Cimarron National Grassland is a 108,000-ac (43,725-ha) property managed by the U. S. Forest Service, and is characterized by shortgrass prairie vegetation with cottonwood (*Populus deltoides*) and saltcedar (*Tamarix ramosissima*) found along the Cimarron River.

Subsequent reintroductions to the Cimarron herd from various source herds (indicated in parentheses) took place in 1982 (Maxwell Wildlife Refuge, n = 6), 1984 (Oregon, n = 2), 1988 (Trinidad, Colorado, n = 3), and 1990 (Moise, Montana, n = 10). Elk from this herd use areas outside of the national grassland boundaries, including parts of northwestern Oklahoma and southeastern Colorado (Bian and West 1997). This herd increased to about 120 elk in the mid 1990s (West 1995) under light hunting pressure (harvest of < 10 elk/year), but was significantly reduced in 1994 and 1995 (total harvest of 80-85 animals in all 3 states) in response to crop damage complaints. Today the herd numbers around 50 elk and is not hunted in Kansas. A second free-ranging herd was established in 1986 on Fort Riley Military Installation in Geary and Riley counties in northeastern Kansas (Fig. 1.1). Fort Riley is an approximately 40,273 ha property managed by the U.S. Army, and training areas are characterized by tallgrass prairie vegetation with some riparian woodland areas. Elk were initially reintroduced to this area with the release of 12 animals from Maxwell Wildlife Refuge (Pitts et al. 1987). Additional elk were introduced to Fort Riley from Maxwell Wildlife Refuge in 1987 (n = 7), 1990 (n = 2), and 1992 (n = 2). Further translocations were made from source herds in Trinidad, Colorado (1988, n = 5), Moise, Montana (1990, n = 8), and Wind Cave National Park, South Dakota (1994, n = 18) for a total of 54 elk released. Like the Cimarron herd, this herd was lightly hunted initially (harvest of < 10 elk/year), but was significantly reduced (by 100 elk) over a 2-year period (1999-2000) as a result of crop damage complaints on neighboring private lands. Today the herd numbers approximately 120 animals and supports an annual harvest of 10-15 elk (Matt Peek, Kansas Department of Wildlife and Parks, unpublished data). The Fort Riley and Cimarron herds are the only free-ranging populations established through reintroduction efforts in the state.

Conclusions

The restoration of elk to Kansas has returned a native species to the tallgrass prairie ecosystem. However, restoration success is measured not only by successful demographic establishment of a population but by restoring the functional role of a species within a system (Higgs 1996). Ungulate populations play a direct role in shaping ecosystem processes (Hobbs 1996) and it is important to understand the ecological interactions of this species within the existing system.

In addition to understanding the ecology of elk in tallgrass prairie, it is also important to understand the dynamics of small and reintroduced populations. Reintroductions have frequently been used as a tool for establishing for conservation purposes (Griffith et al. 1989) and the success of reintroduction efforts may depend on understanding the long-term dynamics of reintroduced populations. Small populations are also frequently targeted for conservation efforts; with the long-term persistence of these populations potentially influenced by resource use patterns, demographic factors, and genetic variability. Understanding the influence of these factors on the elk population at Fort Riley may be useful for developing effective conservation and management strategies for other small or reintroduced populations. The past (Witmer 1990) and ongoing (Telesco et al. 2007) interest in elk reintroductions throughout North America make elk a particularly suitable species for studying the dynamics of reintroduced populations.

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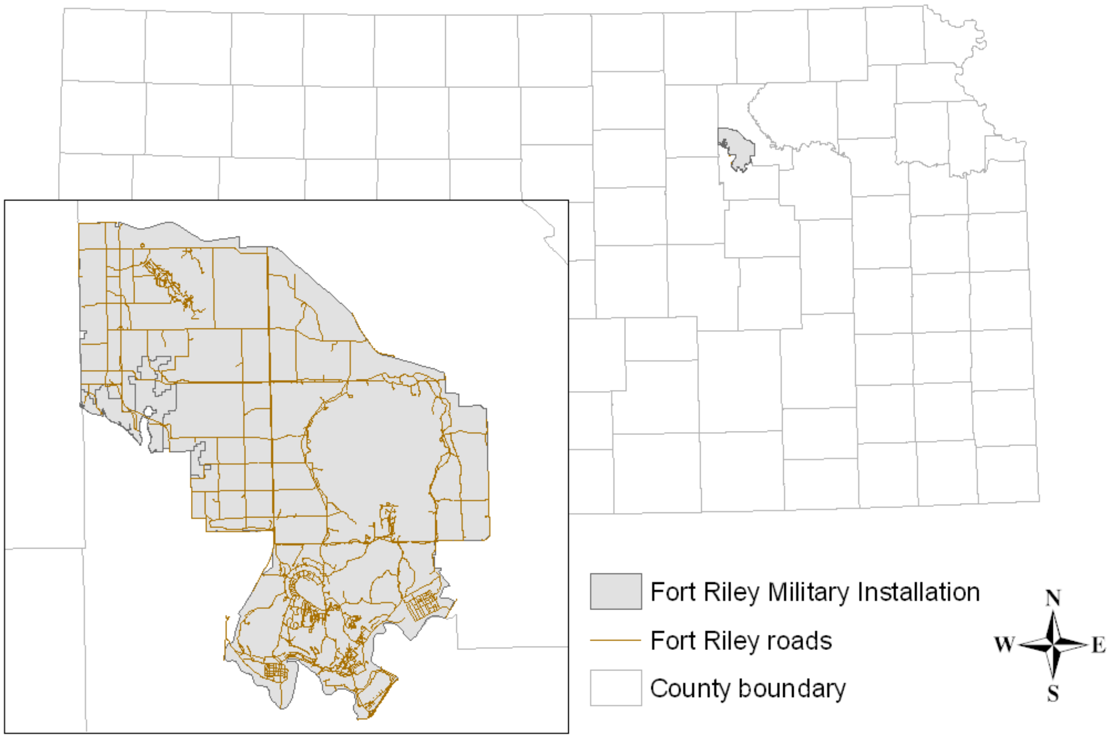
Figure 1.1. Location of Fort Riley Military Installation, Kansas.



CHAPTER 2 - THE INFLUENCE OF TRANSLOCATION STRATEGY AND MANAGEMENT PRACTICES ON GENETIC VARIABILITY IN A RESTORED ELK (*CERVUS ELAPHUS*) POPULATION

Abstract

Reintroduction and restoration efforts typically establish small and isolated populations that may experience reduced genetic variability due to founder effects and genetic drift. Understanding the genetic structure of these populations and maintaining adequate genetic diversity is important for long-term restoration success. We quantified genetic variability at six microsatellite loci for a restored population of elk (*Cervus elaphus*) in northeastern Kansas. Allelic richness, observed and expected heterozygosity were intermediate to levels reported in other North American elk populations. Current levels of genetic variability in restored North American elk populations were not well explained by founding population size, number of founding populations, or number of years since the last translocation. Simulation results suggest that mating system, temporal variability in population size, and population growth rate influence the retention of genetic variability in isolated populations. Our results have implications for understanding how translocation strategies and post-restoration management may influence genetic variability in restored populations.

Introduction

Translocations have frequently been used to reestablish wildlife populations to areas of suitable habitat within their historical range. The successful establishment of a translocated population may depend on the total number of animals released, habitat quality of the release site, location of the release site in relation to the historical range of the species, and biological characteristics of the species (Griffith et al. 1989; Wolf et al. 1996; Wolf et al. 1998). While the initial establishment of a demographically viable population is essential for restoration success, the long-term viability of a population may depend on the maintenance of sufficient levels of genetic variability (Frankham & Ralls 1998). Low levels of genetic variability in a restored population could increase extinction risk (Frankham & Ralls 1998; Saccheri et al. 1998), limit evolutionary potential, or lead to inbreeding depression and lowered reproductive success (Bouzat et al. 1998; Slate et al. 2000; Zachos et al. 2007). Restored populations often have lower levels of genetic variability than source populations (Fitzsimmons et al. 1997; Williams et al. 2002; Mock et al. 2004; Stephen et al. 2005), emphasizing the need to understand the influence of restoration and post-restoration management strategies on the retention of genetic variability.

Restored elk (*Cervus elaphus*) populations provide an opportunity to assess the influence of translocation strategy and management actions on genetic variability. Restored elk populations exhibit characteristics often found in other wildlife populations established through restoration efforts. These characteristics include relatively small initial population sizes (e.g., Williams et al. 2002, Mock et al. 2004, Stephen et al. 2005), a small number of founders (Griffith et al. 1989, Wolf et al. 1996), and relative isolation from existing wild populations (e.g., Maudet et al. 2002). In addition, a harem-breeding system and matriarchal social structure could make restored elk populations particularly susceptible to losing genetic variability (Clutton-Brock et al. 1988). Reduced levels of genetic variability have been associated with inbreeding depression (Zachos et al. 2007) and reduced lifetime breeding success in cervid populations (Slate et al. 2000).

The widespread and ongoing use of translocations as a management tool for restoring elk populations throughout North America (Wolfe et al. 2002) highlights the need to develop effective strategies to retain genetic variability in these populations. Elk were widely distributed in North America prior to European settlement, but their abundance and distribution were sharply reduced during settlement (O'Gara & Dundas 2002). Following this period of population decline, numerous translocations have been used to restore free-ranging elk populations to many locations within their historical range (Polziehn et al. 2000; Williams et al. 2002; Wolfe et al. 2002; Larkin et al. 2003; Hicks et al. 2007; Rosatte et al. 2007). The successful restoration of elk may be important for restoring aspects of ecosystem function; as large ungulate grazers impact carbon and nitrogen cycling (Frank & Grossman 1998), increase above-ground plant biomass (Frank 1998), and enhance the spatial heterogeneity of soil nutrients (Hobbs 1996; Augustine & Frank 2001) in grassland systems.

Elk were native to Kansas (Hoffmeister 1947) but were extirpated prior to 1905 (Cockrum 1952). Elk were restored to the state beginning in 1981 and subsequent restoration efforts beginning in 1986 were successful in establishing a free-ranging elk population at Fort Riley Military Reservation in northeastern Kansas (Conard et al. 2008). This population provides an opportunity to quantify the amount of genetic variability retained in a small, isolated population established using translocations from a variety of source herds. In addition, knowledge of current levels of genetic variability and restoration history for the Fort Riley population and additional restored elk populations in North America (Polziehn et al. 2000; Williams et al. 2002; Hicks et al. 2007) provides the opportunity to quantify the impact of translocation strategies and post-restoration management on the retention of genetic variability in restored elk populations.

The objectives of our research were to: (1) quantify allelic richness and heterozygosity in a restored elk population at Fort Riley, Kansas, (2) compare the level of genetic variability in this population to that present in native and restored herds in North America, (3) determine the influence of restoration strategies on the amount of genetic variability retained within restored herds, and (4) simulate the influence of post-restoration management strategies on future changes in allelic richness and heterozygosity using the Fort Riley population as a model.

Methods

Study area and population history

Fort Riley is located in Geary and Riley Counties in northeastern Kansas. There are 26,400 ha of undeveloped training areas on the installation. Land-cover on training areas of Fort Riley included grassland areas (≈ 80%) along with riparian woodlands and gallery forest (≈ 20%). Grassland areas of Fort Riley are characterized by typical native tallgrass prairie grasses including big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), switchgrass (*Panicum virgatum*), and indiangrass (*Sorghastrum nutans*) along with some areas of non-native vegetation including brome (*Bromus* sp.) and fescue (*Festuca* sp.).

Elk were translocated to Fort Riley beginning in February 1986 from a source herd located at Maxwell Wildlife Refuge near McPherson, Kansas (n = 12). Additional elk from Maxwell Wildlife Refuge were translocated to Fort Riley in 1987 (n = 7), 1990 (n = 2), and 1992 (n = 2). Elk were also released at Fort Riley from source herds located in Trinidad, Colorado (Spanish Peaks State Wildlife Area) (1988, n = 5), Moise, Montana (National Bison Refuge) (1990, n = 8), and Wind Cave National Park, South Dakota (1994, n = 18).

Following restoration, the elk population at Fort Riley grew to an estimated size of 300-350 individuals by 1999, until crop damage complaints on neighboring private lands prompted the state management agency to reduce population size by increasing harvest levels. The population size was between 75 – 100 individuals, with 81 animals counted during a 2007 aerial survey (Alan Hynek, Fort Riley Conservation Division, personal communication.).

Sample collection

Blood samples were drawn from 25 elk captured on Fort Riley between February 2005 and April 2006 (22 females, 3 males), using field procedures approved by the Kansas State University Institutional Animal Care and Use Committee (Protocol #2264). Blood samples were placed in lysis buffer and refrigerated until extraction. DNA was extracted from blood samples using DNeasy Blood and Tissue kits (Qiagen, Inc., Valencia, California). Microsatellite loci used for genetic analysis were: BM5004, BM4208, BM4107, BM888, BM1009 and RM006 (Kossarek et al. 1993; Bishop et al. 1994). These microsatellite loci were originally developed for domestic livestock (Kossarek et al. 1993; Bishop et al. 1994), but are polymorphic in elk (Talbot et al. 1996) and have been used in genetic studies of other elk populations (Williams et al. 2002; Williams et al. 2004; Hicks et al. 2007).

DNA from each sample was amplified in a total volume of 20 µl, which consisted of 2 µl DNA extract, 1 x PCR buffer, 2.7 mM $McCl_2$, 0.2 mM dNTPs, 0.1 µg/µl BSA, 0.8 M Betaine, 0.3 µM forward primer, 0.5 µM reverse primer, 0.5 µM M13 labeled forward primer and 1 unit of Taq polymerase (Promega Corporation, Madison, Wisconsin). Polymerase chain reaction (PCR) products were amplified and sized using a three primer system (Schuelke 2000). The forward primer had an 18 base pair tag (5'-TGTAAAACGACGGCCAGT-3') added to the 5' end. The tag was complementary to the M13 labeled third primer, which became incorporated during PCR, fluorescently labeling the amplicon. Cycle conditions were 94ºC for 5 minutes followed by 40 cycles of 94ºC for 30 sec, 54ºC for 30 sec and 72ºC for 30 sec; the 40 cycles were followed by a 30 minute extension period at 72ºC. Products were visualized on a 6% polyacrylamide gel on a LI-COR® 4300 DNA Analyzer, and analyzed with SAGA Generation 2 software. To ensure consistency in scoring across gels, a previously scored individual was included in subsequent gels. All homozygotes were repeated at least twice, and a portion of heterozygotes were reamplified, such that each single-locus genotype was repeated an average of 2.05 times.

Data analysis

Exact tests for deviation from Hardy-Weinberg equilibrium (HWE) (Guo & Thompson 1992) were conducted using GENEPOP 3.4 software (Raymond & Rousset 1995). If there is no biological basis for an observed deviation from HWE in a population, then significant departure from HWE could be the result of non-amplifying (null) alleles or genotyping errors that could influence subsequent analysis and conclusions (Oosterhout et al. 2004). Tests for linkage disequilibrium were also conducted using GENEPOP 3.4 software (Raymond and Rousset 1995) to determine if genotypes were independent between a given pair of loci (Rousset 2007). Sequential Bonferroni corrections were used to assess the significance of comparisons between loci when testing for linkage disequilibrium (Rice 1989). The average number of alleles per locus (A) and the percent of polymorphic loci were determined using GENALEX software (Peakall & Smouse 2006). Observed heterozygosity (H_O) and unbiased expected heterozygosity (H_e) were calculated using GENEPOP 3.4 (Raymond & Rousset 1995).

These measurements of genetic variability were compared to published data from native (Yellowstone National Park) (Williams et al. 2002) and restored elk populations in North America (Polziehn et al. 2000; Hicks et al. 2007). Direct comparisons were made to restored populations in northwestern Arizona, Oregon, northern New Mexico (Vermejo Park Ranch), Oklahoma (Wichita Mountains Wildlife Refuge), North Dakota (Theodore Roosevelt National Park) (Hicks 2004; Hicks et al. 2007), South Dakota (Custer State Park), and Pennsylvania (Williams et al. 2002). Comparisons of allelic richness (A) and expected heterozygosity (H_e) were made for five loci used in all studies (BM5004, BM4208, BM4107, BM888, and RM006) (Williams et al. 2002; Hicks et al. 2007). Comparisons were also made to Canadian elk populations that were entirely or partially founded by translocations, including populations in Banff National Park (Alberta), Jasper National Park (Alberta), French River (Ontario) and Burwash (Ontario) based on analysis of five microsatellite loci (BM5004, BM4208, BM4107, BM888, and BM1009) (Polziehn 2000; Polziehn et al. 2000). Mean allelic richness and expected heterozygosity were compared between populations with a Kruskal-Wallis test using SigmaStat software (Systat Software, Inc. San Jose, CA). Post hoc pairwise comparisons between populations were made using the Student-Newman-Keuls method.

Multiple linear regression (PROC REG, SAS Institute, Cary, NC) was used to model the influence of predictor variables on the average number of alleles per locus (A) and average expected heterozygosity (H_e) for 12 restored elk populations in the United States and Canada. Predictor variables for each elk population included number of founders, number of source herds used for translocation or supplementation, and number of years since the last known translocation. Founding histories were determined for elk populations in Banff National Park (Alberta), Jasper National Park (Alberta) (Lloyd 1927; Stelfox 1993; Polziehn 2000), French River (Ontario), Burwash (Ontario) (Polziehn 2000; Polziehn et al. 2000), northwestern Arizona, Vermejo Park Ranch (New Mexico), Chesnimus (Oregon), Wichita Mountains Wildlife Refuge (Oklahoma), Theodore Roosevelt National Park (North Dakota) (Halloran & Glass 1959; O'Gara & Dundas 2002; Hicks 2004), Pennsylvania, Custer State Park (South Dakota) (O'Gara & Dundas 2002; Williams et al. 2002), and Fort Riley Military Reservation (Kansas) (Conard et al. 2008). Allelic richness and average expected heterozygosity were calculated based on 4 common loci that were assessed for all populations (BM5004, BM4208, BM4107, and BM888) (Polziehn 2000; Williams et al. 2002; Hicks 2004). Model selection was based on values of Akaike's Information Criterion corrected for small sample size (AIC_c), with smaller AIC_c values indicating better model fit (Burnham & Anderson 1998). Models were considered equally parsimonious if the difference between AIC_c values for competing models was < 2. Normal probability plots of residuals were used to assess regression assumptions of normality (Ott & Longnecker 2001).

Expected future levels of genetic diversity at different potential population sizes were simulated for the Fort Riley elk herd using BOTTLESIM software (Kuo & Janzen 2003). BOTTLESIM estimates future levels of allelic richness, heterozygosity, and fixation probabilities by simulating the effects of genetic drift (random changes in allele frequencies that occur over time) based on initial allele frequencies and population size (Kuo & Janzen 2003). BOTTLESIM simulations are based on input parameters including initial (pre-bottleneck) population size, current population size, age at reproductive maturation, male:female ratio, breeding system (single-male mating vs. random mating), expected longevity, and observed allele frequencies. The degree of generation overlap can be specified, allowing for appropriate simulation of expected changes in genetic variability for populations with overlapping generations (Kuo & Janzen 2003). Input parameters for annual population size can also be specified, making it possible to examine the impact of post-restoration population growth rates on the retention of genetic variability over user-specified time intervals.

Input parameters used to simulate expected changes in genetic variability for the Fort Riley elk herd included a pre-bottleneck population size of 10,653 (based on the combined size of source herds at the time of translocation), longevity of 6 years (average age at capture for elk on Fort Riley), reproductive maturation at 2 years, an estimated current population size of 81 with approximately 65% cows in the population (based on 2007 Fort Riley aerial survey). Parameters for mating system were varied between a single male mating system (one male in the population doing all the breeding) to random mating (all males have an equal chance of reproducing). One hundred iterations were conducted for each simulation.

Projected levels of genetic variability under different management scenarios were simulated to explore the effects of population size, mating system, and population growth rate on future levels of allelic richness. In the first set of simulations, population size was held constant at 81 (current population size), 150 (potential target management level), or 300 (approximate maximum population size following restoration) with a 100 year simulation length. The relationship between annual variation in population size and genetic variability was explored by conducting additional simulations using variable population sizes, with annual population size values generated from a normal distribution with averages of 81, 150, or 300 individuals and a coefficient of variation of 0.20. This level of population variability is within the range reported for other elk populations based on survey data (Smith & Anderson 1998; Lubow et al. 2002). Variable population size values (with the parameters specified above) were generated using the POPTOOLS add-on for Microsoft Excel (Hood 2006). Variability in population growth rates were simulated over a 100 year period under a random mating system based on varying the maximum rate of population growth (r_m). Population size was determined using a discrete time formulation of the logistic growth equation (Johnson 1996) of the form:

$$N_{t+1} = N_t + r_m\,(1 - N_t/K)N_t$$

The maximum rates of population growth (r_m) that were simulated included 0.20 (high growth rate), 0.10 (moderate growth rate), 0.05 (low growth rate), and 0.0 (no population growth). The initial population size (N_t) of 81 and carrying capacity (K) of 300 for all simulations was based on the current census population size and expected maximum sustainable population size for the Fort Riley area. Population sizes at the end of the 100-year period approached carrying capacity (300) for all non-zero growth rates (high growth rate = 299, moderate growth rate = 299, low growth rate = 294). Growth rate values (r_m) were chosen to include a biologically reasonable range of variability in population growth rates, from zero population growth to near maximum growth rates reported for elk populations (Eberhardt et al. 1996).

