Survival, movement, and resource selection of male mule deer and white-tailed deer in western Kansas

by

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Abstract

Abundance and occupied range of mule deer (*Odocoileus hemionus*) in Kansas have been declining for 20 years. The two predominant hypotheses for the reduction of mule deer and concurrent expansion of white-tailed deer (*O. virginianus*) are changes in land use and competitive dominance of white-tailed deer over mule deer. Despite the popularity and income that stem from hunting revenue, there have been no recent studies that provide critical insight on how to improve management and conservation of sympatric populations of either deer species in Kansas. My objectives were to (1) test for differences in annual and weekly survival rates between species, identify temporal mortality patterns, and assess influences of hunting and rut on survival; and (2) examine movement patterns, space use, and population-level resource selection by adult male mule deer and white-tailed deer in western Kansas during three time periods (annually, rut, and 12-day firearm season). I deployed GPS-collared 60 (30 mule; 30 white-tailed deer), 25 (12 mule; 13 white-tailed deer), and 26 (13 mule; 13 white-tailed deer) male mule deer and white-tailed deer at two different study sites (north and south) located in western Kansas in 2018, 2019, and 2020, respectively, maintaining a sample size of 60 at the start of each study year. Each deer was fitted with a high resolution GPS/VHF collar that recorded bi-hourly locations and used an activity sensor to identify mortality events. I assigned each deer to an age class (<3 or ≥3 years old). I analyzed the influence of single variable models (age class, species, study site, year, site and year interaction, and morphological measurements [total body length, chest girth, hind foot, and neck girth]) to identify variables that influenced survival. I calculated average daily and average bi-hourly movement rate for all groups (north mule deer, south mule deer, north white-tailed deer and south white-tailed deer) and analyzed peak movement trends to define the rut periods for each species. I used Biased Random Bridge Movement Models to estimate period home ranges and core use areas by species and sites and tested for species*site interactions. I identified temporal space use of different land cover categories during the annual, rut, and 12-day firearm season periods. I compared used and available proportions of categorical land cover and continuous macro habitat features at second-order resource selection. Annual survival did not differ between species during 2018-2020 (mule deer 0.54 ± 0.05, white-tailed deer 0.58 ± 0.05); pooled survival for combined species was 0.56 ± 0.04. December was the most hazardous time of year for both species. Harvest was the predominant cause of mortality (50% of mortalities [firearm = 42%, archery = 8%]. Other sources of mortality stemmed from natural causes (21%), unknown (25%), and deer-vehicle collisions (4%). Kaplan-Meier cumulative survival results showed that survival of both mule deer and white-tailed deer was affected by harvest season and rut; the two weeks of firearm season heavily reduced survival by 19.6%, and 12.4% for mule deer and white-tailed deer, respectively. Survival was reduced by 10.6% and 9.8% during rut for mule deer and white-tailed deer, respectively. Additionally, site and year interaction ($\omega = 0.38$) was the most parsimonious model for predicting adult male survival, the model site, was also competitive. Localized periods of high mortality occurred; compared to 2018 and 2019, deer survival in the north site during 2020 was drastically lower (0.26 ± 0.09) than other annual species-site combinations. Space use at the landscape scale varied temporally by site and species. Population-level selection of macro habitat differed between species Males reduced both bi-hourly movement rate and daily distance during the 12-day firearm period compared to their rut movements; north mule deer reduced their total daily movement by 35%, south mule deer by 33%, north white-tailed deer by 5% and south white-tailed deer by 32%. Rut (~Nov 5-25 for both species of north deer; ~Oct 29-Nov 18 for south mule deer; ~Oct 29-Nov 25 for south white-tailed deer) begins for both species approximately 3-

4 weeks prior to the 12-day firearm period. Peak movement periods occurred during rut simultaneously for both species, with all deer moving at least twice as fast (bi-hourly) and twice as much (in 24 hr. intervals) during their rut seasons compared to their annual movements. Males reduced movement during the 12-day firearm season compared to their rut movements because of the proximity of the successive 12-day firearm season to the post-rut period; a time in which males may move less in an attempt to recover from the physiological demands of rut. Speculatively, hunters on the landscape may have been a contributing factor to the decrease in movement. To combat the current population trajectory of mule deer abundance and augment the management and conservation of mule deer, I suggest decreasing the harvest limit of male mule deer to directly increase annual survival of adult male mule deer.