Results

Fort Riley population

No evidence for departure from Hardy-Weinberg equilibrium was detected at any locus ($p > 0.05$). Following sequential Bonferroni correction, no evidence of linkage disequilibrium was detected between any pair of loci (table-wide significance level of $\alpha = 0.05$). All loci were polymorphic with an average of 3.0 alleles per locus (SE = 0.516) (Table 2.1). Unbiased expected heterozygosity values ranged from 0.47 - 0.76 with an average value of 0.52 (Table 2.1). Similar values were found for observed heterozygosity, with an average value of 0.52 and a range of 0.48 – 0.68 (Table 2.1).

Population comparisons

Allelic richness differed between elk populations in the United States (Williams et al. 2002; Hicks et al. 2007) (Kruskal-Wallis test, $H_8 = 15.9$, $p = 0.04$). Post hoc comparisons indicated that all populations differed from the restored Pennsylvania elk herd ($p < 0.05$), with fewer alleles present in the Pennsylvania herd. Allelic richness also differed when comparing restored and augmented populations from Canada (Banff, Jasper, French River, Burwash) and the Fort Riley population (Kruskal-Wallis test, $H_4 = 14.5$, $p =$

0.006). Pairwise comparisons indicated that allelic richness for the Fort Riley population was lower than those for the Banff (q = 5.61, $p < 0.05$) and Jasper National Park (q = 4.31, $p < 0.05$) elk populations (Table 2.2). The Banff and Jasper National Park populations had higher levels of allelic richness than the French River and Burwash populations (Table 2.2). No other pair-wise differences in allelic richness were present between populations in the United States or Canada.

Expected heterozygosity (H_e) did not differ between elk populations in the United States (Kruskal-Wallis test, $H_8 = 10.67$, $p = 0.62$) or populations in Canada (Kruskal-Wallis test, $H_4 = 8.27$, $p = 0.08$). The mean levels of heterozygosity and allelic richness observed in the Fort Riley population were intermediate to those found at the same loci in other restored elk populations (Table 2.2).

Modeling genetic variability

Model selection results for allelic richness indicated that all single variable models (number of founders, number of source populations, and number of years since last translocation event) were similarly parsimonious ($\Delta AIC_c < 2.0$) (Table 2.3). However, very little variation in allelic richness was explained by any of these top models ($r^2 < 0.12$ for top models). Top model regression coefficients were only slightly positive for number of founders ($\beta = 0.004$, SE = 0.004), number of source populations ($\beta = 0.12$, SE = 0.22), and number of years since last translocation event ($\beta = 0.009$, SE = 0.01).

Similarly, all single variable models were considered to be equally parsimonious for modeling expected heterozygosity ($\Delta AIC_c < 2.0$), but none of these models explained a substantial amount of the variation in expected heterozygosity in restored elk populations ($r^2 < 0.07$ for top models) (Table 2.3). Regression coefficients in single variable models for expected heterozygosity were also only slightly positive for number of founders (β = 0.0004, SE = 0.0005), number of source populations (β = 0.007, SE = 0.03), and number of years since last translocation event (β = 0.0005, SE = 0.001).

Temporal changes in genetic variability

Simulation results suggest that mating system and variability in population size influence the retention of genetic variability. Reproductive skew (single male mating) resulted in sharply lower levels of expected allelic richness (Fig. 2.1) and higher fixation probabilities (Table 2.4) over all population sizes. Annual variability in population size consistently resulted in decreased allelic richness (Fig. 2.1) and increased fixation probabilities (Table 2.4). Higher population sizes tended to reduce fixation probabilities (Table 2.4) for both single male and random mating systems. Higher population sizes also tended to increase the retention of alleles (Fig. 2.1), with this effect most evident under simulation settings with a random mating system and less pronounced when reproductive skew was simulated (single male mating). There were only slight differences in average allelic richness (A) for high growth rates (A = 2.703, SE = 0.403), moderate growth rates (A = 2.63, SE = 0.393), and low growth rates (A = 2.595, SE = 0.365), with higher growth rates retaining slightly higher average number of alleles/locus. Populations with positive growth rates tended to consistently exhibit higher levels of allelic richness than the stable population (A = 2.390, SE = 0.269).

Discussion

Genetic variability in the Fort Riley elk population was intermediate to levels reported for native and restored Rocky Mountain elk (*Cervus elaphus nelsoni*) populations in North America when compared at the same microsatellite loci (Polziehn et al. 2000;

Williams et al. 2002; Hicks et al. 2007). The observed levels of allelic richness in the Fort Riley population most likely reflect a balance between the potentially diverse genetic input from a range of founding populations (*n* =4) and genetic drift occurring as a result of small population size. The Fort Riley population had significantly higher levels of allelic richness than the Pennsylvania elk population, as did other restored populations in the United States. Low levels of allelic richness documented in the Pennsylvania population have been attributed to a prolonged period of low population size (Williams et al. 2002). Similarly, Canadian elk populations with low observed levels of allelic richness (French River and Burwash) were founded with a relatively small number of individuals and experienced periods of low population size following restoration (Polziehn et al. 2000; Rosatte et al. 2007). The Banff and Jasper National Park elk populations had higher levels of allelic richness than the Fort Riley population, and these populations were characterized by a relatively large number of founders (*n* > 80) and rapid post-restoration population growth (Lloyd 1927; Stelfox 1993). While acknowledging that direct comparisons of genetic variability between populations surveyed at different loci should be made cautiously, it appears that average allelic richness in the Fort Riley population (3.0 alleles / locus) was slightly lower than Rocky Mountain elk from Idaho and Nevada (6.8 alleles/locus) (Meredith et al. 2007), and northern Yellowstone (4.0 alleles/locus) (Williams et al. 2004).

Observed levels of genetic variability in restored elk populations were only weakly related to several variables (number of founding populations, number of years since last translocation event, and number of individuals translocated) generally thought to influence restoration success (Wolf et al. 1996) or retention of genetic variability (Lacy et al. 1987).

Results of our multivariate predictive model indicated that the number of individuals translocated explained the greatest amount of variation in both allelic richness and expected heterozygosity among restored populations. However, this variable only accounted for 6-12% of the observed variation in allelic richness and expected heterozygosity.

The number of individuals translocated may influence the success of restorations (Griffith et al. 1989; Wolf et al. 1996), initial levels of genetic variability, and initial population size. However, ungulate populations grow rapidly under favorable conditions (McCorquodale et al. 1988; Eberhardt et al. 1996) and only a small number of founders ($n > 20$) may be needed to maximize population growth rates in restored populations (Komers & Curman 2000). These characteristics could allow restored elk populations to quickly reach carrying capacity regardless of initial population size and avoid loss of genetic variability associated with prolonged periods of low population size. The total number of individuals translocated may also not be a good index of effective population size. Elk used for restorations may be captured by methods such as corral trapping (i.e., Wichrowski et al. 2005) that favor the capture of individuals from the same matriarchal social group. Thus, capture methods could skew the relatedness of individuals used for translocation and decrease the effective population size. Effective population size may also be influenced by factors including the male:female ratio, number of breeding females, and relative reproductive output of individuals (Primack 2002).

The number of source populations used for translocations should have a positive relationship with the initial number of alleles present within the new population; however, extant elk populations in North America may be quite homogeneous due to a common origin, thus reducing the explanatory power of the number of source populations in our model. Following near-extirpation throughout much of North America, extensive restoration efforts were undertaken using elk from populations from Yellowstone National Park and adjacent areas including Jackson Hole, Wyoming as the source for populations reestablished throughout Canada (Lloyd 1927; Stelfox 1993) and the United States (O'Gara & Dundas 2002). This translocation strategy has resulted in many current elk populations that are directly or indirectly descended from elk in the Yellowstone area (O'Gara & Dundas 2002), potentially resulting in little genetic differentiation between source herds. Previous studies have indeed found relatively low levels of genetic differentiation among translocated elk herds in the United States (Hicks et al. 2007). Our findings suggest that the number of source populations may not have a strong relationship with current levels of genetic variability in restored elk populations if source populations were originally descended from Yellowstone National Park or adjacent areas.

The number of years since the most recent translocation event was also not strongly related to observed levels of heterozygosity or allelic richness. In small and isolated populations, heterozygosity is expected to decline as a function of time and population size (Primack 2002), but the addition of even a few migrants can quickly offset the effects of genetic drift (Mills & Allendorf 1996). Although geographic isolation makes high levels of genetic exchange unlikely for the Fort Riley population and some other populations reviewed (Pennsylvania, Wichita Mountains Wildlife Refuge), the dispersal capability of elk (Petersburg et al. 2000) suggests that this possibility cannot be excluded for other translocated elk populations (Hicks et al. 2007). Some of the restored populations also grew rapidly following reintroduction and achieved large ($n > 1000$) population sizes

(Lloyd 1927; Hicks 2004), which could have reduced the loss of alleles due to genetic drift that may have otherwise occurred over time (Frankham 1996).

Results from simulations used to explore the expected number of alleles per locus under various scenarios indicated that a single-male mating system (an extreme case of the harem mating system of elk) resulted in drastically reduced levels of allelic richness when compared to a random mating system. This highlights the importance of considering species-specific breeding biology when designing conservation strategies and restoration efforts. Species with harem-mating systems may require additional measures (continued occasional translocations, sustained large population size, functional connectivity with other populations) to minimize loss of alleles due to genetic drift.

Our simulation results are consistent with previous findings indicating that retention of alleles in a population depends on population size (Frankham 1996). For restored populations, maximizing post-restoration population size should reduce loss of alleles due to genetic drift. Based on observed allele frequencies for the Fort Riley population, our findings suggest that isolated restored populations with harem-mating systems will require sustained population sizes greater than 300 to avoid the loss of alleles through genetic drift within a 100-year period. Future restoration strategies concerned with the retention of genetic variability should be designed to ensure that biological and social carrying capacities at the restoration site will allow for sufficient population growth and sustained population size. If an isolated restored population cannot be maintained at sufficient population size, continued translocations to facilitate genetic exchange with other populations may be necessary to maintain genetic variability. Since there is not a well-defined threshold for the level of genetic variability needed to avoid the effects of inbreeding depression, and it may be useful to monitor indicators of inbreeding depression (reproductive rates, calf survival, morphological characteristics) to determine when genetic input is necessary.

Our simulations consistently indicated that variability in annual population size resulted in a higher rate of allelic loss when compared to a constant population size. This pattern implies that conservation efforts designed to maintain genetic variability should focus on maintaining a stable population size. Harvest levels can be managed to reduce fluctuations in population size and managing range conditions to ensure adequate winter forage may be useful to ameliorate the effects of unusually harsh winters. This finding also suggests that increased demographic stochasticity in small populations (resulting in higher rates of variation in annual population sizes) will reduce genetic variability.

Our findings support previous management recommendations suggesting that positive post-restoration population growth may enhance the retention of genetic variability by allowing a population to reach carrying capacity and reducing the length of time that a population exists at a low effective population size (Fitzsimmons et al. 1997; DeYoung et al. 2003). Elk populations with lower levels of allelic richness than the Fort Riley population (including the Pennsylvania, French River, and Burwash populations) all experienced periods of low population size following restoration (Polziehn et al. 2000; Williams et al. 2002; Rosatte et al. 2007). Studies on the restoration of other wildlife populations have suggested that post-reintroduction population growth rates influence the retention of genetic variability (Wisely et al. 2008). Williams et al. (2002) speculated that differences in post-restoration population growth were responsible for variation in allelic richness and heterozygosity among restored elk populations. We observed a positive relationship between population growth rates and allelic richness, although the magnitude of differences in projected allelic richness across a range of population growth rates was relatively small. Our results suggest that as long as population growth remains positive that it may be more efficient to focus available resources on maximizing post-restoration carrying capacity rather than maximizing the rate at which a population approaches carrying capacity.

Management Implications

The widespread use of translocations for conserving small or endangered populations (Griffith et al. 1989) and the recognized importance of maintaining genetic variability for long-term population viability (Frankham & Ralls 1998; Saccheri et al. 1998) underscores the importance of understanding factors that influence the retention of genetic variability in translocated populations. Our findings suggest that maintaining positive population growth rates, increasing population size, and maintaining population stability are strategies that will favor the retention of genetic variability in restored populations. It may be possible to maximize post-restoration population growth and population size by designing restoration sites to include high quality habitat, limiting initial harvest levels, and using founding populations familiar with the types of predation risks present in the restoration site (Frair et al. 2007). Our findings may be particularly relevant for the management of recently translocated ungulate populations with polygynous or harem mating systems (i.e. Rosatte et al. 2007; Parker et al. 2008). Continued monitoring of genetic variability in restored populations is expected to further elucidate the impacts of restoration strategies and post-restoration management on the retention of genetic variability in wildlife populations.

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Table 2.1. Sample size (N), number of observed alleles (*A*), unbiased expected hetrozygosity (*He)*, and observed heterozygosity (*Ho*) at six microsatellite loci for the Fort Riley Military Reservation elk population.

	N	*A*	H_e	H_o
BM5004	25	2	0.47	0.48
BM4208	24	2	0.47	0.63
BM4107	25	2	0.41	0.32
BM888	25	3	0.36	0.44
BM1009	25	5	0.76	0.68
RM006	25	4	0.62	0.56
Mean		3.0	0.52	0.52
Standard Deviation		1.26	0.13	0.15

Table 2.2. Mean allelic richness (A), expected heterozygosity (He), and sample size (N) for the Fort Riley elk population and other restored and source herds in the United States and Canada. * indicates data from Williams et al. (2002), + indicates data from Hicks (2004). Comparisons to these populations were made at loci BM5004, BM4208, BM4107, BM888, and RM006. Comparisons to populations described by Polziehn et al. (2000) (#) were made at loci BM5004, BM4208, BM4107, BM888, and BM1009.

Population	*N*	A (SD)	H_e (SD)
Fort Riley	25	2.6 (0.89)	0.47 (0.09)
Yellowstone N.P.*	20	3.6 (0.89)	0.61 (0.09)
South Dakota (Custer State Park)*	30	3.2 (1.30)	0.58 (0.08)
Pennsylvania*	55	1.6 (0.54)	0.29 (0.31)
Arizona$^+$	40	4.0 (0.71)	0.58 (0.05)
Oregon$^+$	27	3.6 (0.89)	0.61 (0.10)
Oklahoma$^+$ (Wichita Mountains Wildlife Refuge)	43	3.2 (0.84)	0.58 (0.13)
New Mexico (Vermejo Ranch)$^+$	34	3.0 (1.22)	0.50 (0.18)
Theodore Roosevelt N.P.$^+$	22	3.2 (1.10)	0.56 (0.09)
Fort Riley	25	2.8 (1.30)	0.49 (0.15)
Banff National Park$^\#$	28	4.2 (1.30)	0.49 (0.20)
Burwash, Ontario$^\#$	14	2.0 (0.71)	0.39 (0.24)
French River, Ontario$^\#$	10	2.2 (0.44)	0.42 (0.11)
Jasper National Park$^\#$	56	4.8 (1.92)	0.49 (0.15)

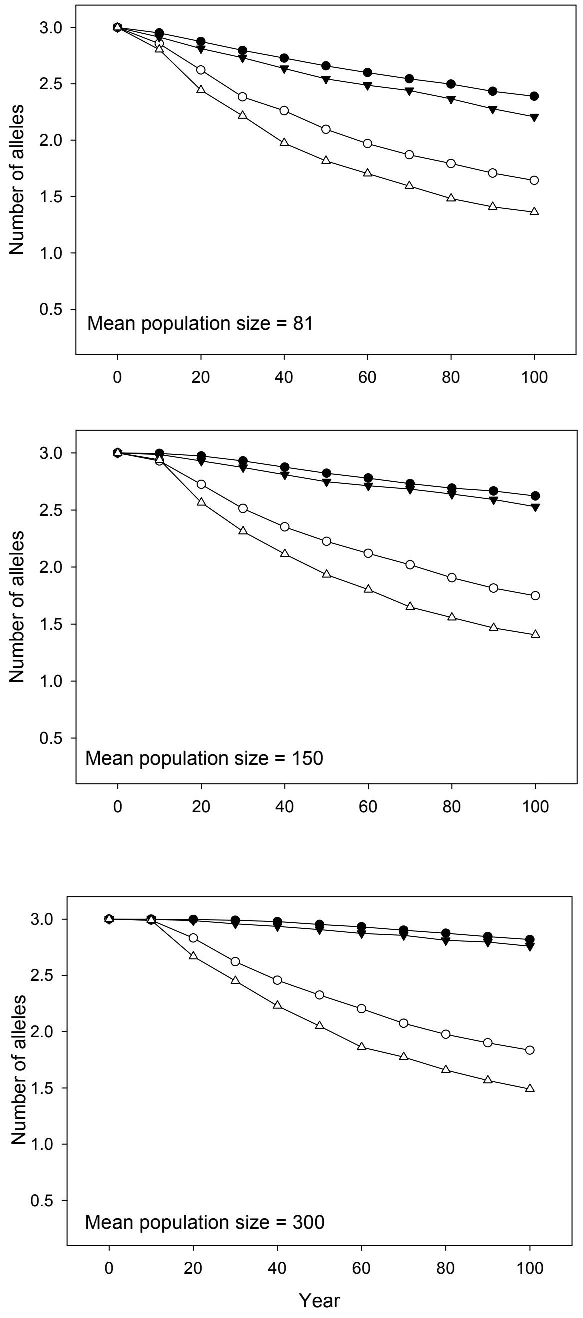
Table 2.3. Models for allelic richness and expected heterozygosity for restored elk populations throughout North America. Model fit is described by Akaike's Information Criterion corrected for small sample size (AICc), the difference in the value of AICc (ΔAICc), and the coefficient of determination (r^2). Variables in candidate models include number of founding individuals (Founders), number of source herds (Source) and years since last translocation event (Years). Dependent variables of allelic richness and mean expected heterozygosity were based on 4 loci in common across studies (BM5004, BM4208, BM4107, BM888).

Model	AICc	ΔAICc	r^2
Dependent Variable: Mean allelic richness			
Founders	2.73	0	0.12
Years	3.29	0.56	0.07
Source	3.89	1.16	0.03
Founders, Years	6.71	3.98	0.17
Founders, Source	7.43	4.70	0.12
Years, Source	7.56	4.83	0.11
Founders, Years, Source	12.99	10.67	0.17
Dependent Variable: Mean expected heterozygosity			
Founders	-45.1	0	0.067
Years	-44.5	0.63	0.017
Source	-44.4	0.75	0.006
Founders, Years	-40.5	4.59	0.076
Founders, Source	-40.4	4.65	0.072
Years, Source	-39.8	5.24	0.024
Founders, Years, Source	-34.3	10.85	0.079

Table 2.4. Fixation probabilities for each of 6 microsatellite loci based on simulations of 100 iterations projected for a 100 year time period. Constant population sizes had the same population size for each year of the simulation, annual values for variable population sizes were generated using a mean value with coefficient of variation of 0.20. Mating systems were either random mating (Random) or with mating only conducted by a single male (Single male).

Population Size	Mating System	BM5004	BM4208	BM4107	BM888	BM1009	RM006
81 (Constant)	Random	0.04	0.01	0.08	0.14	0	0.01
81 (Variable)	Random	0.11	0.15	0.23	0.28	0.02	0.03
81 (Constant)	Single male	0.37	0.44	0.51	0.53	0.23	0.31
81 (Variable)	Single male	0.62	0.70	0.72	0.71	0.53	0.66
150 (Constant)	Random	0	0.01	0.01	0.03	0	0
150 (Variable)	Random	0	0	0.04	0.06	0	0
150 (Constant)	Single male	0.38	0.36	0.51	0.45	0.18	0.21
150 (Variable)	Single male	0.63	0.7	0.67	0.71	0.39	0.59
300 (Constant)	Random	0	0	0	0	0	0
300 (Variable)	Random	0	0	0	0.01	0	0
300 (Constant)	Single male	0.32	0.36	0.4	0.43	0.1	0.13
300 (Variable)	Single male	0.67	0.61	0.49	0.61	0.38	0.49

Figure 2.1. Projected average number of alleles per locus in the Fort Riley elk herd over a 100 year time interval with mean population size of 81, 150 or 300. Simulation settings include random mating and constant population size (closed circles), single male mating system and constant population size (open circles), random mating system and variable population size (closed triangles), single male mating system and variable population size (open triangles).



CHAPTER 3 - ELK (*CERVUS ELAPHUS*) SURVIVAL AND POPULATION DYNAMICS IN NORTHEASTERN KANSAS

Abstract

Understanding the relationship between demographic vital rates and rate of population change (λ) is important for determining effective strategies for population management and conservation. We examined the relative impacts of various demographic vital rates on λ within the range of temporal variability observed in a harvested elk (*Cervus elaphus*) population to test the hypothesis that adult survival rates in ungulates are relatively invariant when compared to other vital rates and that variability in calf survival has a greater influence on rates of population change than adult survival. We estimated demographic vital rates of an elk population at Fort Riley, Kansas for time periods including October 2003 – February 2007. Adult survival rates were similar to other harvested populations, and models including a negative relationship between survival and age received the highest levels of support. Prime-age adult survival had the highest stage-specific elasticity value, indicating a high contribution of this vital rate to λ. Results from life-stage simulation analysis indicated that variation in calf survival had the highest correlation with variation in λ. Our results suggest that adult survival in harvested populations may experience variability, but that calf survival has the greatest relative influence on λ due to the wider range of variability in this vital rate.