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Dedication

I would like to dedicate my thesis to my parents; Roxanna and Gary Kinlan. Thank you for instilling the love of the outdoors and wildlife in me at an early age. Thank you mom for encouraging me and supporting me in all of my wildlife technician pursuits and for teaching me to work hard and always have faith in myself. I would like to thank my sister, my uncle Clay, and my aunt Kimmie for all of your love and support, especially throughout the last year. Lastly, I would like to thank my dogs, Liam and Apache, for always boosting morale, travelling with me across the country and being the best friends anyone could ask for.

Chapter 1 - Introduction

Mule deer (Odocoileus hemionus) abundance has fluctuated in Kansas, USA, over the past century. In 1804, the famed explorer Meriwether Lewis, of Lewis and Clark Expedition, wrote this passage in his journal about Kansas; “immense herds of deer which we saw in every direction feeding on the hills and plains” Clark, further described seeing an unknown deer species as “a curious kind of deer, the ears large and long, a small receptacle under the eyes, the species of deer jumps like a goat or sheep” (Moulton 2003). Approximately one hundred years later, as the settlement of Kansas had diffused east to west, D.E. Lantz of the United States Department of Agriculture wrote mule deer were “still found in western Kansas in 1884, but has now (1903) probably entirely disappeared”; he also wrote white-tailed deer (Odocoileus virginianus) were “probably extinct” in Kansas in 1903 (Lantz 1903). Overharvest stemming from market hunting, a series of harsh winters, human settlement, overgrazing, and drought transformed the once immense deer herds to dwindling remnants (Madson 1953, Severson 1981). By 1947, the conservationist considered to be the father of wildlife ecology, and renowned environmentalist, Aldo Leopold, postulated “There is only one deer-less state: Kansas” (Leopold et al. 1947). Over time populations of mule deer and white-tailed deer rebounded in Kansas in part by effects from implementation of the 1900 Lacey Act (McCabe and McCabe 1984) and 1937 Pittman-Robertson Act (Kauffman et al. 2018); Kansas held its first season of regulated deer harvest in 1965 (Jaster et al. 2019).

Since the resurgence of both white-tailed deer and mule deer populations in the 1960s, abundance ratios between species have fluctuated within the state. Anecdotal observations from Kansas bowhunters of mule deer sightings since 1998, and spotlight surveys performed by the state management agency, Kansas Department of Wildlife, and Parks (KDWP), suggest that mule deer population abundance and harvest has diminished, while the occupied range of white-tailed deer has continuously expanded westward (Jaster 2019; Fig. 1.1). Although some populations of mule deer are stable, most are below management objectives throughout the Great Plains (Mule Deer Working Group 2020).

There are several factors for why mule deer populations are disappearing from areas in Kansas and other Great Plains states. Declines in contemporary mule deer population abundance and occupied range relative to their historic North American range is suspected to be related to habitat loss, altered environmental conditions (frequent intensive drought), intensive grazing, landscape fragmentation, and vegetation succession of invasive plant species (Fig. 1.2; Mule Deer Working Group 2019). In addition, occupancy of the historical eastern distribution of mule deer in the Great Plains is thought to be potentially limited by some combination of temperature, disease, humidity, physical features, predation, and parasites (Fox et al. 2009). Physical features or perhaps the lack of them may be increasing competition between mule deer and white-tailed deer. For example, in most areas of sympatry, mule deer and white-tailed deer segregate based on differential use across an elevation gradient (Martinka 1968, Krausman 1978, Brunjes et al. 2006). However, in western Kansas, there is less opportunity for deer to segregate along an elevation gradient. This lack of topographical segregation could be increasing the geographical overlap of mule deer and white-tailed deer populations, which may increase the likelihood of interspecific competition and be contributing to the contraction of mule deer populations in the western portion of the Great Plains (Hygnstrom et al. 2008, VerCauteren and Hygnstrom 2011; Fig. 1.3).

Changes in land cover and use may also be a driving force behind mule deer decline. Because both deer species share the same resources in western Kansas, there is speculation that white-tailed deer would have the competitive advantage in acquiring resources because of alterations in land cover (i.e., increased woody areas compared to historical grassland), which drives the hypothesis that white-tailed deer are competitively dominant over mule deer, because white-tailed deer are commonly associated with areas of woody cover (Mackie 1981, Mackie et al. 1998). Mule deer may not be as adaptable to changing land use practices as their competitor, the habitat generalist white-tailed deer (Grovenburg et al. 2009). Increasing woody encroachment resulting from long-term fire suppression and other large landscape-scale changes has led to shifts in available habitat in favor of edge species, such as white-tailed deer rather than mule deer (Williamson and Hirth 1985). White-tailed deer have adapted to fragmented landscapes throughout the Great Plains, finding food resources almost everywhere (Sparrowe and Springer 1970) - including areas of woody cover, agricultural areas, suburban/urban development, and river bottoms (Mackie 1981). In turn, white-tailed deer have expanded their range westward in the Great Plains invading spaces never before occupied by the species (VerCauteren and Hygnstrom 2011).