Introduction

Knowledge of demographic rates of wildlife populations can be used to assess habitat quality, estimate population viability, and determine conservation or management strategies (Beissinger and Westphal 1998, Eberhardt 2002, Morris and Doak 2002). Principal demographic vital rates in ungulate populations include adult survival, yearling survival, calf survival, and fecundity (number of female offspring/female/year). Each of these vital rates may be differentially influenced by factors including climate (Garrott et al. 2003), population density (Stewart et al. 2005), nutritional condition (Bender et al. 2008), management actions (Cole et al. 1997), predation (Kunkel and Pletscher 1999) and harvest (Ballard et al. 2000). The relative contribution of a vital rate to the rate of population change (λ) can be assessed by comparing elasticity (e_{ij}) values for each vital rate (Caswell 2001). Elasticity values measure the proportional change in λ that would occur as a result of a proportional change for a given vital rate (Caswell 2001), with higher elasticity values indicating a greater influence of a vital rate on λ. In long-lived vertebrates, adult female survival is the vital rate that generally has the greatest proportional influence on λ (Nelson and Peek 1982, Gaillard et al. 2000). However, adult survival typically exhibits little temporal variability in response to environmental variation (Gaillard et al. 1998, Pfister 1998, Gaillard et al. 2000). In contrast to juvenile survival and reproductive output, adult survival is also relatively invariant in response to changes in population density (Gaillard et al. 2000, Eberhardt 2002, Stewart et al. 2005). Vital rates with high variability may be more important for determining the actual rate of population change than invariant vital rates with higher elasticity values (Pfister 1998, Wisdom et al. 2000, Raithel et al. 2007). However, for harvested populations annual changes in harvest regulations and success rates could result in a higher level of variability in adult survival than would otherwise occur. Similarly, small populations may experience increased variability in vital rates simply as a result of demographic stochasticity (Primack 2004). Therefore, it is important to determine if observed vital rates and rates of population change in small / harvested populations are consistent with the hypothesis that adult survival rates in ungulates are relatively invariant when compared to other vital rates (Gaillard et al. 1998, Gaillard et al. 2000), and that variability in calf survival has a greater influence on λ than adult survival (Raithel et al. 2007).

Adult survival is generally the vital rate with the highest elasticity for long-lived vertebrates (Gaillard et al. 2000, Eberhardt 2002). Primary sources of adult mortality for free-ranging ungulate populations include harvest, predation, disease, and winter mortality (DelGiudice et al. 2002, Raedeke et al. 2002). However, in areas without wolves (*Canis lupus*) or other large predators, predation may not regulate survival of adult elk (Ballard et al. 2000, Larkin et al. 2003). Similarly, winter mortality may not have a large influence on adult survival rates for elk in areas with relatively mild climates (Ballard et al. 2000, Larkin et al. 2003). Starvation resulting from the inability to acquire adequate nutritional resources also may not be a leading cause of mortality except in populations at high densities or in marginal habitats (Bender et al. 2007).

Although marked variation in adult survival rates may not occur in response to changes in population density or environmental conditions, human-caused mortality by legal harvest, wounding, poaching, or vehicle collisions may directly influence variation of this vital rate. Factors related to harvest and other human-caused mortality sources may have the most readily discernable influence on adult survival rates in areas where natural factors including predation, population density and winter conditions have relatively little impact on adult survival. Given that the realized influence of a vital rate on λ is influenced by both the elasticity and variability of that vital rate (Wisdom et al. 2000), it is critical to identify factors that influence variability in adult female survival in managed populations.

Elk (*Cervus elaphus*) are a suitable species for studying the influence of adult survival and other vital rates on population growth rates in managed populations of ungulates. Elk populations are present throughout the United States in areas where the primary causes of adult mortality are human-related (Unsworth et al. 1993, Cole et al. 1997, Ballard et al. 2001, Raedeke et al. 2002). Management practices directly influence the relative impact of human-related mortality on elk survival rates. For example, harvest rates may depend on road density, hunter access (Gratson and Whitman 2000, Hayes et al. 2002), or the total number of permits issued. Limiting road access also reduces elk mortality from poaching and vehicle collisions (Cole et al. 1997). Use of concealment cover within the home range and the relative amount of time spent in refuge areas may influence the vulnerability of harvested species to human-caused mortality (Unsworth et al. 1993, Beringer et al. 1998).

Nutritional condition also influences the relative vulnerability of elk to mortality (Bender et al. 2006, Bender et al. 2008). Elk that are in poor nutritional condition may be less alert, more willing to use foraging areas with higher mortality risk, and be less likely to flee from perceived threats than elk in good nutritional condition. Similarly, gestation, parturition, and lactation impose high energetic demands on adult female elk and influence survival rates (Moyes et al. 2006). Individual characteristics including age and condition of elk may also influence hunter selection, with a potentially increased mortality risk for mature animals. Survival rates for large herbivores may also be lower in older age classes (Festa-Bianchet et al. 2003).

The goals of this study were to: 1) estimate monthly and annual survival rates for female elk at Fort Riley Military Reservation, Kansas; 2) determine the influence of habitat use, nutritional condition, and harvest-related variables on female elk survival rates; 3) compare female elk survival rates and mortality causes to rates reported for other elk populations; 4) estimate overall rates of population change (λ) and underlying vital rates elasticities; and 5) estimate the relative contribution of these vital rates to expected changes in λ within the range of variability in vital rates observed for the Fort Riley elk population.

Study area

The study was conducted at Fort Riley Military Installation, Kansas (39° N, 97° W). Fort Riley is a 40,273 ha military reservation located in portions of Geary, Riley and Clay counties in the Flint Hills of northeastern Kansas. Undeveloped training areas comprised approximately 26,400 ha of the installation and training activities included artillery firing, small arms firing, combat vehicle operations, and field encampments (US Army 1994). Military training activities regularly resulted in the temporary closure of various training areas within the installation. The training areas of the installation included a contiguous 5,600 ha artillery and range firing impact area (Impact Zone) with a core area impacted by munitions firing and a surrounding buffer zone. The Impact Zone was off limits at all times to civilians and military personnel.

The topography of Fort Riley is typical of the Flint Hills region, with rolling hills of upland prairie interspersed with gallery forest along ravines and lowland areas. Grassland sites at Fort Riley were generally characterized by native prairie grasses including big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), Indiangrass (*Sorghastrum nutans*), and switchgrass (*Panicum virgatum*) (United States Army 1994). Common shrubs and forbs included rough-leaf dogwood (*Cornus drummondii*), smooth sumac (*Rhus glabra*), Missouri goldenrod (*Solidago missouriensis*), and common sunflower (*Helianthus annuus*). Crops including winter wheat (*Triticum aestivum*), corn (*Zea mays*), alfalfa (*Medicago sativa*), grain sorghum (*Sorghum bicolor*), and soybeans (*Glycine max*) were planted on areas of Fort Riley for the benefit of wildlife.

Elk were reintroduced to the Fort Riley area with the release of 12 animals from Maxwell Wildlife Refuge, KS in 1986 (Pitts et al. 1987). Additional elk were introduced to Fort Riley from Maxwell Wildlife Refuge in 1987 (n = 7), 1990 (n = 2), and 1992 (n = 2). Further translocations were made from source herds in Trinidad, Colorado (1988, n = 5), Moise, Montana (1990, n = 8), and Wind Cave National Park, South Dakota (1994, n = 18) for a total of 54 elk released. A limited annual harvest was initiated beginning in 1990. From 2003-2006, from 15 to 33 antlerless-only elk permits were issued annually with firearms season taking place from 1 October – 31 December. An additional 6-9 any-elk permits (allowing harvest of either a bull or cow elk) have also been issued annually from 2003-2006. Each firearms season was divided into 3 monthly segments (1–31 October, 1-30 November, and 1-31 December) and each elk permit holder was designated a particular segment of the firearms season for hunting. Off-post firearms elk harvest was allowed for permit holders from 1 January – 15 March. We conducted phone interviews with hunters who held a Fort Riley cow elk permit between 2003-2006 to determine if hunters preferentially harvested or avoided harvesting elk with collars. During phone interviews, we first asked if hunters observed elk with collars while hunting on Fort Riley. If hunters had observed collared elk, we asked if the presence of a collar influenced the decision of the hunter to harvest a given animal. Interviewed hunters indicated that selection for cow elk was based primarily on availability (positioning / distance of a given animal in a way that allowed the opportunity for a successful shot), and that the presence of a collar on an elk was not a factor that influenced the decision to either harvest or not harvest a given animal.

Methods

We captured 34 female elk during capture periods including 26-27 October 2003, 4-5 February 2005, 11-13 November 2005, and 14 April 2006 at Fort Riley, Kansas. We captured elk by aerial darting using carfentanil citrate (3.0 mg/elk) and xylazine hydrochloride (100 mg/elk) for immobilization. We removed a vestigial upper canine from immobilized elk to determine age by counting cementum annuli (Braun 2005). We scored rump body condition (rBCS), and measured subcutaneous rump fat thickness levels (using an ultrasonograph) for elk on each capture occasion (Stephenson et al. 1998). We outfitted each captured elk with a global positioning system (GPS) radio-collar equipped with a very high frequency (VHF) transmitter (164 mHz range), remote-release mechanism and mortality sensor (G2000, Advanced Telemetry Systems, Inc. Isanti, MN) or a VHF radio-collar equipped with a mortality sensor (Telemetry Solutions, Concord, CA). Following processing of immobilized elk, we administered naltrexone

(300 mg/elk; ½ subcutaneous, ½ intravenous) and tolazoline (800 mg/elk intravenous) as an antagonist. We captured an additional 4 female elk (1 yearling, 3 adults) using corral trapping during the study period and these elk were also outfitted with GPS radio collars (G2000, Advanced Telemetry Systems, Inc. Isanti, MN). All capture and handling procedures were approved by the Kansas State University Institutional Animal Care and Use Committee (Protocol #2264).

Age structure of captured female elk included yearlings (1.5 years old); (n = 7), prime-age adults (2.5-9.5 years old); (n = 19), and old-age adults (10.5+ years old); (n =4). We have no evidence to suggest that our capture methods were biased towards any age class, and believe that age classes of captured elk were generally representative of the Fort Riley population. We attempted to recapture and place new radio-collars on previously captured female elk (n = 12) during subsequent capture periods. Following capture, we monitored elk survival using radio-telemetry until either mortality occurred, collars failed, or collars were removed. We attempted to determine locations of all elk 1-2 times/week, and estimated elk locations based on triangulation of >2 signal bearings taken from known geographic locations within a 10-20 minute time period. During telemetry monitoring we located elk using a 3-element Yagi antenna and took compass bearings in the direction of the strongest VHF signal. Geographic locations (UTM coordinates) were recorded using a hand held GPS unit (Garmin, Olathe, KS) at the location from which each compass bearing was taken. Geographic locations and compass bearings were used to estimate elk locations and associated error ellipses using the Program LOCATE II (Nams 1990).

We estimated survival rates using the ‘nest survival’ model (Dinsmore et al. 2002) in Program MARK (White and Burnham 1999). The ‘nest survival’ model in Program MARK is a known-fate model that can be used to estimate survival rates based on telemetry data collected at irregular intervals (i.e., Hartke et al. 2006, Mong and Sandercock 2007). We estimated survival rates on a monthly time interval to match the time-scale of some covariates used for modeling (number of hunting permits, training area accessibility). Program MARK provides an effective framework for estimating survival rates using maximum-likelihood methods (White and Burnham 1999) and allows for model selection using an information-theoretic approach (Burnham and Anderson 2002). The ‘nest survival’ model in Program MARK can accommodate models with variation in survival rates over time and allows for the inclusion of both environmental and individual covariates. The model requires the following encounter history information: the month following collar deployment (k), the last month that an elk was known to be alive (l), the month during which an elk died or was last located (m), and the fate of each elk (1 = died, 0 = survived). We coded the month following collar deployment as the initial monthly interval (k). We used this approach because several capture periods occurred near the end of a given month, so survival to the beginning of the next month would not reflect survival over a full monthly time period and could bias survival estimates high.

Environmental covariates that we used for modeling elk survival included an index to hunter accessibility (average number of days/month that training areas were open for hunting during firearms season) and the number of anterless-only elk permits issued for elk harvest on Fort Riley. Individual covariates related to habitat-use patterns that we considered in the candidate model set included: proportion of telemetry locations in the Impact Zone, proportion of telemetry locations < 250 m from the nearest publicly accessible road, and proportion of telemetry locations < 500 m from the nearest publicly accessible road. We included individual covariates for average girth and average percent ingesta-free body fat (IFBF) in candidate models as indices to elk body condition. Girth and fat levels were measured during capture periods including 26-27 October 2003, 4-5 February 2005, and 11-13 November 2005. The level of IFBF was estimated based on rump body conditions scores (rBCS) and subcutaneous rump fat thickness levels using the equation:

$$\text{IFBF} = -7.153 + 7.323(X) - 0.989(X^2) + 0.057(X^3)$$

Where X = (rBCS + subcutaneous rump fat thickness – 0.3) (Cook et al. 2001). If IFBF could not be estimated using subcutaneous rump fat thickness levels due to low body fat levels, IFBF was estimated based on rBCS (L. Bender, unpublished data) using the equation:

$$\text{IFBF} = 4.478 \times \text{rBCS} - 4.618$$

Individual covariate values for average girth and fat levels were calculated as the mean value across all capture occasions during which an individual elk was captured or recaptured. Cow elk were captured one (n = 22), two (n = 9), or three (n = 3) times during the study period. Additional details of methodology related to body condition measurements, pregnancy determination, and aging are reported by Piasecke (2006).

We included age as a time-varying individual covariate (Cooch and White 2008) with initial age values determined based on counts of cementum annuli from a tooth extracted during capture. Age values for subsequent years were determined by adding one year to the initial age estimate on 1 October of the following year. Thus, age estimates increased annually for individual elk throughout the study period. We coded annual values for age as separate columns in the encounter histories file and the design matrix was coded so that elk were considered to remain the same age from 1 October – 30 September of the following year.

We examined correlations among individual covariates using Pearson correlation coefficients (PROC CORR, SAS Institute, Cary N.C.). When multiple individual covariates were highly correlated ($r > 0.70$), we selected only a single covariate for inclusion in candidate models. Individual covariates that were highly correlated included average IFBF with average girth ($r = 0.79$, $P < 0.001$), and proportion of locations < 250 m from the nearest road with proportion of locations < 500 m from the nearest road ($r = 0.85$, $P < 0.001$). For these pairs of highly correlated covariates we included average IFBF and proportion of locations < 500 m from the road in candidate models because we felt that these variables would be most likely to influence elk survival (Bender et al. 2008).

Four elk were harvested by hunters before telemetry locations could be collected, and all available information (capture locations, recorded sightings, mortality locations) indicated that each of these elk were initially captured, lived, and died > 6 km outside of the Impact Zone. For modeling purposes, we assigned these elk a proportion of locations in the Impact Zone of "0", which better reflected the actual use of the Impact Zone by these individuals than the overall population average value (0.40) for this covariate. We could not measure percent IFBF for three adult and one yearling elk captured using corral trapping and these elk were assigned the overall mean value for this covariate (11.5%).

A mean annual age value was also assigned to the three adult elk captured using corral trapping (5.8 years).

We generated an *a priori* suite of 42 candidate models based on environmental and individual covariates and allowed survival rates to vary between (but not within) hunting season (1 October – 31 March) and non-hunting season (1 April - 30 September) time periods. We believe that this model structure was reasonable as it was logical to assume that adult survival in a harvested population would differ between time periods encompassing firearms season (1 Oct – 15 March) and time periods during which legal harvest did not occur. Candidate models were fitted using design matrices in Program MARK. We used Akaike's Information Criterion corrected for small sample size (AICc) and Akaike weights (w_i) to determine the most appropriate model. We considered models to be equally parsimonious if the difference between AICc values was < 2.0.

To account for model selection uncertainty when examining temporal variation in monthly survival throughout the study period, we averaged monthly survival estimates from across the candidate model set using model-averaging procedures in Program MARK. We also considered models without covariates that included: constant survival across all months of the study period ($S.$) and full time dependence (S_{monthly}), in which survival estimates could vary for each monthly interval within the study.

We estimated annual cow elk survival rates for 12-month time periods including October 2004 – September 2005 ($\hat{S}_{2004\text{-}2005}$), and October 2005 – September 2006 ($\hat{S}_{2005\text{-}2006}$). We chose these time periods instead of calendar years so that annual survival rates would better reflect conditions that were constant across a given hunting season (October – March) time period. To estimate annual survival rates for each of these time periods, we constructed a model in which survival varied between years and between hunting season (October – March) vs. non-hunting season months (April – September). Monthly survival rates were held constant at 1.0 for all non-hunting season months, as no collared elk died during these time periods. We estimated annual survival rates as a product of monthly hunting season ($\hat{S}_{\text{hunting season}}$) and non-hunting season ($\hat{S}_{\text{non-hunting season}}$) survival estimates within each annual time period

$$\hat{S}_{\text{annual}} = [\hat{S}_{\text{hunting season}}]^6 \text{ x } [\hat{S}_{\text{non-hunting season}}]^6.$$

As our study included additional survival data outside of the time period 2004-2006, we calculated an overall annual survival rate to include survival information from our entire monitoring period. We extrapolated a point estimate of overall annual survival ($\hat{S}_{\text{overall}}$) based on a model in which survival estimates were allowed to vary between hunting ($\hat{S}_{\text{overall hunting season}}$) and non-hunting season months ($\hat{S}_{\text{overall non-hunting season}}$) across the study period. Survival during non-hunting season months was fixed at 1.0. The overall estimate of annual survival was calculated as:

$$\hat{S}_{\text{overall}} = [\hat{S}_{\text{overall hunting season}}]^6 \text{ x } [\hat{S}_{\text{overall non-hunting season}}]^6.$$

We calculated variance for annual and overall survival estimates with the delta method as described by Powell (2007). As non-hunting season survival rates were held constant at 1.0, variance calculated using the delta method was based on variance for hunting season survival rates. Covariation or dependence between variables used to estimate overall and annual survival rates were not accounted for in these delta method variance calculations because overall and annual estimates were derived from the product of only a single variable (hunting season monthly survival estimates).

Real parameter estimates for survival across a range of ages were calculated using the model (S_{age}) and specifying age values for individual covariates in Program MARK ranging from 0.5 -10.5 years. Age-specific elk survival estimates were calculated for hunting seasons, as no mortalities occurred during non-hunting season and survival estimates were 1.0 for these months.

To accommodate the uncertainty associated with the fate of one elk lost during the study, we conducted an initial analysis with this elk considered alive and right-censored following the last known location and a second analysis with this elk considered to have died following the last recorded location (Murray 2006). Monthly survival estimates and model selection results were similar for both analyses, thus only results for the analysis with this elk coded as dead are presented.

We estimated fecundity for adult cows based on pregnancy rates determined by levels of serum progesterone and/or pregnancy specific protein b (PSPB) in blood samples collected during February 2005, November 2005, and April 2006 capture periods (*see* Piasecke 2006). Fecundity is a measure of the number of female offspring/female/year, which is a product of conception, intrauterine mortality, and successful parturition rates. Intrauterine mortality is generally rare in brucellosis-free elk herds in adequate nutritional condition (Cook 2002), and our fecundity calculations assumed no intrauterine mortality. Calf production was assumed to consist of a single calf per female, as the occurrence of twins has rarely been documented in elk (Hudson and Haigh 2002) and was not observed during our study. Sex ratios at birth for elk calves are assumed to not differ substantially from a 1:1 ratio (Raedeke et al. 2002). Therefore, we estimated fecundity as the overall pregnancy rate (including data pooled from all capture periods) multiplied by 0.5 (to account for male calves). All captured yearlings were pregnant, but due to a small sample size for this segment of the population we calculated a single overall fecundity rate based on combined data for both yearling and adult cows.

We calculated annual calf survival rates based on lactation rates obtained during October 2003 and November 2005 for adult cows. Lactation by adult cows indicates that nursing by a calf has taken place within the past 3-11 days (Bender et al. 2002) and has been used as an indicator of calf survival (Bender et al. 2002, Bender et al. 2006). Lactation rates can be related to calf survival ($\hat{S}_{calf}$) with knowledge of the number of lactating females sampled ($n_{\mathrm{lactating}}$), total number of females sampled (n_{sampled}), and pregnancy rates (p) using the equation:

$$\hat{S}_{\mathrm{calf}} = n_{\mathrm{lactating}} / (n_{\mathrm{sampled}} \times p)$$

We did not use lactation data from capture periods in February 2005 and April 2006 because the proportion of lactating cows steadily declines as calves are weaned beginning in early winter (Hudson and Haigh 2002). To incorporate additional data from the study period subsequent to the last capture period (April 2006) we conducted an aerial survey count of cow:calf ratios during March 2007 to estimate calf survival from birth through late winter (Eberhardt et al. 1996, Sargeant and Oehler 2007). We conducted the aerial survey within a single day using multiple observers from 2 Black Hawk military helicopters assigned to separate search areas on Fort Riley. We estimated calf survival ($\hat{S}_{\mathrm{calf}}$) based on number of adult females observed (n_{females}), number of calves observed (n_{calves}), annual adult survival estimated for the previous year ($\hat{S}_{2006}$), and overall pregnancy rates (p); using a modification of an estimator presented by Sargeant and Oehler (2007):

$$\hat{S}_{\text{calf}} = (n_{\text{calves}} \times \hat{S}_{2006}) / [p \times n_{\text{females}}]$$

This estimator accounts for potential overestimation in calf survival that would otherwise occur if the estimator were calculated without accounting for adult mortality (Sargeant and Oehler 2007). The total number of females sighted during late winter aerial surveys includes both adult females (> 2 years old) and yearling females (1.5 years old). Only adult females would have been capable of producing a calf during the previous calving season, therefore we did not count yearling females when calculating the number of potentially reproductive females in the population (n_{females}). We calculated the number of adult females as the total number of females – number of yearling females to better estimate the number of cows in the population capable of producing calves during the previous calving period. As we could not readily distinguish yearling from adult females during the aerial survey, we assumed that the number of yearling females was equal to the number of yearling males (spike bulls) that we observed during the aerial survey. Dispersal rates of yearling bulls are generally low (Raedeke et al. 2002) and similar mortality rates were observed during this study for yearling cows and a small number of collared bull calves and yearling bulls (n = 3), suggest that it would not be unreasonable to observe near equal male:female yearling sex ratios during late winter aerial surveys.

We calculated an overall point estimate of annual calf survival by averaging calf survival estimates obtained from lactation rates and aerial survey data. This rate represents a maximum estimate of calf survival, as it does not account for mortality that could occur during late winter or spring. The primary sources of mortality for elk calves are summer predation, hunting, and over-winter mortality due to malnutrition (Singer et al. 1997, Smith and Anderson, 1998). Therefore, late winter / spring calf survival rates were expected to approach 1.0 (similar to non-hunting season adult mortality rates) on Fort Riley during the study period due to relatively mild winters, adequate late winter forage availability (food plots on Fort Riley and winter wheat fields on adjacent private lands), the absence of large predators on our study site, and high documented survival of yearling and adult cows during non-hunting season periods.

We parameterized a deterministic, female-based, stage-structured, pre-breeding matrix model with a one-year projection interval based on age-specific estimates of cow elk survival from the model (S_{age}), overall calf survival, and overall fecundity. We could not estimate age-specific fecundity from our data, and a single overall fecundity value was used for all reproductively capable stage classes in the matrix model. The stage classes in the projection matrix included: calves (<1 year old), yearlings (1 year old), prime-age adults (2-9 years old), and old-age adults (10-14+ years old) (Raithel et al. 2007), resulting in a 3 x 3 projection matrix (**A**):

$$\mathbf{A}= \begin{pmatrix} 0 & S_0F & S_0F \\ S_1 & S_2(1-\gamma) & 0 \\ 0 & S_2\gamma & S_3 \end{pmatrix}$$

Survival rates for calves (S_0) were based on lactation rates and aerial survey data. Survival rates for other age classes were based on age-specific estimates of survival from the model S_{age} (age included as an individual covariate) in Program MARK using user-specified individual covariate values for age (Morris and Doak 2002). Age values used to estimate stage-specific survival rates were specified at the age for the midpoint of each stage in the life cycle. We calculated transition probabilities (the probability of an individual moving from one stage in the life cycle to the next stage) (γ) as the reciprocal of the number of years within a stage for the prime-age stage (Brault and Caswell 1993). As the yearling stage lasts only a single year, we fixed the transition probability for this stage at 1.0. While yearling survival is generally thought to be slightly lower than prime age adult survival (Raithel et al. 2007), we documented no cases of mortality occurring in the yearling segment of our population, and surmise that high yearling survival may be due to hunters selectively harvesting larger more mature females. Therefore, we believe that the assignment of a slightly higher value for yearling survival than prime-age adult survival is a reasonable reflection of biological processes occurring in the Fort Riley population.

The observed vital rates (calculated as described above) were used to parameterize the projection matrix (**A**). The parameterized matrix (**A**) had the following matrix element values:

$$\mathbf{A}= \begin{pmatrix} 0 & 0.353 & 0.353 \\ 0.911 & 0.676 & 0 \\ 0 & 0.097 & 0.374 \end{pmatrix}$$

The finite rate of population change (λ) was estimated by determining the dominant eigenvalue of the projection matrix (**A**) (Caswell 2001). A prospective analysis was conducted to determine elasticities (e_{ij}) of λ to changes in individual matrix elements (a_{ij}) (Caswell 2000, Caswell 2001) for the elk population at Fort Riley. Elasticity analysis was used to assess the proportional change in λ that would occur as a result of a change of an individual matrix element (a_{ij}) (Caswell 2000, de Kroon et al. 2000). Elasticity values for all matrix elements sum to 1, and can be used to compare the relative influence on λ for vital rates measured on different scales (i.e., fecundity and survival) (de Kroon et al. 2000). Each matrix element consisted of a single vital rate except for the upper ("recruitment") row of the projection matrix, which was a product of calf survival and fecundity. The elasticities for these matrix elements can be interpreted as stage-specific recruitment contributions to the population growth rate. We estimated the relative contributions to λ for various vital rates by summing elasticities for all matrix elements that included a given vital rate. Vital rates included: yearling survival (1 year old survival), prime-age adult survival (2-9 year old survival), old age survival ($10\text{-}14^{+}$ year old survival), prime-age recruitment (the product of fecundity and calf survival for age classes 2-9), and old-age recruitment (the product of fecundity and calf survival for age class 10-14+).

We did not estimate lower-level elasticities for matrix elements that were a product of multiple vital rates, as lower level elasticities for vital rates do not sum to 1 and cannot be interpreted as a direct measure of the contribution of a vital rate to λ (Caswell 2001). Instead, we estimated the influence of individual vital rates on λ within the range of vital rate variability observed at Fort Riley using Life Stage Simulation

Analysis (LSA) (Wisdom et al. 2000). Life-stage simulation analysis allows the specification of a range of possible values for each vital rate based on observed or expected levels of variability, and repeatedly samples possible combinations of matrix vital rates and calculates projected population growth rates based on these combinations of vital rates (Wisdom et al. 2000). We used linear regression to determine the proportion of variation in λ explained by the variation in each vital rate based on the observed output from 500 projection matrix simulations (Wisdom et al. 2000). We conducted LSA analysis in Program MATLAB (Student Version R2007A, Mathworks, Inc. Natick, MA) using a modification of the limitsens.m code from Morris and Doak (2002). It was not possible for us to estimate process variance for fecundity and calf survival because within-year variances for these vital rates could not be estimated from our data. Therefore, we sampled simulated values for all vital rates from a uniform distribution ranging from the minimum and maximum annual or overall vital rate estimates observed during our study (Morris and Doak 2002).

Results

The overall annual survival rate for the entire study period was 0.76 (var($\hat{S}_{overall}$)= 0.005), with higher estimates of survival for 2004-2005 ($\hat{S}_{2004\text{-}2005}$ = 0.83, var($\hat{S}_{2004\text{-}2005}$) = 0.012) and 2005-2006 ($\hat{S}_{2005\text{-}2006}$ = 0.89, var ($\hat{S}_{2005\text{-}2006}$)= 0.01). The lower overall annual survival rate was due primarily to mortalities (n = 3) that occurred during the 2003 Fort Riley firearms season. We documented eight mortalities out of 34 female elk tracked during this study, and all causes of mortality were human-related. Five elk were harvested during the Fort Riley firearms season, one elk was legally harvested on private land off Fort Riley, one elk was found dead on Fort Riley during firearms season presumably dying as a result of being wounded and not recovered (Tom Duckworth, Fort Riley Conservation Officer, personal communication), and one cow was euthanized by a Kansas Department of Wildlife and Parks conservation officer after reports of strange behavior. This individual was old and in poor nutritional condition, so the ultimate cause of death could also have been attributed to malnutrition/starvation. One cow elk died while immobilized during the capture process and we excluded this mortality event from survival estimates. No other elk deaths were attributed to capture, handling, or presence of a collar. We did not attribute the cause of any elk deaths to military training activities, vehicle collisions, or predation.

We considered five models to be equally parsimonious (Δ AICc ≤ 2.0), and age was included as a variable in all of these models either as a main or additive effect (Table 3.1). Age had a slight but significant negative relationship with elk survival in all top models (Table 3.2). For covariates other than age, β-coefficient standard errors were large and 95% confidence intervals overlapped 0, indicating that the inclusion of these covariates explained very little additional variation in survival when compared to the top model S_{age} (Table 3.2).

Survival estimates were lower during hunting seasons and higher during all non-hunting seasons for all years (Fig. 3.1) based on model-averaged estimates from all candidate models. Non-hunting season survival was estimated at near 1.0, and this estimate is reasonable as no mortalities were recorded outside hunting season. Age-specific parameter estimates from the model S_{age} indicated that elk survival generally decreased with age. Monthly survival rates for yearlings approached 1.0 with progressively lower survival rates for older cows (Fig. 3.2).

Fecundity values for cow elk on Fort Riley were generally high, with an overall estimate of 0.481. Calf survival based on lactation rates for adult cows was variable, with lower lactation rates observed during 2003 (0.636) than 2005 (1.0). Calf survival based on aerial survey estimates from 2007 indicated a lower rate of calf survival during this time period (0.567). We estimated an overall calf survival rate of 0.734 based on averaging annual calf survival rate estimates.

Based on deterministic matrix projections from observed vital rates, we predicted the elk population at Fort Riley to have a slightly positive overall rate of population change ($\lambda = 1.033$). Summed elasticities were highest for prime-age adult survival matrix elements (0.493), followed by yearling survival (0.244), and prime-age recruitment (0.213) (Fig. 3.3). Life-stage simulation analysis results indicated that the greatest amount of variation in λ was explained by variation in calf survival ($r^2 = 0.606$) and prime-age adult survival ($r^2 = 0.367$). Other vital rates including yearling survival ($r^2 = 0.002$), old-age survival ($r^2 = 0.006$), prime-age fecundity ($r^2 = 0.004$), and old-age fecundity ($r^2 = <0.001$) explained little of the observed variation in λ.

Discussion

Understanding factors that influence variability in vital rates and the subsequent influence of these vital rates on λ is essential for determining conservation strategies or management actions. Life-history theory suggests that vital rates with a high influence on population growth rates should exhibit reduced levels of variation in response to environmental variability (Pfister 1998, Gaillard and Yoccoz 2003). This hypothesis has been supported based on findings of high elasticity coupled with low temporal variability in adult survival rates and low elasticity coupled with high temporal variability for juvenile survival rates in ungulates (Gaillard et al. 1998, Gaillard et al. 2000, Raithel et al. 2007). However, it is important to understand whether these findings can be generalized to small harvested populations. In harvested populations, increased variability in vital rates with high elasticities (adult survival) may occur due to changes in harvest regulations or hunter success rates. Vital rates in small populations may also be influenced by demographic stochasticity, manifested as variability in vital rates that occur exclusively due to stochastic variation in survival or birth rates in a small population (Primack 2004). The results from this study provide valuable knowledge for assessing how changes in specific vital rates could influence ungulate population dynamics in small harvested populations.

Variation in adult elk survival rates were explained primarily by age, with older age-class adults having lower survival rates. Similar results have been found for cervid populations with large predators present (Kunkel and Pletscher 1999) where older individuals may be more susceptible to predation than prime-age adults (Wright et al. 2006). Our results suggest that previous findings of age-dependence in adult survival for ungulates (Loison et al. 1999, Gaillard et al. 2000, Festa-Bianchet et al. 2003) are also supported for a population under carrying capacity where harvest is the primary source of mortality. It is possible that the negative relationship between survival and age in the Fort Riley population is due in part to a tendency for hunters to selectively harvest mature prime-age individuals (Wright et al. 2006). In addition, some deaths may occur in this population as a result of age-related declines in nutritional condition.

The primary observed cause of adult female mortality was due to hunting or wounding, which is similar to mortality causes in other harvested populations (Unsworth et al. 1993, Ballard et al. 2000). However, no mortality due directly to natural causes was documented during the course of this study. This differs from mortality causes reported for elk populations in Idaho (Unsworth et al. 1993), Montana (Kunkel and Pletscher 1999), and Banff National Park (Hebblewhite et al. 2002). This suggests that effects of winter, predation, or other natural causes are secondary to harvest as a source of mortality in the Fort Riley population. Without these sources of natural mortality, hunting is the predominant factor influencing adult survival and consequently is expected to have a strong influence on λ, especially if harvest focuses selectively on prime-age classes (Wright et al. 2006) with high elasticity values.

Annual estimates of survival for this population were comparable in magnitude to those reported for other harvested populations. Annual survival estimates for adult cow elk ranged from 0.78 – 1.0 in Idaho (Unsworth et al. 1993), 0.82 – 0.96 in Oregon (Stussy et al. 1994), 0.99 in northern Arizona (Ballard et al. 2000), 0.64 – 0.88 in Montana (Kunkel and Pletscher 1999), and 0.74 – 1.0 across populations in Washington and Oregon (Bender et al. 2008). The overall survival estimate at Fort Riley was lower than the overall average female adult survival rate (0.87) reported for 12 elk studies in the western United States (Raithel et al. 2007). Annual estimates of survival for the Fort Riley population exhibited temporal variation, but were within the range of survival estimates reported for elk survival in other areas (Unsworth et al. 1993, Stussy et al. 1994, Kunkel and Pletscher 1999, Bender et al. 2008).

High elasticity values for prime-age adult and yearling survival rates suggest that changes in these vital rates will have a large influence on λ. This finding is not unexpected, as survival is generally recognized as the vital rate with the highest level of elasticity for long-lived species (Eberhardt 2002). Although adult survival may be relatively invariant in response to environmental variability, management actions (number of permits issued / harvest regulations) that directly influence adult survival can be an effective tool for managing rates of population change. These findings suggest that regulating population size in the Fort Riley population could be achieved by influencing prime-age survival rates through harvest management strategies including number of permits issued, hunter access regulations, or season length.

However, life-stage simulation analysis based on empirical data from the Fort Riley population supports the hypothesis that high variability in calf survival rates strongly influences variation in population growth rates (Raithel et al. 2007). Although adult survival rates have higher elasticity values, the wider range of variability in calf survival may ultimately result in a greater influence on observed rates of population change. These observations suggest that management actions that impact calf survival may also influence population growth rates in managed elk populations. We did not assess the underlying mechanisms responsible for the high variability in elk calf survival as part of this study, but it is known that calf survival can be influenced by anthropogenic disturbance (Shively et al. 2005, Phillips and Alldredge 2000), birth weight (Cook 2002), winter nutritional condition (Singer et al. 1997, Cook et al. 2001), and summer predation (Singer et al. 1997). Management actions to increase calf survival could include reducing disturbance during calving seasons by restricting off-road access to calving areas or by enhancing late-winter forage availability to increase adult female nutritional condition during gestation.

While our results support the hypothesis that calf survival ultimately has a greater influence on λ than adult survival, it is important to note that the variability in λ explained by adult survival in the small, harvested Fort Riley population ($r^2 = 0.367$) was several times greater than that reported over a range of elk populations ($r^2 = 0.164$) (Raithel et al. 2007). These findings suggest that further work may be necessary to determine how population size and harvest status influence the relative variability of adult and calf survival rates and the realized influence of these vital rates on λ.

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Table 3.1. Top models for monthly cow elk survival at Fort Riley, Kansas from October 2003 – February 2007. Model fit assessed by AICc (Akaike's Information Criterion corrected for small sample size), Akaike weights (w_i), number of parameters (K), and deviance (Dev).

Model structure	AICc	ΔAICc	w_i	K	Dev.
S_{age}	72.9	0.0	0.15	3	66.9
$S_{\text{age + avg fat}}$	74.8	1.8	0.06	4	66.7
$S_{\text{age + impact zone}}$	74.8	1.9	0.06	4	66.7
$S_{\text{age + woodlands}}$	74.9	2.0	0.05	4	66.8
$S_{\text{age + 500m}}$	74.9	2.0	0.05	4	66.9

Table 3.2. Beta coefficients (β) and 95% confidence intervals for covariates included in top models ($\Delta AIC_c < 2.0$) of elk survival at Fort Riley, Kansas.

Model structure	Parameter	β	95% confidence interval
S_{age}	AGE	-0.18	(-0.34, -0.02)
$S_{\text{age + avg fat}}$	AGE	-0.20	(-0.39, -0.02)
	AVG FAT	-0.05	(-0.26, 0.16)
$S_{\text{age + impact zone}}$	AGE	-0.19	(-0.37, -0.02)
	IMPACT ZONE	-0.44	(-2.49, 1.61)
$S_{\text{age + woodlands}}$	AGE	-0.17	(-0.34, -0.01)
	WOODLANDS	-0.97	(-8.07, 6.13)
$S_{\text{age + 500m}}$	AGE	-0.18	(-0.34, -0.02)
	500M	-0.48	(-4.39, 3.42)

Figure 3.1. Model-averaged estimates of monthly cow elk survival (+/- SE) at Fort Riley, KS for 40 monthly intervals beginning November 2003 and ending February 2007.

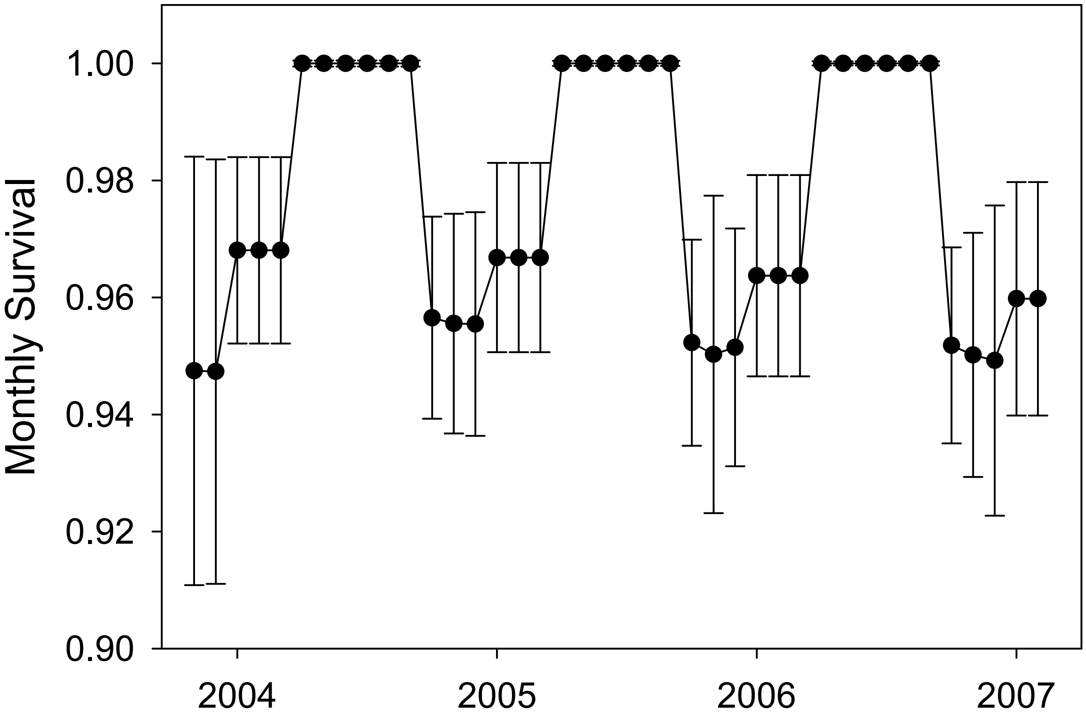

Figure 3.2. Age-specific monthly survival estimates (+/- SE) for cow elk from the model S_{age} during hunting seasons at Fort Riley, Kansas.