The decline in abundance and occupied range of mule deer has been recognized as a priority conservation need by the Kansas Department of Wildlife and Parks (KDWP). The state management goal of Kansas is to maintain herd size at socially acceptable levels to provide ample hunting opportunities in terms of hunter viewing and harvest opportunities, while also minimizing deer vehicle strikes and property damage. Because mule deer abundance is currently below social carrying capacity, the management goal of KDWP is to increase mule deer numbers in response to landowner and hunter concerns in the eastern portion of their range in Kansas, while also augmenting mule deer numbers in the western portion of their range without increasing crop depredation, which has been a landowner concern in some areas (Jaster et al. 2019).

Reduction in the abundance of mule deer is occurring throughout their occupied range in Kansas. However, rate of decline is most apparent along the eastern portion of occupied range in Kansas (Fig. 1.4). Annually, KDWP implements a fall spotlight survey to estimate density and population size of mule deer in Kansas. The 2020 population density of mule deer in Kansas was estimated to be 5.2 mule deer/km2 (95% CI: 3.36-7.77) and 0.28/km2 (95% CI: 0.02-1.19) in the western and eastern zones, respectively. In total, the pre-harvest population estimate prior to firearm season was 53,400 mule deer (Jaster 2021). The western zone had a buck: doe ratio of 33.7:100. The ratio for the eastern zone had an insufficient sample size (only 8 mule deer over 1346.53 km2 of private land spotlight transects) and KDWP was not able to estimate the buck: doe ratio (Jaster 2021). In response to the declining mule deer numbers, KDWP allowed mule deer to be harvested on 16% of either sex deer permits in 2020 (Jaster 2021). However, in an attempt to limit mule deer harvest, for the fifth successive year, KDWP did not issue antlerless tags that permitted the harvest of female mule deer (Jaster 2021). In 2019, Kansas had the lowest estimated mule deer harvest of 1,732, of which 1,620 were males, since 1983 when 1,412 total mule deer were harvested (Fig. 1.1; Jaster 2020). Male mule deer made up 2.07% of the total male deer harvest in 2019-2020 (Jaster et al. 2020). This is a sharp decline from the 12.3% of total harvest for mule deer during 1978-1987 (L. Fox, Kansas Department of Wildlife Parks and Tourism, unpublished data). Despite recent significant reductions in antlerless mule deer permits, the declining trend in mule deer continues. Additional information is essential to develop management strategies in a way that positively alters the trajectory of mule deer abundance.

Reductions in mule deer population abundance can have significant effects on the Kansas economy. In 2018-2019, hunters in Kansas spent >1.1 million days hunting with 179,247 total deer permits sold, including 106,896 total male permits. (Jaster et al. 2019). During 2018, KDWP Fisheries and Wildlife program expenditures totaled US$27,541,397 with revenue for all deer permits (resident, nonresident, and other) totaling US$12,854,025; 47% of agency budget (2018 Kansas Department of Wildlife Parks and Tourism Annual Report, https://ksoutdoors.com/KDWPT-Info/Annual-Quarter-Reports, accessed 1 Apr 2021). The state agency is dependent on annual fees paid by resident and nonresident deer hunters who come to Kansas to have the opportunity to observe, and potentially harvest, a trophy buck. Without the deer permit revenue, wildlife management and the overall health of the economy within the state may depreciate.

Knowledge of survival rates, timing of mortality, and source of mortality is important to surveil overall health of deer herds. The ability to balance age classes and sex ratios in alignment with Kansas management goals is only achievable with this information. Currently, no literature exists on estimated survival rates, sources of mortality, and timing of mortality of male mule or white-tailed deer in Kansas. Without this information, state management is limited in developing strategies to accurately maintain socially acceptable herd sizes and sex ratios and unable to effectively model future population trajectories of male mule deer.

Hand-in-hand with survival is understanding associated movement patterns, space use, and resource selection by male deer. Male movement is affected by temporal periods such as season of the year and daily periods (Sparrowe and Springer 1970, Walter et al. 2011, Simoneaux et al. 2016), perceived threats on the landscape (hunters or natural predators [Marantz et al. 2016]), and, most importantly, by the onset of rut (Ozoga and Verme 1985, Foley et al. 2015, Simoneaux et al. 2016). To comprehend complexities of adult male population movement dynamics, it is important to understand that the effects of rut are greater than only the summation of successful or unsuccessful breeding attempts.