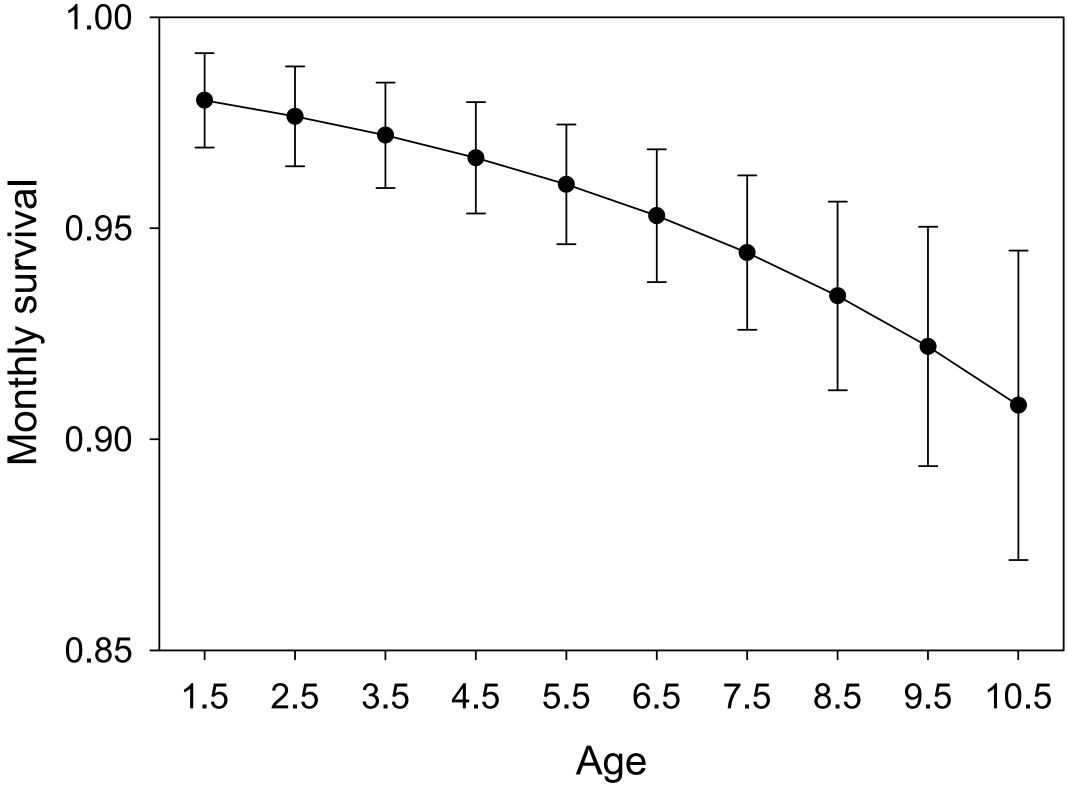

Figure 3.3. Elasticity matrix (E), indicating elasticities (*e_{ij}*) for individual matrix elements (*a_{ij}*) based on vital rates estimated for an elk population at Fort Riley, Kansas.

$$\mathbf{E}= \begin{pmatrix} 0 & 0.213 & 0.031 \\ 0.244 & 0.462 & 0 \\ 0 & 0.031 & 0.018 \end{pmatrix}$$

CHAPTER 4 - LANDSCAPE AND HOME RANGE SCALE HABITAT SELECTION BY ELK (*CERVUS ELAPHUS*) IN A GRASSLAND SYSTEM

Abstract

Habitat selection may occur over a range of spatial scales, with scale-dependent patterns of habitat selection emerging as a result of decisions made at the landscape scale and within the home range. We assessed habitat selection across spatial scales by comparing locations used by elk to available locations in the surrounding landscape and within the home range. We assessed the relative influence of risk-related and resource-related factors to habitat selection at each of these scales by comparing predictor variables included in resource selection function models generated seasonally for a reintroduced elk population at Fort Riley, Kansas. All predictor variables, with the exception of fall and spring prescribed burns, were included in top models across seasons at both spatial scales. Elk selected low-elevation areas, gentle slopes, edge habitat, and areas close to streams at both spatial scales. At the landscape scale, elk generally avoided roads and preferred areas on or near Fort Riley. At both spatial scales, elk used riparian woodlands more frequently than grasslands. Elk selected for agricultural crops on food plots and private lands when seasonally available. These findings do not support the idea that risk-related factors have a stronger influence on resource selection by elk at the landscape scale, as has been found for ungulates in areas with natural predators present.

Introduction

Habitat-selection is driven by the need to enhance individual fitness by acquiring adequate resources while minimizing predation risk (Sih 1980, Lima and Dill 1990). The outcomes of individual behavioral decisions are manifested as the location of the home range within the landscape and specific locations used within the home range. Therefore, the distribution of animal locations on a landscape across various spatial scales may reflect the distribution or heterogeneity of limiting resources (forage, water, cover) or predation risk (Ripple and Beschta 2004, Hernandez and Laundre 2005). The influence of environmental factors on habitat selection can vary across spatial scales (Boyce et al. 2003, Anderson et al. 2005, Bowyer and Kie 2006), but the mechanisms for this variation have not been widely explored. Rettie and Messier (2000) hypothesize that there is a direct relationship between the relative importance of limiting factors on individual fitness and the scale at which these factors have the greatest influence on habitat selection. This hypothesis suggests that habitat selection at coarser scales (i.e. placement of the home range within the landscape) should occur as a response to the limiting factor that most strongly influences individual fitness (Rettie and Messier 2000). If coarse-scale habitat selection is successful at mitigating the influence of the primary limiting factor, habitat selection at finer scales (i.e. within the home range) should be less directly influenced by this factor and more strongly reflect the influence of secondary factors, whose impact may not be as evident at coarser scales of investigation (Rettie and Messier 2000). In areas with gray wolves (*Canis lupus*) present, habitat selection by ungulates is influenced by predation risk at the landscape scale, while habitat selection within the home range is related to forage availability (Rettie and Messier 2000, Anderson et al. 2005).

The location of elk (*Cervus elaphus*) on a landscape at various spatial scales may be influenced by predation risk or the distribution of resources. Elk fitness, as measured by survival and reproduction, is directly influenced by nutritional condition (Cook et al. 2001, Cook et al. 2004, Bender et al. 2006, Bender et al. 2008) which in turn is determined by resource acquisition. Therefore, it is necessary for elk to acquire forage of sufficient quality and quantity to maximize survival and reproductive success. Elk may select for native graminoid plant species, with woody vegetation (browse) and forbs generally constituting less important components of the diet (Christianson and Creel 2007). Forage quantity may directly influence elk habitat selection as grassland areas with high forage biomass are often selectively used by elk (Wallace et al. 1995, Anderson et al. 2005). In prairie systems, elk diets may include large proportions of native prairie grasses during both growing and non-growing seasons (Walter 2006). In addition to graminoids, agricultural crops including winter wheat (*Triticum aestivum*), grain sorghum (*Sorghum bicolor*), and alfalfa (*Medicago sativa*) are consumed by elk on a seasonal basis (Walter 2006). In tallgrass prairie systems, burning of grassland vegetation promotes the dominance of graminoid species and enhances the total amount of aboveground biomass available for ungulate grazers (Abrams et al. 1986). In addition, net primary production of tallgrass prairie vegetation can be influenced by topographic position (Knapp et al. 1993) with higher levels of biomass found on lowland prairie sites than upland sites (Abrams et al. 1986). Water may also be an important limiting resource for elk, and the availability of free water can influence the distribution of elk (Skolvin et al. 2002).

The importance of altered prey behavior in response to predation risk (behaviorally-mediated indirect effects) is now increasingly recognized (Lima 1998, Werner and Peacor 2003). Predation risk can influence vigilance patterns, social group structure, and spatial or temporal patterns of habitat use by prey species (Ripple and Beschta 2004, Creel et al. 2005, Mao et al. 2005). Elk responses to predation risk may be sex-specific, with females exhibiting a stronger response to predation risk in terms of their habitat selection and vigilance behavior than males (Childress and Lung 2003, Winnie and Creel 2007).

Harvest is the leading cause of mortality for many elk populations (Unsworth et al. 1993, Ballard et al. 2000), and habitat selection by elk in harvested populations is expected to reflect anti-predator behavior designed to reduce mortality risk from harvest or poaching. During hunting season, elk are found less frequently in areas with high densities of hunters (Millspaugh et al. 2000) and may move to refuge areas where hunting is not allowed (Viera et al. 2003). These observations suggest that the behavioral responses of herbivores to mortality risk from harvest are expected to be strong, measurable, and similar to responses to natural predation risk.

Behavioral responses of elk to predation or harvest pressure can be measured based on elk use of landscape features that minimize mortality risk. When foraging under the risk of predation, elk may increase use of woodland areas (McCorquodale 2003, Wolff and Van Horn 2003) or selectively forage in grassland areas that are located in close proximity to woodland cover. Harvest rates of elk may increase as road density increases (Hayes et al. 2002) and the avoidance of roads by ungulates (Witmer and DeCalesta 1985, Rowland et al. 2000) may be a means of reducing mortality risk. When predators are present, elk locate home ranges distant from predator territories (Anderson et al. 2005) or use refuge areas where predators are absent (Ferguson et al. 1988).

When wolves are present, habitat selection by ungulates at a coarse-scale (i.e. home range location within the landscape) may be most influenced by predation risk, while habitat use within the home-range reflects resource availability (Rettie and Messier 2000, Anderson et al. 2005). However, this scale-dependent pattern of habitat selection has not been examined in ungulate populations where natural predators are absent and hunting is the primary cause of mortality. We sought to determine if this same pattern was present in an ungulate population where mortality risk from harvest was the primary cause of mortality. To this end, we studied a harvested elk population without natural predators located at the Fort Riley Military Installation, Kansas.

The impact of adult survival on population growth rates is generally large for long-lived vertebrates (Eberhardt 2002), suggesting that factors influencing adult survival generally have a large influence on fitness for these species. For the Fort Riley elk population, natural predators were absent and harvest was the primary cause of adult mortality. Under these conditions, we expected that harvest mortality would be an important limiting factor and exert a strong influence on elk distributions and habitat selection. Forage availability was not expected to be a primary limiting factor for this population due to the ready availability of native and agricultural crops for forage and the absence grazers including bison (*Bos bison*) or cattle (*Bos taurus*) on Fort Riley. Resource limitation for this population was also unlikely because the population was under ecological carrying capacity (Piasecke and Bender 2009) and female elk attained levels of body fat adequate for successful reproduction and survival (Piasecke 2006).

Our objectives were: 1) to determine elk locations in relation to habitat features related to morality risk and forage availability, 2) to assess the magnitude and direction of the relationship between these factors and elk locations at two spatial scales using resource selection functions (RSF), and 3) to determine the relative influence of risk-related and resource-related variables on coarse- and fine-scale habitat selection patterns by elk. Specifically, we predicted that mortality risk would explain elk distribution at the landscape scale and that elk locations would be closer to areas without hunting pressure, farther from roads, and occur more frequently in woodland areas when compared to available locations throughout the study area. We expected risk-related factors to have a reduced influence on elk distribution within the home range and that factors related to resource availability (including topographic variables, stream distance, food plots, burned areas and grassland habitats) should have a stronger influence on elk habitat use at this scale.

Methods

Study area - Fort Riley is a 40,273 ha military training facility located in the Flint Hills of northeastern Kansas (39° N, 97° W) (Fig. 4.1). On Fort Riley, approximately 26,400 ha of the installation are designated as field training areas that are used for artillery firing, small arms firing, combat vehicle operations, and field encampments (US Army 1994). These training areas include a contiguous 5,600 ha artillery and range firing impact area (Impact Zone) with a core area impacted by munitions firing and a surrounding buffer zone. The Impact Zone is off-limits at all times to civilians and military personnel.

Training areas of the installation are primarily tallgrass prairie vegetation with scattered riparian woodlands associated with streams and lowland areas. Brome (*Bromus sp.*) and fescue (*Festuca sp.*) remain the dominant grass species in some areas used for agriculture prior to acquisition by the US Army in 1965 (Freeman and Delisle 2004). A variety of crops are planted in cultivated fields on Fort Riley (food plots) for the benefit of wildlife. These crops include soybeans (*Glycine max*), wheat (*Triticum aestivum*), corn (*Zea mays*), alfalfa (*Medicago sativa*), and grain sorghum (*Sorghum bicolor*). Prescribed burning takes place annually throughout training areas of the installation. Training areas are burned on a 3-year burn interval, with approximately 1/3 of the installation burned each year to achieve this management objective (Alan Hynek, Fort Riley Conservation Division, personal communication).

Field methods – We captured female elk at Fort Riley, Kansas by flying a helicopter to locate elk and then shooting elk with tranquilizer darts containing carfentanil citrate (3.0 mg/elk) and xylazine hydrochloride (100 mg/elk). During February 2005, we captured and placed radio-telemetry collars equipped with store-on-board global positioning system (GPS) receivers (Advanced Telemetry Systems, Isanti, MN) and a remote release mechanism on 16 female elk. We captured additional female elk in November 2005 (5 recaptures and 4 new captures) and April 2006 (6 recaptures and 2 new captures). We also captured elk in a corral trap during January-February 2006 (4 new captures). We placed GPS collars on a total of 26 female elk during the study. We programmed GPS collars to record locations at 4.5-h intervals during the calving season (1 May – 15 July), and at 7-h intervals during the rest of the year. The increased frequency of locations obtained during the calving season was designed to assess habitat use and movement patterns at a finer temporal scale during the times preceding, during, and immediately following calving. The increased location frequency was also chosen to provide data for an additional separate analysis of fine-scale movement patterns during the calving period.

Data analysis- We used logistic regression to compare characteristics of locations used by elk to available locations at the landscape and home-range scale (Manly et al. 2002, Anderson et al. 2005). Logistic regression is a suitable technique for analyzing patterns of wildlife habitat selection based on a comparison of used and available locations (use-availablity design) (Johnson et al. 2006). We generated resource selection functions separately for winter (January – February), spring (March-April), calving (May – July), late summer (August-September), and rut / hunting season (October – December). We conducted a separate analysis for each season because elk habitat requirements change seasonally (Ager et al. 2003) and the relative importance of risk-related and resource-related variables may vary on a seasonal basis. For example, risk-related variables may be more important for explaining elk habitat selection during hunting season when harvest-related mortality risk is high, while resource-related variables may have a greater influence on elk habitat selection during early spring when limited forage is available. Seasonal analysis was also specifically appropriate for our study because the types and quality of available forage differed between growing and non-growing seasons on our study site and elk home ranges on Fort Riley shifted seasonally during 2005 (Fig. 4.2) and 2006 (Fig. 4.3).

While the exact number of GPS locations recorded per elk within a given season varied (March-April 2005: $\mu = 170.6$ ($\sigma = 36.6$), May-July 2005: $\mu = 306.9$ ($\sigma = 71.1$), August-September 2005: $\mu = 122.1$ ($\sigma = 41.4$), October-December 2005: $\mu = 143.1$ ($\sigma = 44.2$), January-February 2006: $\mu = 145.3$ ($\sigma = 59.2$), March-April 2006: $\mu = 142.6$ ($\sigma = 55.8$), May-July 2006: $\mu = 387.7$ ($\sigma = 76.8$), August-September 2006: $\mu = 152.2$ ($\sigma = 40.6$), October-December 2006: $\mu = 244.4$ ($\sigma = 48.6$)) we felt that this variation was not substantial enough to justify the loss of data that would have occurred by equalizing sampling sizes through sub-sampling or excluding elk with a high or low number of locations. Furthermore, when resource selection patterns are consistent across individuals in a population, β coefficient estimates from logistic regression may be robust to variation in sample size (number of locations / animal) between individuals (Gillies et al. 2006). Therefore, we used all recorded GPS locations for subsequent analysis for both the landscape and home-range scales.

We determined top models from a predefined set of candidate models by comparing differences in values of Akaike's Information Criterion (AIC) between a given model and the model with the lowest AIC value in the candidate set (ΔAIC) (Burnham and Anderson 2002). We also computed Akaike weights (w_i) for models in the candidate set, with values for Akaike weights indicating the relative support for a given model when compared to other models in the candidate set (Burnham and Anderson 2002). We assessed the goodness-of-fit of the top model based on overall likelihood chi-square tests (Allison 1999), with significance levels < 0.05 indicating that at least one model coefficient was not equal to 0. Likelihood chi-square tests for all top models across scales and seasons were significant ($P < 0.05$), indicating that top models fit better than null models in all cases.

We determined maximum likelihood estimates of β coefficients for predictor variables in each logistic regression model using SAS statistical software (PROC LOGISTIC, SAS Institute, Inc., Cary, N.C.). We modeled elk habitat selection within the home range using conditional logistic regression. Conditional logistic regression can be used to model binary response data (used vs. available locations) in cases where locations used by an animal are matched to locations available specifically to that animal (*i.e.* Nielsen et al. 2002, Anderson et al. 2005). We considered used and available location data from each individual elk as paired when conducting conditional logistic regression analysis. This design allowed us to account for dependence between used and available data for individual elk, and estimate overall effects of predictor variables on resource selection while controlling for differences between individual elk (Stokes et al. 2000). With this design, conditional maximum likelihood estimation was used to obtain overall estimates of slope coefficients (β) while removing the removing the effect of individual elk (Stokes et al. 2000).

We assessed the influence of predictor variables on elk habitat use across spatial scales by comparing regression coefficients (β) and odds ratio values for variables included in top models at the level of the home range and at the landscape scale. Positive values for logistic regression coefficients indicate a positive relationship between the predictor variable and the independent variable, while negative values for regression coefficients indicate a negative relationship between the predictor and independent variable (Allison 1999, Hosmer and Lemeshow 2000). Odds ratios indicate the relative odds of an event (elk use) occurring, with odds ratios greater than one indicating that an increase in the value of a predictor variable increases the odds of an event occurring

(Allison 1999). Odds ratios of less than one indicate that an increase in the value of a predictor variable results in a decrease in the odds of an event occurring (Allison 1999).

We characterized used locations at the landscape scale based on GPS telemetry locations recorded for each elk. We characterized available habitat by generating an equal number of random points within the study area using the Hawth's Analysis Tools extension for ArcGIS (Beyer 2004). We defined the study area as the area within a 400 m buffer of a minimum convex polygon (MCP) encompassing all recorded elk locations on and around Fort Riley for a given season. Using this approach, the spatial extent of available habitat varied seasonally but generally included the majority of training areas on Fort Riley and some areas of private land < 800 m from the installation boundary. While home ranges of elk were centered on Fort Riley throughout the study period, home ranges of individual elk did not encompass all training areas within the installation during a given season (Fig. 4.2, Fig. 4.3). Thus, our definition of availability allowed us to consider available habitat to include both unused areas between elk home ranges on Fort Riley and areas of private land beyond the periphery of elk home ranges.

For analysis of elk habitat selection within the home range, we determined locations used by elk from GPS telemetry locations recorded for individual elk. We defined available locations by generating random points within the seasonal 100% MCP home range for each female elk. We set the number of random point locations generated within the home range of each elk equal to the number of GPS telemetry locations for that elk. We chose this number of random points so that used and available locations from within the home range of each elk would have an equal sample size for conditional logistic regression analysis.

Predictor variables for each point location included land-cover type, distance to nearest maintained road, nearest stream, Impact Zone, Fort Riley boundary, burned locations from the previous spring, burned locations from the previous fall, slope, elevation, and curvature. To characterize points located in grassland edge (grassland areas <100 m from woodlands), a dummy variable was created in which points located in grassland cover types within 100 m of woodlands were assigned a "1" and all other points assigned a "0".

We did not consider unimproved roads (tank trails) in our analysis because their accessibility and vehicle-use patterns differed from maintained roads on Fort Riley. Military vehicles used unimproved roads less frequently than maintained roads and unimproved roads were not accessible to the public for hunting access or other purposes. We felt that elk would avoid roads primarily as a means of reducing hunting pressure and felt that this effect would be most evident for maintained roads.

We screened predictor variables for multicollinearity by examining correlation coefficients and variance inflation factors (Allison 1999). We excluded predictor variables from further analysis for a given season if they were highly correlated with other individual predictor variables ($r > 0.70$) or had a high variance inflation factor (VIF > 3.0). Variance inflation factors provide an index to the degree of correlation between a single variable and all other predictor variables in the candidate set (Allison 1999).

We measured land-cover types on Fort Riley using GIS layers provided by the Fort Riley Integrated Training Area Management program that defined vegetation categories as woodland (> 15% canopy cover), grassland, urban, or water. These land-cover layers were originally derived from Kansas GAP analysis vegetation data (Troy

Livingston, Fort Riley Integrated Training Area Management, *personal communication*) and land-cover classifications were generally consistent with National Agricultural Image Program (NAIP) aerial images (2005) based on a qualitative visual comparison. We excluded points located in urban or water land-cover classes from further analysis. In addition, we classified agricultural crops planted on Fort Riley (food plots or firebreak fields) and on surrounding areas of private land and included these cover types in our analysis. We did not use Fort Riley vegetation maps with finer resolution of vegetation classes due to incomplete coverage of the Impact Zone (Freeman and Delisle 2004). We digitized private-land field boundaries surrounding Fort Riley based on GPS waypoints taken around accessible field borders and National Agricultural Imagery Program (NAIP) aerial images (2005). We determined crop types for each private land field twice annually by visual inspection. Firebreaks (cultivated areas located along the border of the installation) on Fort Riley were leased to agricultural producers and planted to a variety of row-crops with a portion of crops planted in all firebreak fields left for wildlife use. We also digitized firebreak field boundaries as described above and determined crop types twice annually. Food-plot planting data were obtained from the Fort Riley Conservation Division and we assigned crop types as an attribute to existing GIS food-plot layers.

We mapped spring and fall burns (including prescribed burns and wildfires) by taking GPS locations around edges of accessible burned areas on Fort Riley. We used these GPS locations to create digitized GIS layers for spring and fall burned areas. We recorded spring and fall burns separately because burn timing may influence vegetation composition (Towne and Kemp 2003), timing of vegetation regrowth, and seasonal availability of forage biomass. We recorded the dates of prescribed burns from burn data obtained from the Fort Riley Conservation Division and added these dates as an attribute for each burned area.