Rut encompasses the physiological and behavioral changes that occur leading up to and during breeding and differs from the temporal estimate of doe estrus. In temperate climates, rutting activities are facilitated by seasonal fluctuations in photoperiod (Goss 1983). Both intrinsic and environmental factors manipulate the physiological processes that institute rut and lead to successful mating (Wallmo 1981). These physiological changes are evident in adult males through the growth of antlers, neck girth expansion, increased activity, aggressive behavior, and a marked drop in food intake (Wallmo 1981). It is inaccurate and misleading to assign only the act of breeding with rut because males are physically able to breed long before females enter estrus (Tomberlin 2007). Females are only receptive to breeding during estrus, which is typically only 24 hours, lasting up to 48 hours if not successfully bred (Knox et al. 1988, DeYoung and Miller 2011). Raised male testosterone levels and potentially pheromone signals projected from females may be the catalyst that begins behavioral courtship (Marchinton and Hirth 1984). Courtship (a stage within rut) occurs during the time in which bachelor herds dissipate and mature-aged males increase movements and home ranges in an attempt to find receptive does in estrous (Beier and McCullough 1990). During courtship displays and breeding attempts, males often relocate seasonal home ranges or expand them to gain access to females in estrous (Tomberlin 2007). I defined rut as the embodiment of male physiological and behavioral changes that incur increased bouts of activity (quantifiable through movements and home range sizes [Beier and McCullough 1990, Tomberlin 2007]) that take place following a decrease in photoperiod (Goss 1983). The ultimate goal of rut-based activities is to enhance individual’s fitness through successful breeding attempts. I determined the occurrence of rut through peaks in weekly mean bi-hourly movement rate, sum of weekly movement across the annual cycle, and significant augmentations or fluctuations in mean home range size.

An animal's home range, the space that includes 95% of its known locations, is indicative of its relationship between the deer's social hierarchy among intrasexual conspecifics and reflective of available resources (i.e., does in estrus during rut and the quality of available food resources). Home range area and placement can also be clues of limiting factors for mule deer. If there are sufficient food resources available within an animal's home range, then perhaps space or some other unperceived necessity is the limiting factor contributing to mule deer decline. In addition to home range area providing insight into available or limiting resources, mule deer movement trends may have broad applications for future harvest management. Effects of hunting and rut on male movement are largely understudied for sympatric populations of mule deer and white-tailed deer occupying only private land in the Great Plains.

Conservation planning for management on private lands necessitates an understanding of mule deer response to common land use practices throughout western Kansas (e.g., grazing management, Conservation Reserve Program, row-crop agriculture). Response to land use practices can be identified through space use and resource selection by mule deer. By identifying macrohabitat features (e.g., land cover type, slope, aspect, elevation) that influence resource selection by mule deer, management strategies can prioritize enhancement of land cover types to augment mule deer abundance.

In most areas, sympatric mule deer and white-tailed deer segregate based on differential use across an elevational gradient (Martinka 1968, Brunjes et al. 2006). However, in western Kansas, there is less opportunity for deer to segregate along an elevation gradient, making competition between the two species more probable. Investigating space use and resource selection by sympatric white-tailed deer and mule deer populations in Kansas has the potential to provide important information to KDWP for managing deer and will contribute to the basic understanding of interactions between these two species. As food is not typically a limiting factor for deer in western Kansas, competition theory indicates that habitat selection may result in niche separation between the species (Hardin 1960). Competition is most likely limited during spring, summer, and fall when food resources are abundant. If competition is occurring, it may be more likely to take place during the resource-sparse winter months and in spaces with limited food availability (Martinka 1968). Additionally, anecdotal evidence supports the hypothesis that white-tailed deer may be displaying interference competition against mule deer; limiting the distribution and abundance of mule deer.

To date, there is a deficit of information in the central and northern Great Plains concerning the influence of hunting seasons (both archery and firearm) on survival of male mule deer and white-tailed deer. There is a need to identify species survival rates, this information could be key to restructuring species harvest limits, which could potentially bolster mule deer abundance. In addition to discerning vulnerable periods of the year and identifying survival rates for mature-aged males, keying on the spatial relationship and distribution of mule deer relative to white-tailed deer during seasons of when they are most vulnerable to mortality (rut and 12-day firearm hunting season) will help determine resources selected by mule deer during their life cycle. Of importance is addressing questions of the potential for white-tailed deer to be interspecific aggressors or are mule deer simply limited by some habitat component or cover type critical to their survival? Identifying available and selected resources by mule deer in the presence of white-tailed deer is essential in pinpointing their limiting factors that could be contributing to their decline.