Elevation data for the study area was based on 10-m resolution elevation rasters from the National Elevation Dataset (NED) (http://ned.usgs.gov). We calculated percent slope and curvature from elevation raster layers using the Spatial Analyst extension for ArcGIS. We calculated curvature as the second derivative of the elevation raster (McCoy et al. 2004) using the Spatial Analyst extension for ArcGIS. Positive curvature values indicate locations at which the surrounding landscape slopes downwards (hilltops and ridgelines) and negative curvature values indicate locations at which the surrounding landscape slopes upwards (valley bottoms and ravines) (McCoy et al. 2004).

We tested the positional accuracy of GPS locations recorded by collars used during the study. To test positional accuracy, we first placed test collars at randomly selected test locations on training areas of Fort Riley. We selected test locations within woodland and grassland habitat types using Hawth's Tools Random Point Generator in ArcGIS (Beyer 2004). We placed stakes at each test location and affixed collars to the stakes approximately 0.5 m above the ground with the GPS receiver of the collar oriented upwards. Collars remained at a given location between 40-96 hours. We determined the positional accuracy of each GPS fix based on the distance from the true geographic location using the formula:

$$(\Delta x^2 + \Delta y^2)^{1/2}$$

with Δx and Δy representing the distance (m) from the x and y coordinates of the true geographic location (Di Orio et al. 2003). We determined the reference geographic coordinates of each test location using a Trimble handheld GPS receiver (Trimble Navigation, Limited, Sunnyvale, CA). The grand mean positional accuracy of collars at grassland test locations (n = 14) was 2.4 m (SD = 1.38, range of means = 0.83 – 5.35) and 9.75 m (SD = 7.6, range of means = 4.6 – 11.6) at woodland test locations (n = 8). We did not differentially correct GPS collar locations used for analysis as the mean positional accuracy for collars at both grassland and woodland locations was within the finest grain size of raster layers that we used for analysis (10-m elevation layers).

Results

Home-range scale model selection

The best supported models ($\Delta AIC < 2.0$) for habitat selection at the home range scale for 2005 included all predictor variables. Global models received the highest level of support, as indicated by low ΔAIC values and Akaike weights for all seasons in 2005 (Table 4.1). Global models were also the best supported models for home-range scale habitat selection during 2006, with the exception of January-February 2006 (Table 4.2). The best supported model for January-February 2006 included all predictor variables except for fall and spring burn distance.

Landscape-scale model selection

The best supported models for landscape-scale habitat selection patterns generally included the majority of predictor variables. Global models consistently had the lowest AIC values and were considered to be the best supported model for all seasons during 2005 (Table 4.3) and for all seasons with the exception of January-February during 2006 (Table 4.4). For January-February 2006, the best supported model included all predictor variables except burn variables (fall burn distance and spring burn distance). Parameter estimates were not model-averaged (Burnham and Anderson 2002) as there was little model uncertainty in the datasets, with top models receiving the greatest amount of support for each season based on values of Akaike weights for top models ($w_i > 0.70$ for all top models).

Model parameters for landscape and home-range scale top models

Risk-related predictor variables included distance from roads, grassland edge, Impact Zone distance, and Fort Riley boundary distance. Parameter estimates for 2006 landscape-scale top models indicated that elk avoided roads (Tables 4.9 - 4.13). This effect was most evident during the hunting season (October – December). Although β coefficients for road distance also tended to be positive for 2005 landscape-scale models, confidence intervals for the odds ratios of road distance overlapped 1.0 for each season (Tables 4.5-4.8). Home-range scale models indicated that elk also avoided roads during 2006, and odds ratios were the same or slightly smaller than corresponding ratios for landscape-scale models. At the home-range scale during 2005, there was no discernable pattern of habitat selection in relation to roads; elk exhibited a slight avoidance of roads during March-April and May-July, no preference during August-September, and a slight preference for being closer to roads during October-December.

Elk strongly selected for grassland edge with this predictor variable having odds ratios > 1.0 across seasons, years, and scales (Tables 4.5 - 4.13). While grassland edge consistently increased the odds of elk use of an area, the relative influence of edge habitat on elk use appeared to vary across scales on a seasonal basis. Grassland edge had a stronger positive influence on the odds of elk using a location (as indicated by larger β coefficients and odds ratios) at the home-range scale than the landscape scale during

May-July (calving season) and October-December (hunting season) during both 2005 and 2006.

Impact Zone distance did not appear to have a strong influence on patterns of elk habitat selection at either the landscape or home-range scale. Although Impact Zone distance was included as a predictor variable in all top models, 95% confidence intervals for odds ratios of this variable included 1.0 during all seasons for 2005 and 2006 at both the landscape and home-range scale. This indicates that elk used the Impact Zone much like other areas on Fort Riley without exhibiting a notable preference or avoidance during any season.

The odds of elk using a location decreased slightly as the distance from Fort Riley increased, as indicated by a negative β coefficient for this predictor variable (with the exception of October-December 2006). Elk selection for areas closer to Fort Riley was manifested more strongly at the landscape scale than within the home range, as indicated by β coefficients and odds ratios that were generally larger at the landscape scale than the home-range scale.

Resource-related predictor variables included streams, spring and fall burns, topographic variables, and land-cover types. Elk selected for areas that were close to streams during all seasons at the landscape and home-range scales. Stream distance was not included in all top models due to correlation with other predictor variables during some seasons. For seasons in which the predictor variable for stream distance was included in top models, the odds of elk using an area decreased as distance from a stream increased (Tables 4.5 - 4.13). Spring and fall burn predictor variables were not included in top models for January-February 2006 and we removed this predictor variable from candidate models for several additional seasons due to multicollinearity (Tables 4.1 -4.4). When burn variables were included in top models, they had little directional impact on elk habitat selection at either the landscape or home-range scale, with no noted preference or avoidance of burned areas during all seasons with the exception of October-December 2005.

Land-cover types were important for elk habitat selection and the selection of land-cover types by elk changed on a seasonal basis. We used woodlands as a reference category and compared elk use of other land-cover types to this category. Elk used grassland less than woodland areas, as indicated by negative β coefficents and odds ratios < 1.0 for all seasons at both scales (Tables 4.5 - 4.13). Elk use of agricultural crops planted on food plots, firebreaks, or private land varied seasonally. Elk selected for winter wheat fields during January-February and March-April at both the landscape and home-range scales. For these seasons, the presence of winter wheat fields had a stronger positive influence on the odds of elk using a location at the landscape than at the home range scale. Land-cover types classified as "other" were primarily fallow agricultural fields and elk consistently selected against these cover types during all seasons at both spatial scales.

Less common crop types included corn, soybeans, milo, forage sorghum, sunflower and alfalfa. The relatively small number of used and available points located in these land-cover types resulted in parameter estimates with large variability and large 95% confidence intervals for odds ratios, making it difficult to determine with confidence the influence of these crop types on habitat selection by elk. Elk used these crops at both scales as they became seasonally available, selecting corn fields during May-July and

August-September, soybean fields during August-September, and forage sorghum during October-September.

At the landscape scale, elk selectively used areas of lower elevations and avoided areas with steep slopes (Tables 4.5 – 4.13). At the home-range scale, elk also avoided areas of high elevation and steep slopes across all seasons with the exception of October – December 2005 (Tables 4.5 – 4.13). Elk exhibited a stronger avoidance of steep slopes at the landscape scale than at the home-range scale, as indicated by smaller β coefficients and odds ratios for slope at the home range scale.

With the exception of August-September 2006, there was limited evidence for a directional effect of curvature on elk habitat use at the landscape scale (based on odds ratio confidence intervals that overlapped 1.0). During August-September 2006, upwardly concave topographic surfaces (ravines / valley bottoms) were selected for by elk, as indicated by a positive β coefficient and odds ratio > 1.0 for this season (Table 4.12). Similar to patterns found at the landscape scale, curvature did not increase or decrease the odds of elk using an area on the landscape during either 2005 or 2006 (Tables 4.5 – 4.13).

Discussion

Patterns of habitat selection can vary across spatial scales. Factors that have the strongest influence on survival and reproduction drive habitat- or resource-use patterns at the landscape scale, and secondary factors influence resource-use within the home range (Rettie and Messier 2000). Studies of ungulates that have examined habitat selection across multiple scales have found that landscape-scale habitat selection is strongly influenced by predator presence (Rettie and Messier 2000, Anderson et al. 2005, Creel et al. 2005, Dussault et al. 2005) and that responses to predation risk may vary seasonally (Mao et al. 2005).

We found little difference among variables included in the best-supported models describing habitat selection at the landscape and home-range scales for elk in a tallgrass prairie landscape. The inclusion of the same suite of predictor variables in both landscape and home-range models could indicate that elk are faced with similar pressures from mortality risk and resource acquisition, and that both of these factors influence habitat selection at landscape and home-range scales. It may also be possible that habitat selection at the landscape scale was not successful at reducing the effects of mortality risk. In this case, risk-related variables would be expected to have a similar influence on habitat selection at both the landscape and home-range scale (Rettie and Messier 2000, Dussault et al. 2005). The influence of specific predictor variables on elk habitat selection was generally consistent at both the landscape and home-range scales.

The main risk-related factor with a directional effect on elk habitat selection was road distance. Elk avoidance of roads at the landscape scale is generally consistent with previous findings (McCorquodale 2003, Stubblefield et al. 2006). Elk may place home-ranges away from roads to minimize vehicle disturbance or reduce mortality risk (Hayes et al. 2002). On Fort Riley, improved roads are open to the public during hunting season and serve as access points for elk hunting. Hunter densities may be negatively related to distance from roads (Stedman et al. 2004), making it logical for elk to place home ranges in areas that would minimize mortality risk and disturbance associated with roads. Within the home range, road distance did not have as strong of a negative influence on elk habitat selection. Elk may have mitigated risks from this factor by selecting areas with low road densities at the landscape scale or may rely on increased use of cover within the home range as a strategy to minimize mortality risk when hunters are present (Millspaugh et al. 2000).

While elk may move to refuge areas during hunting season to avoid harvest pressure (Burcham et al. 1999), elk at Fort Riley did not select for or against refuge areas including the Impact Zone during any season. Elk used the Impact Zone similarly to other areas on Fort Riley over all seasons and across both spatial scales. Elk with home ranges outside the Impact Zone did not generally use this area as a refuge even during hunting season, but elk with home ranges centered on the Impact Zone were observed on multiple occasions to flee to this area when disturbed. It may be possible that elk mitigated mortality risk during the hunting season by increasing use of the Impact Zone during diurnal periods when hunters were allowed access to training areas of the installation. Female elk groups were present in the Impact Zone throughout the year, suggesting that this area meets the majority of year-round habitat requirements for elk. A possible exception was late winter and early spring periods when female elk groups temporarily decreased use of the Impact Zone and increased use of private lands and food plots. The use of artillery and range target areas by elk is similar to that observed for the Sonoran pronghorn (*Antilocapra americana sonoriensis*) in Arizona (Krausman et al. 2005), and further investigation into the generality of this phenomenon may be warranted.

Elk home ranges were centered on Fort Riley and female elk exhibited a strong site fidelity for the installation with no documented dispersal events occurring and no relocation of home ranges to similar habitats on adjacent private lands. While elk are not restricted from moving away from the installation, observational evidence suggests that elk use private land primarily for feeding sites during crepuscular hours and return to Fort Riley during the day. Elk home ranges may be centered on Fort Riley due to a longer elk hunting season on adjacent private lands, the lack of sufficient riparian woodlands to meet cover requirements, higher traffic volume on roads surrounding the installation, or increased levels of disturbance.

While streams were not included in all top models due to multicollinearity, elk preferred to use areas close to streams at both landscape and home-range scales during all seasons in which stream distance was included as a predictor variable. Streams are an important habitat feature for elk in a variety of areas (Skolvin et al. 2002) and water sources may be important for female elk in arid regions, particularly during calving season (McCorquodale et al. 1986, Bian and West 1997). On Fort Riley, perennial streams are a primary source of free water on the landscape and may determine elk distributions in this system.

Spring and fall burns had little discernable impact on elk habitat selection. This result was unexpected, given that prescribed burning in grassland systems increases aboveground biomass in the growing season following fire (Tracy and McNaughton 1997, Knapp et al. 1998) and promotes the dominance of native C_4 grasses that provide forage for grazing ungulates (Walter 2006). Burning may also enhance forage quality by improving both protein (Van Dyke and Darragh 2007) and nutrient content (Tracy and McNaughton 1997). In tallgrass prairie, bison preferentially graze on areas that have been burned the previous spring (Vinton et al 1993, Knapp et al. 1999) and elk also prefer burned areas in rough fescue grasslands (Jourdonnais and Bedunah 1990), sagebrush communities (Van Dyke and Darragh 2006), and grassland-sagebrush communities (Pearson et al. 1995). Perhaps the lack of discernable effect of burning on elk habitat selection was due to the availability of additional forage, including agricultural crops on food plots and private lands. Although a major portion of elk diets can consist of graminoids (Christianson and Creel 2007) including C_4 grasses (Walter 2006), elk may also use forbs or C_3 grasses on a seasonal basis (Wydeven and Dahlgren 1983, Edge et al. 1988). Elk diets on Fort Riley included a variety of forbs during the growing season and C_3 grasses during winter (J.M. Conard, unpublished data). Thus, prescribed burning in tallgrass prairie that increases the dominance of C_4 grasses at the expense of C_3 grasses and forbs (Hartnett and Fay 1998) may not increase elk use of burned areas as has been found in other systems (Pearson et al. 1995, Van Dyke and Darragh 2006). In a system with abundant forage resources and no other large native grazers, elk may not be forage-limited and the increase in forage biomass expected to occur as a result of prescribed burning (Knapp et al. 1998) may not have a large direct influence on habitat selection. While short-term positive responses to fire were not evident in this study, the importance of periodic fires for suppressing woody vegetation and maintaining a grassland system (Hartnett and Fay 1998) may be important for maintaining suitable habitat for elk over a longer time period.

Elk use a variety of land-cover types for foraging habitat, cover, bedding areas, or to aid in thermoregulation. Among native cover types on Fort Riley, woodland areas were used much more frequently by elk than grassland areas. In this tallgrass prairie landscape, riparian or gallery forest areas comprise a relatively small proportion of the landscape (<20%) and may provide important habitat for elk. In areas where closed canopy forest comprises the majority of the landscape, elk use open meadows or grassland areas more often than expected based on availability (Anderson et al. 2005). Elk may also prefer woodland areas when inhabiting landscapes composed of a mixture of grassland and woodland habitats (Stewart et al. 2002). In the few studies that have been conducted on elk in prairie regions of the Great Plains, elk preferentially use riparian and other woodlands (Wydeven and Dahlgren 1985, Robinson 1993, Bian and West 1997). We observed elk on Fort Riley using grassland areas for foraging or travel during crepuscular and night time periods, and woodland areas for bedding and cover during the day. Grassland edges were strongly preferred by elk, which is consistent with previous reports of elk preferring to use areas in close proximity to woodland cover (Cairns and Telfer 1980, Boyce et al. 2003).

Elk used private land fields and food plots when crops were seasonally available on these areas. Elk consistently selected for winter wheat more strongly than woodlands during January-February and March-April, presumably due to the quality forage provided by winter wheat at a time when native vegetation is dormant. Elk use winter wheat frequently when it is available (Walter 2006), and the presence of this crop may influence the placement of elk home ranges within the landscape and habitat selection within the home range.

Elevation and slope influenced elk habitat selection at both the landscape and home-range scales, with elk generally selecting areas of lower elevation and gentler slopes. For slope, this effect was stronger within the home range. Elk in montane areas exhibit seasonal shifts in elevation, with higher elevation areas used for summer ranges and lower elevations used for winter ranges (Irwin 2002). Elk preference for low elevation areas is consistent with observed patterns of elk habitat use in other non-montane areas (McCorquodale et al. 1986), and may be partially explained by elevation-related changes in vegetation productivity or phenology (Stubblefield et al. 2006). On the study area, there is a relatively small range of elevation (1025 – 1365 ft) (Pitts et al. 1987), but even across this range of elevation there may be differences in primary productivity between upland and lowland sites (Knapp et al. 1998). In areas that are regularly burned, upland sites are less productive and lowland sites have higher levels of annual above ground net primary productivity (ANPP) (Knapp et al. 1998) potentially resulting in increased forage quantity for elk. Elk tend to move parallel to ridgelines (Kie et al. 2005), and it may not be energetically advantageous for elk to move uphill to reach higher elevation areas containing lower forage biomass.

Elk use a variety of cover types and landscape areas to meet daily and seasonal habitat requirements (Ager et al. 2003). This shifting pattern of habitat use highlights the importance of considering variation in habitat selection at various temporal and spatial scales. Elk exhibited similar patterns of habitat selection within the home range and at the landscape scale, suggesting that the influence of risk-related factors on habitat selection by elk may not differ across spatial scales in areas where mortality is primarily due to hunting. These findings differ from patterns of habitat selection at the landscape and home-ranges scale exhibited by ungulates in systems with large natural predators (Rettie and Messier 2000, Anderson et al. 2005). In systems with wolves present, habitat selection by elk at the landscape scale is generally driven by risk-related variables (Rettie and Messier 2000, Anderson et al. 2005). This implies that hunting may not influence elk behavior in the same way as natural predation risk. It is also likely that currently observed patterns of elk habitat use in tallgrass prairie differ from the way in which elk were distributed during historical periods when large natural predators were a functional component of the ecosystem.

Understanding factors that influence the distribution of elk may also be useful for understanding the influence of elk on various ecosystem processes. Ungulates directly influence nutrient cycling, vegetation composition, and plant primary productivity (Hobbs 1996, Hartnett and Fay 1998, Schoeneker et al. 2004), and our findings suggest that these impacts may be spatially heterogeneous and depend on factors that influence the distribution of elk across the study area. For instance, impacts of elk herbivory on vegetation may be reduced in close proximity to landscape features that are avoided by elk such as roads and areas with high elevation or slope. Vegetation in areas preferentially used by elk, including grassland edges or woodland areas, is expected to be most strongly impacted by elk herbivory. Nutrient cycling patterns may also be influenced by ungulate distributions, and elk may redistribute nitrogen from areas frequently used for foraging (agricultural crops / grasslands) to areas used for bedding (woodlands). While our findings support the idea that landscape features may influence the spatial distribution of elk, further study is needed to determine the precise influence of elk on vegetation dynamics and nutrient cycling in tallgrass prairie.

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Table 4.1. Model rankings for 2005 home range habitat selection top models. Model fit was assessed separately for each season based on values of Akaike's Information Criterion (AIC) and Akaike weights (w_i). Model parameters (K = number of parameters) included elevation (ELEV), slope (SLOPE), curvature (CURVE), road distance (RD_DIST), stream distance (STRM_DIST), impact zone distance (IZ_DIST), Fort Riley boundary distance (FRTBND_DIS), previous spring burn distance (SPRGBRN), previous fall burn distance (FALLBRN), land cover type (COVER_NAME), and grassland edge habitat (GRASS_EDGE). Global model includes all parameters for a given season.

Season	Rank	Model	K	AIC	ΔAIC	w_i
March-April†	1.	GLOBAL MODEL	11	5971.7	0.0	0.999
	2.	ELEV SLOPE CURVE RD_DIST STRM_DIST IZ_DIST FRTBND_DIS GRASS_EDGE COVER_NAME	9	6008.4	36.7	< 0.001
	3.	FALLBRN RD_DIST STRM_DIST GRASS_EDGE COVER_NAME	6	6021.4	49.8	< 0.001
May-July*	1.	GLOBAL MODEL	10	10912.0	0.0	> 0.999
	2.	SLOPE CURVE RD_DIST STRM_DIST IZ_DIST FRTBND_DIS GRASS_EDGE COVER_NAME	9	11012.0	100.0	< 0.001
	3.	SPRGBRN FALLBRN RD_DIST STRM_DIST GRASS_EDGE COVER_NAME	6	11049.3	137.2	<0.001
August– September	1.	GLOBAL MODEL	11	4714.23	0.0	>0.999
	2.	SPRGBRN FALLBRN RD_DIST STRM_DIST GRASS_EDGE COVER_NAME	6	4777.84	63.6	<0.001
	3.	STRM_DIST COVER_NAME GRASS_EDGE	3	4831.45	117.2	<0.001
October-December	1.	GLOBAL MODEL	11	2151.53	0.0	>0.999
	2.	SPRGBRN FALLBRN RD_DIST STRM_DIST GRASS_EDGE COVER_NAME	6	2314.69	163.2	<0.001
	3.	ELEV SLOPE CURVE SPRGBRN FALLBRN STRM_DIST GRASS_EDGE COVER_NAME	8	2367.07	215.5	<0.001

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†Spring burn predictor variable removed as burn data were not available from the previous spring.

* Elevation (ELEV) predictor variable was removed due to convergence problems.

Table 4.2. Model rankings for 2006 home range habitat selection models. Model fit was assessed separately for each season based on values of Akaike's Information Criterion (AIC) and Akaike weights (*w_i*). Model parameters (*K* = number of parameters) included elevation (ELEV), slope (SLOPE), curvature (CURVE), road distance (RD_DIST), stream distance (STRM_DIST), impact zone distance (IZ_DIST), Fort Riley boundary distance (FRTBND_DIS), previous spring burn distance (SPRGBRN), previous fall burn distance (FALLBRN), land cover type (COVER_NAME), and grassland edge habitat (GRASS_EDGE). Global model includes all parameters for a given season.