The goals of my thesis research were to (1) test for differences in annual and weekly survival rates between species by estimating annual and weekly cumulative survival rates, identify periods of their annual cycle where male mule deer are most vulnerable to mortality factors, and examine the influence of harvest and rut on both species, (2) discern the influence of the 12-day firearm hunting season and rut period on male mule deer and white-tailed deer movements and home ranges relative to the rest of the year, and, lastly, (3) understand how resource selection of different land-cover types differs between mule deer and white-tailed deer across spatial scales. Western Kansas supplies a unique environment in which to address a current information gap concerning management of sympatric populations of male deer inhabiting private land with the intent of improving mule deer abundance.

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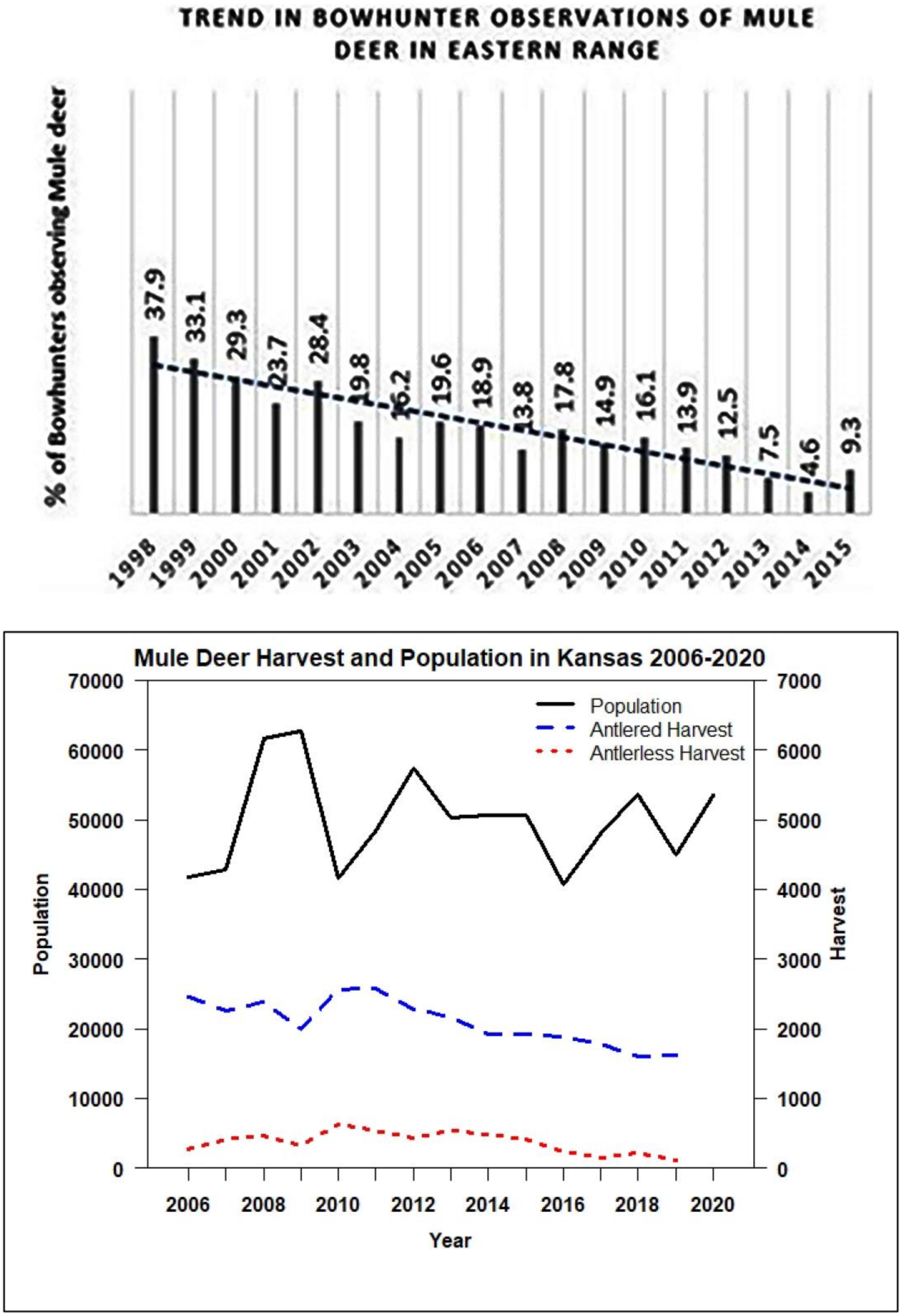

Figure 1.1. Decreasing number of bow hunter observations of mule deer in the eastern zone of Kansas, USA, from 1998-2015 (top; L. Fox, Kansas Department of Wildlife and Parks, unpublished data). Number of harvested mule deer in Kansas with 2019 being the lowest value since 1983 (bottom; Jaster 2021).

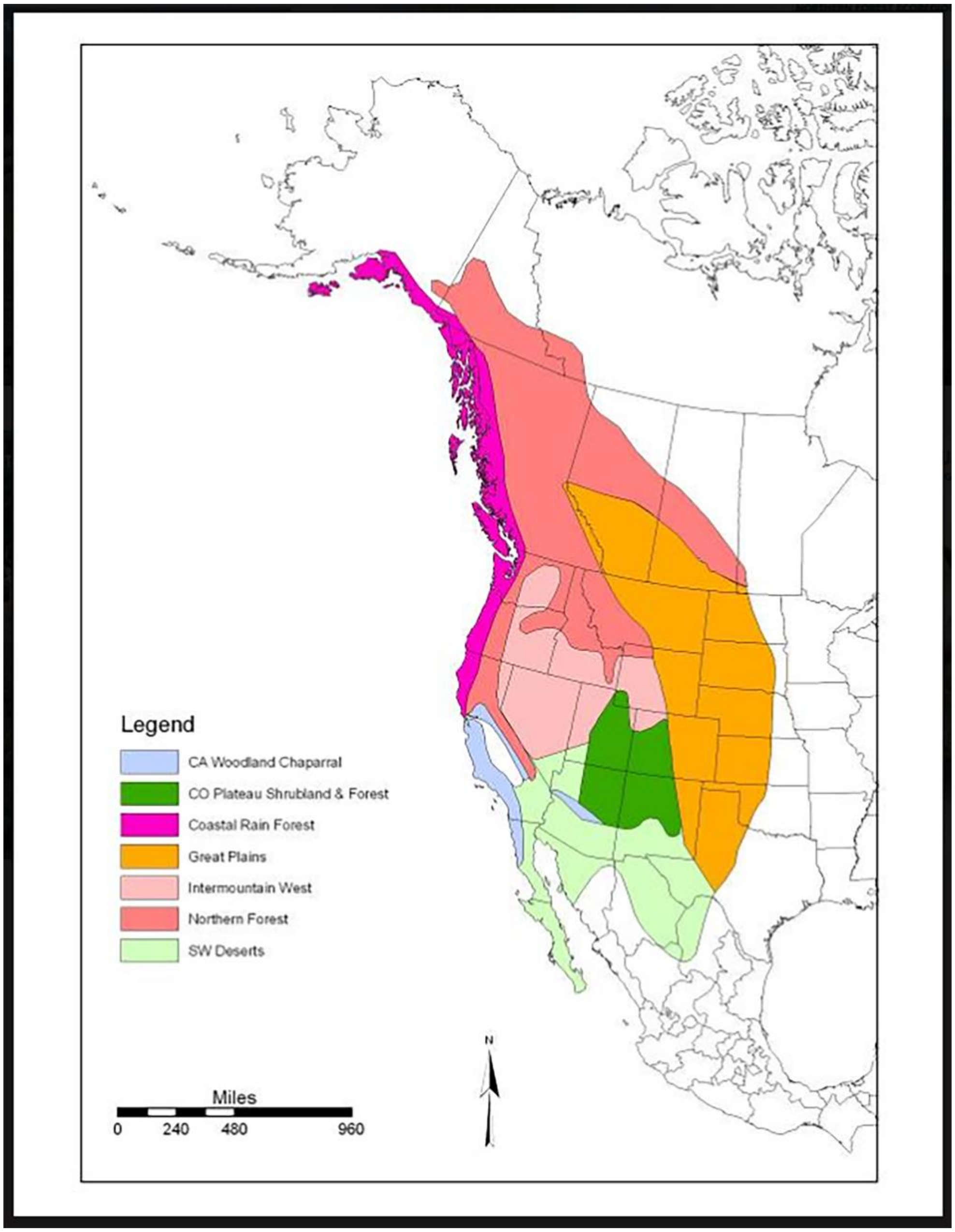

Figure 1.2. Current range of mule deer in North America. In western Kansas, USA, mule deer are located within the Great Plains Ecoregion, which is colored tangerine (Mule Deer Working Group 2019).

Figure 1.3. Distribution of white-tailed deer (lightest shade) and mule deer (darkest coloration) in North America (Hygnstrom et al. 2008). The overlapping range of mule deer and white-tailed deer is depicted by the medium shading.