Season	Rank	Model	K	AIC	ΔAIC	w_i
January-February	1.	ELEV SLOPE CURVE RD_DIST STRM_DIST IZ_DIST FRTBND_DIS GRASS_EDGE COVER_NAME	9	3212.5	0.0	0.83
	2.	GLOBAL MODEL	11	3215.7	3.2	0.16
	3.	RD_DIST COVER_NAME GRASS_EDGE IZ_DIST	4	3345.9	133.5	<0.001
March-April	1.	GLOBAL MODEL	11	4301.4	0.0	0.96
	2.	ELEV SLOPE CURVE RD_DIST STRM_DIST IZ_DIST FRTBND_DIS GRASS_EDGE COVER_NAME	9	4307.6	6.2	0.04
	3.	SPRGBRN FALLBRN RD_DIST STRM_DIST GRASS_EDGE COVER_NAME	6	4317.9	16.6	< 0.001
May-July†	1.	GLOBAL MODEL	9	11698.4	0.0	> 0.99
	2.	SLOPE CURVE RD_DIST STRM_DIST IZ_DIST FRTBND_DIS GRASS_EDGE COVER_NAME	8	11747.9	49.6	< 0.001
	3.	SLOPE CURVE FALLBRN STRM_DIST GRASS_EDGE COVER_NAME	6	11768.0	69.7	< 0.001
August-September*	1.	GLOBAL MODEL	10	4538.3	0.0	> 0.999
	2.	RD_DIST COVER_NAME GRASS_EDGE IZ_DIST	4	4645.6	107.3	< 0.001
	3.	FALLBRN RD_DIST STRM_DIST GRASS_EDGE COVER_NAME	5	4753.3	215.0	< 0.001
October – December†	1.	GLOBAL MODEL	9	5086.6	0.0	>0.999
	2.	FALLBRN RD_DIST STRM_DIST GRASS_EDGE COVER_NAME	5	5160.6	81.3	<0.001
	3.	SLOPE CURVE RD_DIST STRM_DIST IZ_DIST FRTBND_DIS GRASS_EDGE COVER_NAME	8	5176.9	97.9	<0.001

†Elevation variable removed due to convergence problems, spring burn variable removed due to high correlation with multiple other variables.

* Spring burn predictor variable removed due to high correlation with multiple other variables.

Table 4.3. Model rankings for 2005 landscape scale habitat selection models. Model fit was assessed separately for each season based on values of Akaike's Information Criterion (AIC) and Akaike weights (w_i). Model parameters (K = number of parameters) included elevation (ELEV), slope (SLOPE), curvature (CURVE), road distance (RD_DIST), stream distance (STRM_DIST), impact zone distance (IZ_DIST), Fort Riley boundary distance (FRTBND_DIS), previous spring burn distance (SPRGBRN), previous fall burn distance (FALLBRN), land cover type (COVER_NAME), and grassland edge habitat (GRASS_EDGE). Global model includes all parameters for a given season.

Season	Rank	Model	*K*	AIC	ΔAIC	w_i
March-April*†	1.	GLOBAL MODEL	9	5586.7	0.0	>0.99
	2.	ELEV SLOPE CURVE RD_DIST IZ_DIST FRTBND_DIS GRASS_EDGE COVER_NAME	8	5647.6	60.9	<0.01
	3.	RD_DIST FALLBRN GRASS_EDGE COVER_NAME	4	5698.4	111.7	<0.01
May-July	1.	GLOBAL MODEL	11	9180.8	0.0	>0.99
	2.	ELEV SLOPE CURVE RD_DIST STRM_DIST IZ_DIST FRTBND_DIS GRASS_EDGE COVER_NAME	9	9238.7	57.9	<0.01
	3.	SPRGBRN FALLBRN RD_DIST STRM_DIST GRASS_EDGE COVER_NAME	6	9524.8	343.9	<0.01
August-September	1.	GLOBAL MODEL	11	4079.7	0.0	>0.99
	2.	ELEV SLOPE CURVE RD_DIST STRM_DIST IZ_DIST FRTBND_DIS GRASS_EDGE COVER_NAME	9	4162.8	83.1	<0.01
	3.	ELEV SLOPE CURVE SPRGBRN FALLBRN STRM_DIST GRASS_EDGE COVER_NAME	8	4458.1	378.4	<0.01
October-December	1.	GLOBAL MODEL	11	2447.8	0.0	>0.99
	2.	ELEV SLOPE CURVE SPRGBRN FALLBRN STRM_DIST GRASS_EDGE COVER_NAME	8	3096.7	648.9	<0.01
	3.	SPRGBRN FALLBRN RD_DIST GRASS_EDGE COVER_NAME	6	3123.5	675.8	<0.01

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*Spring burn predictor variable not included as no burn data were available for spring 2004.

†Stream distance variable not included due to high correlation with other predictor variables.

Table 4.4. Model rankings for 2006 landscape scale habitat selection models. Model fit was assessed separately for each season based on values of Akaike's Information Criterion (AIC) and Akaike weights (w_i). Model parameters (K = number of parameters) included elevation (ELEV), slope (SLOPE), curvature (CURVE), road distance (RD_DIST), stream distance (STRM_DIST), impact zone distance (IZ_DIST), Fort Riley boundary distance (FRTBND_DIS), previous spring burn distance (SPRGBRN), previous fall burn distance (FALLBRN), land cover type (COVER_NAME), and grassland edge habitat (GRASS_EDGE). Global model includes all parameters for a given season.

Season	Rank	Model	K	AIC	ΔAIC	w_i
January-February[†]	1.	ELEV SLOPE CURVE RD_DIST IZ_DIST FRTBND_DIS GRASS_EDGE COVER_NAME	8	2834.8	0.0	0.79
	2.	GLOBAL MODEL	10	2837.9	2.7	0.20
	3.	RD_DIST COVER_NAME GRASS_EDGE IZ_DIST	4	2847.8	12.9	< 0.01
March-April	1.	GLOBAL MODEL	11	3889.9	0.0	0.95
	2.	ELEV SLOPE CURVE RD_DIST STRM_DIST IZ_DIST FRTBND_DIS GRASS_EDGE COVER_NAME	9	3895.9	58.6	0.04
	3.	SPRGBRN FALLBRN RD_DIST STRM_DIST GRASS_EDGE COVER_NAME	6	3902.5	123.9	<0.01
May-July*	1.	GLOBAL MODEL	11	10091.8	0.0	> 0.99
	2.	ELEV SLOPE CURVE RD_DIST STRM_DIST IZ_DIST FRTBND_DIS GRASS_EDGE COVER_NAME	9	10242.3	150.5	<0.01
	3.	FALLBRN RD_DIST STRM_DIST GRASS_EDGE COVER_NAME	5	10569.6	477.8	<0.01
August-September	1.	GLOBAL MODEL	11	3958.3	0.0	> 0.99
	2.	ELEV SLOPE CURVE RD_DIST STRM_DIST IZ_DIST FRTBND_DIS GRASS_EDGE COVER_NAME	9	4016.9	58.6	<0.01
	3.	SPRGBRN FALLBRN RD_DIST STRM_DIST GRASS_EDGE COVER_NAME	6	4082.2	123.9	<0.01
October-December	1.	GLOBAL MODEL	11	4002.8	0.0	>0.99
	2.	ELEV SLOPE CURVE RD_DIST STRM_DIST IZ_DIST FRTBND_DIS GRASS_EDGE COVER_NAME	9	4077.4	73.4	<0.001
	3.	RD_DIST COVER_NAME GRASS_EDGE IZ_DIST	4	4153.9	195.6	<0.001

[†] Predictor variable stream distance removed due to high correlation with other variables.

Table 4.5. Logistic regression coefficients and odds ratios for March-April 2005 landscape and home range scale top models. Parameters for milo could not be estimated at the home range scale due to complete separation resulting from small sample sizes.

	Landscape Scale				Home range Scale			
Parameter	β	SE	Odds Ratio	Odds C.I.	β	SE	Odds Ratio	Odds C.I.
Elevation	0.002	0.98	1.00	0.99 – 1.01	- 0.002	0.003	0.998	0.992 – 1.004
Slope	-0.064	0.01	0.94	0.92 – 0.96	- 0.067	0.013	0.935	0.912 – 0.959
Curvature	0.055	0.03	1.06	0.99 – 1.12	0.048	0.030	1.049	0.989 – 1.113
Road Distance	0.002	<0.01	1.00	1.00 – 1.00	0.001	< 0.001	1.001	1.001 – 1.001
Impact zone dist.	<0.001	<0.01	1.00	1.00 – 1.00	> - 0.001	< 0.001	1.000	0.999 – 1.000
Fall burn dist.	>-0.001	<0.01	1.00	1.00 – 1.00	< 0.001	< 0.001	1.000	1.000 – 1.000
Fort boundary dist.	-0.001	<0.01	0.99	0.99 – 1.00	0.001	< 0.001	1.001	1.000 – 1.002
Grassland edge	0.920	<0.01	2.51	2.09 – 3.00	0.837	0.092	2.308	1.928 – 2.764
Land cover type								
Alfalfa	0.78	0.82	2.17	0.43 10.91	- 0.447	0.672	0.640	0.171 – 2.387
Corn	1.23	1.06	3.44	0.43 27.54	1.144	1.069	3.139	0.386 – 25.505
Forage Sorghum	-0.40	0.44	0.67	0.28 1.57	- 0.414	0.519	0.661	0.239 – 1.829
Grassland	-1.64	0.11	0.19	0.16 0.24	- 1.899	0.111	0.150	0.120 – 0.186
Milo	-2.85	1.16	0.06	0.01 0.56				
Other	-2.26	0.24	0.07	0.06 0.17	- 1.375	0.292	0.253	0.143 – 0.448
Wheat	0.98	0.35	2.66	1.35 5.24	0.397	0.317	1.487	0.798 – 2.769

Table 4.6. Logistic regression coefficients and odds ratios for May-July 2005 landscape and home range scale top models. Elevation not included in home range scale model due to problems with model convergence.

	Landscape Scale				Home range Scale			
Parameter	β	SE	Odds Ratio	Odds C.I.	β	SE	Odds Ratio	Odds C.I.
Elevation	- 0.044	0.003	0.96	0.95 – 0.96				
Slope	- 0.041	0.009	0.96	0.94 – 0.98	-0.064	0.007	0.938	0.925 – 0.952
Curvature	0.036	0.022	1.04	0.99 – 1.08	-0.015	0.018	0.985	0.951 – 1.022
Road distance	0.001	0.001	1.00	1.00 – 1.00	0.001	<0.001	1.001	1.000 – 1.001
Stream distance	>- 0.001	<0.001	0.99	0.99 – 1.00	-0.002	<0.001	0.998	0.997 – 0.998
Impact zone dist.	<0.001	<0.001	1.00	1.00 – 1.00	>-0.001	<0.001	1.000	1.000 – 1.000
Spring burn dist.	>-0.001	<0.001	1.00	1.00 – 1.00	<0.001	<0.001	1.000	1.000 – 1.000
Fall burn distance	>-0.001	<0.001	1.00	1.00 – 1.00	<0.001	<0.001	1.000	1.000 – 1.000
Fort boundary dist.	-0.002	<0.01	0.99	0.99 – 1.00	0.002	0.002	1.002	0.999 – 1.006
Grassland edge	1.409	0.067	2.51	3.58 – 4.66	1.522	0.057	4.580	4.093 – 5.125
Land cover type								
Alfalfa	- 0.41	1.18	0.67	0.07 6.68				
Corn	1.75	0.30	5.76	3.19 10.39	2.929	0.459	18.725	7.607 – 46.088
Forage Sorghum	0.48	0.27	1.61	0.94 2.76	0.413	0.286	1.511	0.862 – 2.648
Grassland	- 1.53	0.08	0.22	0.19 0.25	- 1.624	0.067	0.197	0.173 – 0.225
Other	- 3.34	0.41	0.04	0.02 0.09	- 1.340	0.483	0.262	0.102 – 0.674
Soybeans	- 5.81	1.03	<0.01	<0.01 0.02	- 4.079	1.124	0.017	0.002 – 0.153
Sunflower	1.41	0.44	4.09	1.74 9.64	2.821	0.725	16.801	4.055 – 69.608
Wheat	- 1.55	0.47	0.21	0.08 0.53	- 1.309	0.551	0.270	0.092 – 0.795

Table 4.7. Logistic regression coefficients and odds ratios for August-September 2005 landscape and home range scale top models. Odds ratios for land cover types are based on comparison to woodland land cover type as a reference category.

	Landscape Scale				Home range Scale			
Parameter	β	SE	Odds Ratio	Odds C.I.	β	SE	Odds Ratio	Odds C.I.
Elevation	-0.170	0.004	0.96	0.95 – 0.96	-0.013	0.001	0.987	0.986 – 0.988
Slope	-0.106	0.015	0.96	0.94 – 0.98	-0.082	0.012	0.922	0.900 – 0.944
Curvature	-0.014	0.035	1.04	0.99 – 1.08	-0.024	0.029	0.977	0.922 – 1.035
Road distance	<0.001	<0.001	1.00	1.00 – 1.00	< 0.001	< 0.001	1.000	1.000 – 1.000
Stream distance	-0.002	<0.001			-0.001	< 0.001	0.999	0.998 – 0.999
Impact zone dist.	>-0.001	<0.001	1.00	1.00 – 1.00	> -0.001	< 0.001	1.000	1.000 – 1.000
Spring burn dist.	>-0.001	<0.001	1.00	1.00 – 1.00	< 0.001	< 0.001	1.000	1.000 – 1.000
Fall burn distance	< 0.001	<0.001	1.00	1.00 – 1.00	< 0.001	< 0.001	1.000	1.000 – 1.000
Fort boundary dist.	-0.015	0.006	0.99	0.99 – 1.00	0.462	0.398	1.587	0.728 – 3.464
Grassland edge	0.647	0.103	2.51	2.09 – 3.00	0.425	0.087	1.530	1.289 – 1.816
Land cover type								
Corn	1.889	0.333	6.62	3.45 – 12.71	2.754	0.371	15.700	7.593 – 32.462
Forage Sorghum	2.668	0.484	14.42	5.58 – 37.26	1.986	0.395	7.284	3.361 – 15.786
Grassland	- 0.992	0.134	0.37	0.28 – 0.48	-0.624	0.109	0.536	0.433 – 0.664
Other	- 1.107	0.629	0.33	0.09 – 1.13	-1.378	1.067	0.252	0.031 – 2.044
Soybeans	0.038	0.513	1.04	0.38 – 2.84	1.308	0.634	3.699	1.068 – 12.814
Sunflower	2.417	1.034	11.21	1.47 – 85.17	3.260	1.041	26.049	3.387-200.370
Wheat	0.589	0.804	1.80	0.37 – 8.71	1.379	1.087	3.972	0.472 – 33.450

Table 4.8. Logistic regression coefficients and odds ratios for October-December 2005 landscape and home range scale top models. Odds ratios for land cover types are based on comparison to woodland land cover type as a reference category.

		Landscape Scale				Home range Scale		
Parameter	β	SE	Odds Ratio	Odds C.I.	β	SE	Odds Ratio	Odds C.I.
Elevation	- 0.002	0.005	0.989	0.989 – 1.008	0.014	0.006	1.014	1.003 – 1.025
Slope	- 0.104	0.019	0.901	0.868 – 0.935	-0.078	0.021	0.925	0.888 – 0.964
Curvature	0.063	0.054	1.065	0.959 – 1.183	0.073	0.056	1.076	0.965 – 1.200
Road distance	> - 0.001	<0.001	1.000	0.999 - 1.000	- 0.001	<0.001	0.999	0.999 – 0.999
Stream distance	- 0.001	<0.001	0.999	0.998 – 0.999	- 0.001	<0.001	0.999	0.998 – 1.000
Impact zone dist.	>- 0.001	<0.001	1.000	0.999 – 1.000	>-0.001	<0.001	1.000	1.000 – 1.000
Spring burn dist.	0.003	<0.001	1.003	1.002 – 1.003	0.003	<0.001	1.003	1.003 – 1.003
Fall burn distance	> -0.001	<0.001	1.000	1.000 - 1.000	<0.001	<0.001	1.000	1.000 – 1.000
Fort boundary dist.	- 0.003	0.002	0.997	0.994 – 1.000	-0.001	0.002	0.999	0.994 – 1.003
Grassland edge	0.319	0.135	1.377	1.055 – 1.797	0.636	0.149	1.889	1.410 – 2.531
Land cover type								
Alfalfa	2.12	1.097	8.29	0.970 – 71.300	- 0.232	1.619	0.793	0.033 – 18.964
Corn	-2.77	1.310	0.06	0.005 – 0.818	- 3.756	1.178	0.023	0.002 – 0.235
Forage Sorghum	3.09	0.737	21.94	5.180 – 92.900	1.501	0.443	4.486	1.883 – 10.685
Grassland	- 1.26	0.168	0.28	0.201 – 0.388	- 1.799	0.187	0.165	0.115 – 0.239
Other	-1.92	0.474	0.15	0.058 – 0.372	- 2.871	0.517	0.057	0.021 – 0.156
Wheat	-0.12	0.853	0.88	0.166 – 4.701	- 0.168	1.501	0.845	0.045 – 16.028

Table 4.9. Logistic regression coefficients and odds ratios for January - February 2006 landscape and home range scale top models. Odds ratios for land cover types are based on comparison to woodland land cover type as a reference category.

	Landscape Scale				Home range Scale			
Parameter	β	SE	Odds Ratio	Odds C.I.	β	SE	Odds Ratio	Odds C.I.
Elevation	<0.001	0.003	1.000	0.995 – 1.006	-0.002	0.002	0.998	0.994 – 1.003
Slope	-0.058	0.015	0.943	0.917 – 0.971	-0.035	0.013	0.966	0.942 – 0.991
Curvature	0.048	0.038	1.049	0.974 – 1.130	0.069	0.033	1.071	1.003 – 1.145
Road distance	<0.001	< 0.001	1.001	1.001 – 1.001	<0.001	< 0.001	1.000	1.000 – 1.001
Impact zone dist.	<0.001	< 0.001	1.000	1.000 – 1.000	<0.001	< 0.001	1.000	1.000 – 1.000
Fort boundary dist.	>0.001	< 0.001	0.999	0.998 – 1.000	0.005	0.001	1.005	1.004 – 1.006
Grassland edge	1.047	0.123	2.848	2.244 – 3.616	0.364	0.112	1.440	1.155 – 1.794
Land cover type								
Alfalfa	0.347	1.136	1.415	0.153 – 13.125	-0.657	0.776	0.518	0.113 – 2.372
Corn	-2.456	1.211	0.086	0.008 – 0.920	-0.429	0.933	0.651	0.104 – 4.058
Forage Sorghum	-0.516	0.456	0.597	0.244 – 1.457	-1.131	0.392	0.323	0.149 – 0.697
Grassland	-2.483	0.135	0.084	0.064 – 0.109	-0.781	0.109	0.458	0.370 – 0.568
Other	-2.145	0.309	0.117	0.064 – 0.215	-1.029	0.299	0.357	0.199 – 0.643
Wheat	1.367	0.424	3.922	1.709 – 9.002	0.169	0.209	1.185	0.786 – 1.788
Soybeans	-0.855	0.547	0.425	0.146 – 1.243	-0.755	0.586	0.470	0.149 – 1.482

Table 4.10. Logistic regression coefficients and odds ratios for March - April 2006 landscape and home range scale top models. Odds ratios for land cover types are based on comparison to woodland land cover type as a reference category.

	Landscape Scale				Home range Scale			
Parameter	β	SE	Odds Ratio	Odds C.I.	β	SE	Odds Ratio	Odds C.I.
Elevation	0.002	0.003	1.002	0.996 – 1.007	-0.010	0.003	0.990	0.984 – 0.995
Slope	- 0.021	0.013	0.979	0.956 – 1.004	-0.033	0.011	0.968	0.947 – 0.989
Curvature	- 0.020	0.037	0.981	0.913 – 1.053	-0.012	0.031	0.988	0.931 – 1.049
Road distance	0.001	<0.001	1.001	1.001 – 1.001	0.001	< 0.001	1.001	1.001 – 1.001
Stream distance	>- 0.001	<0.001	0.999	0.999 – 1.000	> -0.001	< 0.001	1.000	0.999 – 1.000
Impact zone dist.	> -0.001	<0.001	1.000	1.000 – 1.000	> -0.001	< 0.001	1.000	1.000 – 1.000
Fall burn dist.	> -0.001	<0.001	1.000	1.000 – 1.000	> -0.001	< 0.001	1.000	1.000 – 1.000
Fort boundary dist.	-0.001	<0.001	0.999	0.998 – 1.000	< 0.001	< 0.001	1.000	0.999 – 1.002
Spring burn dist.	> -0.001	<0.001	1.000	1.000 – 1.000	> -0.001	< 0.001	1.000	1.000 - 1.000
Grassland edge	0.808	0.107	2.244	1.817 – 2.771	0.653	0.103	1.921	1.569 – 2.352
Land cover type								
Corn	- 0.049	1.211	0.609	0.057 – 6.537	- 2.378	1.214	0.093	0.009 - 1.002
Forage Sorghum	0.572	0.401	1.771	0.807 – 3.888	1.322	0.544	3.749	1.291 – 10.890
Grassland	- 2.011	0.123	0.134	0.105 – 0.170	-1.545	0.117	0.213	0.169 – 0.268
Other	- 1.940	0.277	0.144	0.084 – 0.248	- 1.047	0.315	0.351	0.189 – 0.651
Wheat	2.252	0.513	9.509	3.477 – 26.005	1.724	0.441	5.609	2.366 – 13.301
Soybeans	- 1.580	0.694	0.206	0.053 – 0.803	- 1.072	0.817	0.342	0.069 – 1.700

Table 4.11. Logistic regression coefficients and odds ratios for May - July 2006 landscape and home range scale top models. Odds ratios for land cover types are based on comparison to woodland land cover type as a reference category. Elevation not included in home range scale analysis due to problems with convergence. Corn, sunflower, and forage sorghum parameters could not be estimated at the home range scale due to complete separation resulting from small sample sizes.