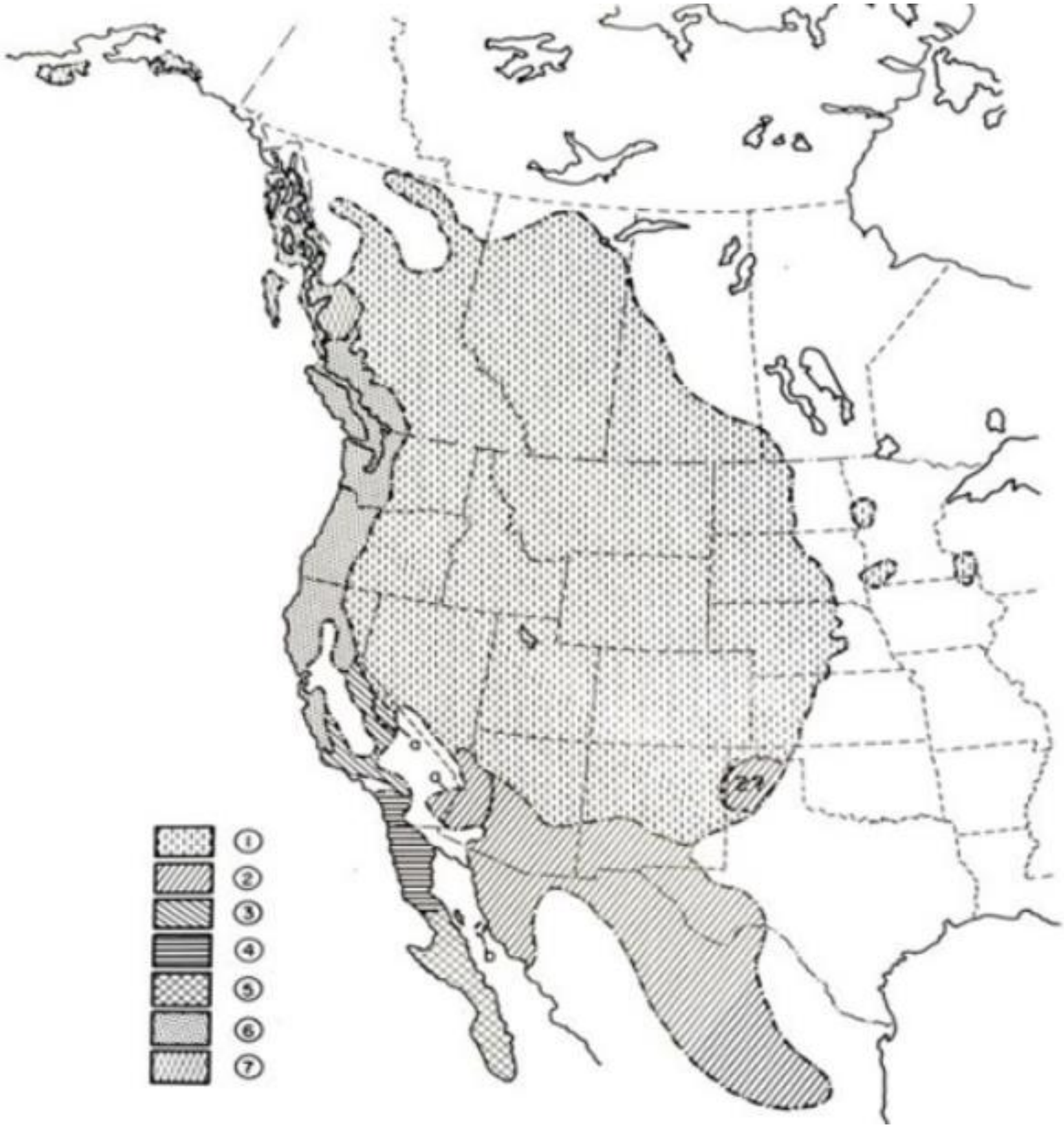

Figure. 1.4. Historic range of mule deer subspecies in North America; (1) *O.h. hemionus* is currently found in the western third of Kansas, USA, within the Great Plains. Other subspecies include (2) *O.h. crooki*; (3) *O.h. californicus*; (4) *O.h. fuliginatus*; (5) *O.h. peninulae*; (6) *O.h.columbianus*; and (7) *O.h. sitkensis* (Leopold 1959).