	Landscape Scale				Home range Scale			
Parameter	β	SE	Odds Ratio	Odds C.I.	β	SE	Odds Ratio	Odds C.I.
Elevation	- 0.044	0.003	0.957	0.952 – 0.962				
Slope	-0.041	0.009	0.959	0.943 – 0.976	- 0.059	0.006	0.943	0.932 – 0.954
Curvature	0.036	0.022	1.037	0.993 – 1.083	0.026	0.016	1.027	0.994 – 1.060
Road distance	<0.001	<0.001	1.001	1.001 – 1.001	< 0.001	< 0.001	1.000	1.000 – 1.000
Impact zone dist.	<0.001	<0.001	1.000	1.000 – 1.000	> -0.001	< 0.001	1.000	1.000 – 1.000
Fort boundary dist.	>-0.001	0.001	1.000	0.998 – 1.002	> -0.001	< 0.001	0.999	0.997 – 1.001
Grassland edge	1.409	0.067	4.090	3.589 – 4.662	1.521	0.056	4.578	4.100 – 5.109
Fall burn dist.	<0.001	< 0.001	1.000	1.000 – 1.000	< 0.001	< 0.001	1.000	1.000 – 1.000
Land cover type								
Alfalfa	-0.405	1.176	0.667	0.067 – 6.684	2.119	1.021	8.319	1.124 – 61.53
Corn	1.750	0.302	5.756	3.188- 10.394				
Forage Sorghum	0.476	0.275	1.610	0.939 – 2.759				
Grassland	-1.533	0.080	0.216	0.185 – 0.253	- 1.897	0.064	0.150	0.132 – 0.170
Other	-3.139	0.409	0.043	0.019 – 0.097	- 0.437	0.208	0.646	0.429 – 0.972
Wheat	-1.555	0.469	0.211	0.084 – 0.529	- 0.081	0.397	0.922	0.423 – 2.008
Soybeans	-5.812	1.027	0.003	< 0.001 – 0.022	0.519	0.325	1.680	0.889 – 3.174
Sunflower	1.409	0.437	4.092	1.737 - 9.643				

Table 4.12. Logistic regression coefficients and odds ratios for August - September 2006 landscape and home range scale top models. Odds ratios for land cover types are based on comparison to woodland land cover type as a reference category. Spring burn distance not included in home range scale model due to correlation with other variables. Milo and forage sorghum parameters could not be estimated at the home range scale due to complete separation resulting from small sample sizes.

	Landscape Scale				Home range Scale			
Parameter	β	SE	Odds Ratio	Odds C.I.	β	SE	Odds Ratio	Odds C.I.
Elevation	- 0.024	0.003	0.977	0.971 – 0.982	- 0.014	< 0.001	0.987	0.986 – 0.988
Slope	- 0.075	0.014	0.928	0.902 – 0.954	- 0.086	0.011	0.918	0.899 – 0.937
Curvature	0.081	0.034	1.084	1.014 – 1.160	0.009	0.029	1.009	0.954 – 1.067
Spring burn dist.	< 0.001	<0.001	1.000	1.000 – 1.000				
Road distance	0.001	<0.001	1.001	1.001 – 1.001	< 0.001	< 0.001	1.000	1.000 – 1.000
Stream dist.	-0.001	<0.001	0.999	0.998 – 0.999	- 0.001	< 0.001	0.999	0.999 – 1.000
Fall burn dist.	< 0.001	<0.001	1.000	1.000 – 1.000	< 0.001	< 0.001	1.000	1.000 – 1.000
Impact zone dist.	< 0.001	<0.001	1.000	1.000 – 1.000	< 0.001	< 0.001	1.000	1.000 – 1.000
Fort boundary dist.	-0.007	0.002	0.994	0.989 – 0.998	- 0.001	0.004	0.999	0.991 – 1.007
Grassland edge	0.827	0.106	2.287	1.858 – 2.815	1.019	0.094	2.771	2.303 – 3.334
Land cover type								
Alfalfa	2.423	1.035	11.278	1.485 – 85.659	2.203	1.029	7.592	1.009 – 57.103
Forage Sorghum	- 0.753	1.426	0.471	0.029 – 7.702				
Grassland	- 1.163	0.131	0.313	0.242 – 0.404	- 1.246	0.109	0.288	0.232 – 0.356
Milo	- 3.012	1.219	0.049	0.005 – 0.537				
Other	- 2.029	0.436	0.313	0.056 – 0.309	- 0.752	0.602	0.472	0.145 – 1.535
Wheat	- 2.210	0.737	0.110	0.026 – 0.465	- 1.426	0.846	0.240	0.046 – 1.261
Soybeans	0.736	0.259	2.088	1.256 – 3.471	2.342	0.522	10.406	3.744 – 28.923

Table 4.13. Logistic regression coefficients and odds ratios for October - December 2006 landscape and home range scale top models. Odds ratios for land cover types are based on comparison to woodland land cover type as a reference category. Elevation not included due to convergence problems and spring burn distance not included in home range scale models due to correlation with other variables. Forage sorghum parameters could not be estimated at the home range scale due to complete separation resulting from small sample size.

		Landscape Scale				Home range Scale		
Parameter	β	SE	Odds Ratio	Odds C.I.	β	SE	Odds Ratio	Odds C.I.
Elevation	-0.012	0.003	0.988	0.983 – 0.993				
Slope	-0.060	0.013	0.942	0.918 – 0.966	-0.082	0.009	0.921	0.904 – 0.940
Curvature	0.050	0.034	1.051	0.984 – 1.124	0.029	0.026	1.030	0.978 – 1.084
Spring burn	>-0.001	<0.001	1.000	0.999 – 1.000				
Road distance	0.002	<0.001	1.002	1.002 – 1.002	0.001	< 0.001	1.001	1.001 – 1.001
Stream distance	-0.001	<0.001	0.999	0.998 – 0.999	> -0.001	< 0.001	0.999	0.999 – 1.000
Impact zone dist.	>-0.001	<0.001	1.000	1.000 – 1.000	> -0.001	< 0.001	1.000	1.000 – 1.000
Fall burn distance	>-0.001	<0.001	1.000	1.000 – 1.000	> -0.001	< 0.001	1.000	1.000 – 1.000
Fort boundary dist.	<0.001	0.001	1.001	1.000 – 1.002	0.002	0.001	1.002	1.001 – 1.004
Grassland edge	0.443	0.110	1.560	1.258 – 1.934	0.884	0.093	2.420	2.018 – 2.902
Land cover type								
Alfalfa	1.914	0.792	6.779	1.436 – 31.997	0.668	0.671	1.951	0.523 – 7.269
Corn	0.044	0.801	1.045	0.218 – 5.016	- 0.946	0.671	0.388	0.104 – 1.447
Forage Sorghum	0.997	1.496	2.709	0.144 – 50.821				
Grassland	-1.331	0.136	0.264	0.202 – 0.345	- 1.356	0.101	0.258	0.211 – 0.314
Other	-1.287	0.334	0.276	0.143 – 0.531	- 1.564	0.307	0.209	0.115 – 0.382
Wheat	0.011	0.423	1.011	0.441 – 2.317	- 1.195	0.445	0.303	0.127 – 0.724
Soybeans	0.518	0.314	1.680	0.909 – 3.105	0.513	0.256	1.671	1.101 – 2.760

Figure 4.1. Boundary map of Fort Riley Military Installation, Kansas.

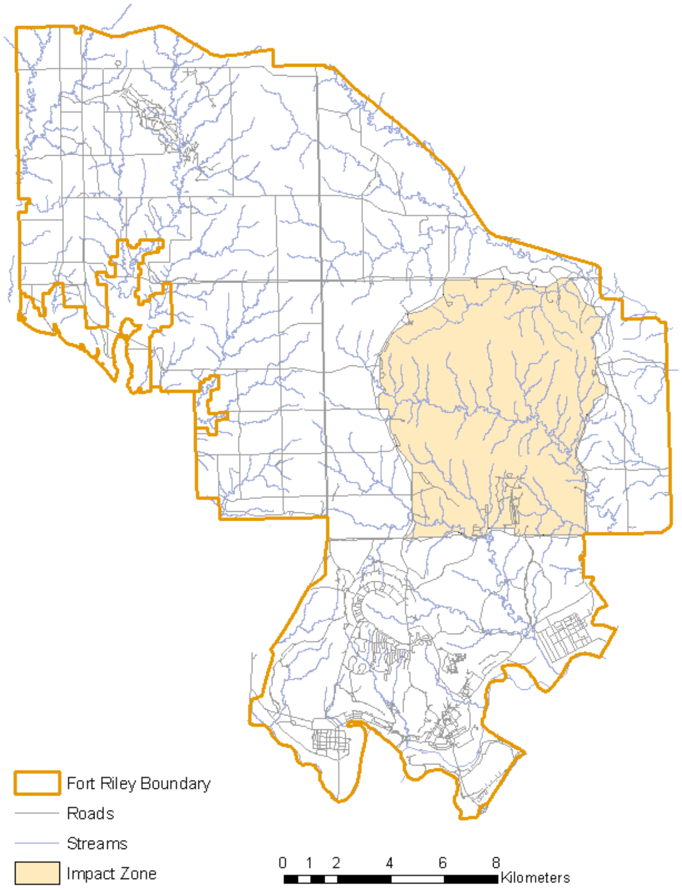

Figure 4.2. 100% minimum convex polygon home ranges for individual female elk on Fort Riley, Kansas during 2005. Home ranges estimated for seasons including (a) March-April, (b) May-July, (c) August-September, and (d) October-December.

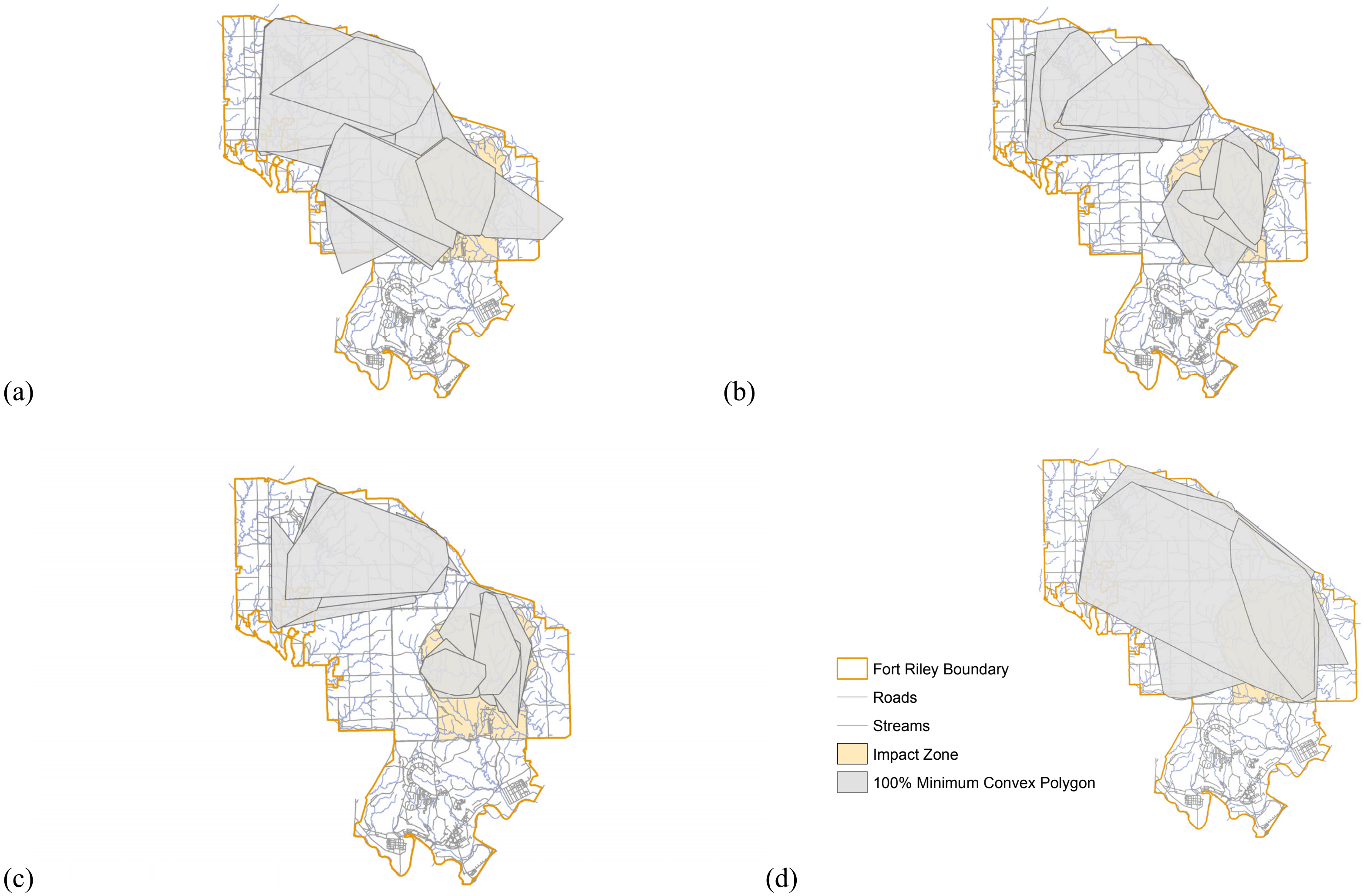

Figure 4.3. 100% minimum convex polygon home ranges for individual female elk on Fort Riley, Kansas during 2006. Home ranges estimated for seasons including (a) January-February, (b) March-April, (c) May-July, (d) August-September, and (e) October-December.

CHAPTER 5 - CONCLUSIONS

The translocation of elk (*Cervus elaphus*) to Fort Riley Military Installation restored a component of the tallgrass prairie fauna that had been absent for over a century. Restoration of a free-ranging elk population to the Flint Hills region provided the unique opportunity to study the ecology of elk in a tallgrass prairie system. Current knowledge of elk resource selection and demography is important for assessing the ecological role of elk in modified prairie landscapes. Knowledge gained from the study of the Fort Riley elk population may also be applicable to the management and conservation of other small and / or reintroduced populations, or for identifying potential sites for future reintroductions of elk in prairie areas. My primary research objectives were to: 1) compare the level of genetic variability in the Fort Riley population to other source and reintroduced elk populations, 2) characterize relationships between demographic vital rates and variation in the rate of population change (λ), and 3) examine patterns of resource selection by elk at the landscape and home-range scales.

My findings suggest that at the current population size, levels of genetic variability in the Fort Riley population are likely to decline as alleles are lost through genetic drift over time. Continued loss of genetic variability in the Fort Riley population has the potential to reduce calf survival and reproductive success (Slate et al. 2000). In species with harem-mating systems, population sizes of greater than 300 appear to be necessary to retain genetic variability over a 100-year time period. These findings suggest that elk restoration programs are most likely to be successful for the long-term (greater than 100 years) on sites where biological and human / social carrying capacity will allow for a minimum sustained population size of over 300 individuals. Post-restoration management should attempt to maintain positive rates of population growth and minimize annual fluctuations in population size. Translocations of additional elk into small (< 300) and isolated populations is a management option for restoring genetic variability lost due to drift.

Demographic vital rates ultimately determine the size and viability of a population. In the Fort Riley elk population, changes in adult and yearling survival rates are expected to result in the greatest proportional change in population growth rate (λ). Survival of adult elk was less variable than calf survival based on demographic vital rates observed for the Fort Riley population. This is consistent with predictions from life-history theory suggesting that vital rates with the greatest influence on λ should exhibit low levels of variability (Pfister 1998). Survival of yearling, prime-age, and old-age elk in the Fort Riley population is directly influenced by harvest, and harvest levels could be used to influence vital rates with high elasticity values (prime-age adult and yearling survival). Calf survival on Fort Riley was highly variable, and the observed variation was strongly correlated with variation in λ. The underlying mechanisms responsible for the variability of this vital rate were not assessed as part of this study, and further work is needed to understand factors that are related to variation in calf survival. My findings are consistent with previous work suggesting that calf survival is the vital rate with the highest correlation to variation in λ for ungulate populations (Raithel et al. 2007). However, variation in prime-age adult survival for the Fort Riley population was more correlated with variation in λ than has been reported for other elk populations (Raithel et al. 2007). It is possible that adult survival is generally more variable in small and harvested populations than in large populations that are not harvested. Further study is needed to determine how population size, harvest, and natural predation influence the relationship between demographic vital rates and variation in λ for ungulate populations.

Patterns of resource selection by elk are expected to influence vital rates, and individuals are likely to select habitats that maximize fitness. Actual patterns of resource use that maximize fitness may depend on population density, interspecific competition, and predation pressure. Historically, resource selection by elk in tallgrass prairie may have been driven by predation pressure from wolves (*Canis lupus*) and competition with bison (*Bos bison*) for forage. Hunting of elk by humans in prairie systems occurred in historical time periods (Molloy 1993) and may also influence the distribution of elk in the modern landscape. It is important to note that current patterns of habitat use by elk are influenced by different competitive and predatory interactions than elk historically encountered in prairie systems. The availability of resources on the landscape also differs from historical time periods, with agricultural crops providing an additional forage resource for the current elk population on Fort Riley.

This study is one of the first to document patterns of resource selection by elk in a predominantly tallgrass prairie landscape, and is one of the few studies to examine resource selection by elk in the Great Plains (Wydeven and Dahlgren 1985, Robinson 1993, Bian and West 1997, Walter 2006). My findings suggest that elk on Fort Riley preferred land-cover types including woodlands, grassland edge, and agricultural crops. Elk also used areas close to streams while avoiding areas of steep slope or high elevation. Patterns of resource-selection by elk were consistent across spatial scales with both risk-related and resource-related predictor variables influencing resource selection at the landscape scale and within the home range.

The topography and vegetation of Fort Riley are similar to other prairie regions of the Flint Hills. However, military training on Fort Riley is a unique type of disturbance that may impact the landscape in different ways than natural disturbance events (Quist et al. 2003). Although it was not possible to quantitatively assess the relationship between military training patterns and elk distribution on Fort Riley, it is likely that military training had some influence on elk locations and distribution patterns. Elk on Fort Riley did not avoid using artillery and small-arms target areas (Impact Zone), and appear to have habituated to noise from artillery and small-arms firing. Elk use of target areas is similar to that observed for the Sonoran pronghorn (*Antilocapra americana sonoriensis*) on military areas in Arizona, where military activities may enhance forage (Krausman et al. 2005). The potential for direct disturbance of elk by military vehicles is reduced by frequent elk use of woodland habitats (Chapter 4) that are not extensively used by military vehicles (Haugen et al. 2003). Elk may avoid main roads on Fort Riley to reduce hunting pressure or to avoid military vehicle traffic, especially since the majority of military vehicle training activities occur along existing roads (Haugen et al. 2003).

Military training lands on Fort Riley appear to provide important areas of habitat for elk, with limited observation of conflict between elk and military training activities. Elk also exhibited a strong fidelity for the installation, with home ranges of female elk centered on Fort Riley during all seasons of the study (Chapter 4; Fig. 4.2, Fig. 4.3). Although troop training loads were relatively light during the study period, changes in training loads and vehicle-use patterns that alter vegetation structure or composition could certainly influence patterns of elk distribution and resource selection in the future. Further monitoring of elk population numbers and elk responses to military vehicle training may provide important indicators of training impacts on the installation, and further investigation into the utility of elk as an indicator species may be warranted (Rowland et al. 2004).

The long-term success of a reintroduced population ultimately depends on maintaining survival and reproductive rates at levels that maintain a viable population size. The primary research topics of this study (genetics, demography, and resource selection) are expected to have interacting effects on elk vital rates. Managing for increased levels of genetic variability may prevent reductions in reproductive output that may otherwise occur as a result of inbreeding depression, while knowledge of preferred habitat characteristics may be useful for managing elk habitat in ways that increase survival and reproductive success. By examining factors that influence genetic variability, demography, and resource selection this research integrates findings from these areas in ways that can be used for the management and conservation of small and reintroduced populations of elk and other species.

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