Chapter 2 - Effects of Hunting and Rut on Survival of Adult Male Mule Deer and White-tailed Deer

Current population trajectories of mule deer (*Odocoileus hemionus*) and white-tailed deer (*O. virginianus*) in western Kansas, USA, are diverging. Mule deer populations in Kansas are becoming constrained in occupied range, and abundance is declining based on Kansas Department of Wildlife and Parks (KDWP) survey data (Jaster et al. 2020). A similar pattern of decline is also being reported throughout the western Great Plains. However, catalysts driving the decline of mule deer are currently ambiguous. While mule deer population distribution is decreasing and potentially contracting westward (Ballard et al. 2001, Shallow et al. 2015), concomitantly white-tailed deer populations are ostensibly expanding (Martinka 1968, Baker 1984, Van der Hoek et al. 2002). It is crucial to understand factors affecting the demography of sympatric populations of white-tailed deer and mule deer in the Great Plains to develop management strategies to offset the decline of mule deer populations.

Mule deer are of both social and economic significance in Kansas. Big game hunting is a major source of revenue for the Kansas economy; if mule deer populations continued to recede, the loss of income afforded through mule deer permits will incite a rippling effect throughout the state (Chapter 1). To forestall the further decline of mule deer, it is pivotal to determine if harvest is affecting population demography, and potentially contributing to deferential survival of male deer between species in Kansas.

As sympatric deer populations in western Kansas share resources such as food, space, and cover, there is potential for one of these resources to be limiting, which could be contributing to the declining trend of mule deer populations through effects on annual survival. To elucidate factors that may be limiting adult male mule deer in Kansas, it is essential to discern if there are differences in survival between mule deer and white-tailed deer. Shifts in population abundance related to environmental changes may increase survival of white-tailed deer relative to mule deer in marginal mule deer habitats (Whittaker and Lindzey 2001). Estimating species survival is paramount to understanding the dynamics and demographics between these overlapping populations, as survival rates, and the unknown factors governing survival, can have meaningful effects on harvest management, population dynamics, and overall herd health (Brinkman et al. 2004, Webb et al. 2007, Anderson et al. 2015).

Simultaneously estimating survival, timing of mortalities, and causes of mortality is necessary to successfully manage population dynamics and demographics of deer (DeYoung 1989, Dusek et al. 1992, Webb et al. 2007). The KDWP currently uses information acquired through general survey trends (hunter surveys to estimate harvest rates, deer-vehicle collisions as an index to deer abundance, and distance sampling to estimate density) to monitor deer populations. By obtaining estimates of vital rates for deer populations, management capacity would greatly improve, and those estimates would help provide the information needed to set accurate species harvest limits. This would prevent the overexploitation of hunted populations, which becomes possible without the knowledge of region-specific, temporal mortality patterns (Nelson and Mech 1986). Although the underlying causes for diverging population trends between mule deer and white-tailed deer are unclear, harvest regulations directly affect mortality and may contribute to discrepancies in annual survival between species.

Rut encompasses the physiological and behavioral changes that occur leading up to and during breeding and differs from the temporal estimate of doe estrus. Rut is an important biological time period for adult males, in which males increase movements and home ranges to seek out estrus does and secure breeding opportunities to increase fitness (Beier and McCullough 1990, Marchinton and Hirth 1984, Tomberlin 2007). Males that engage in rutting activities rely on stored energy reserves acquired before rut, as their primary focus during rut is successful acts of breeding (Wallmo 1981, DeYoung 1989, Ditchkoff et al. 2001). Males may lose up to 30% of their body mass during rut (DeYoung 1989, Ditchkoff et al. 2001), which makes them more susceptible to mortality after rut (Harrison et al. 2011). Rut is a vulnerable time period for adult males, because rutting males may be more predisposed to forms of natural mortality from physical exhaustion and inadequate nutrition (Klein and Olson 1960, Clutton-Brock 1982 et al. 1982, Ditchkoff et al. 2001).

The influence of hunting and rut temporal periods on survival of white-tailed deer has been reported. Ditchkoff et al. (2001) estimated survival among different age classes of primarily mature male white-tailed deer in Oklahoma, USA. Overall annual survival of male deer was 0.68; the greatest source of mortality was hunting. Webb et al. (2007) estimated annual survival to be 0.49 for adult male white-tailed deer in Texas, USA; all but one non-harvest-related mortality occurred during rut or post-rut periods. However, factors affecting survival have not been reported for free ranging male mule deer or for sympatric populations of non-migratory mule deer and white-tailed deer in the Great Plains, with the intention of informing management. As one of the few studies on sympatric deer species in the Great Plains, Whittaker and Lindzey (2001) found no difference in survival between species for sympatric populations of unhunted mule deer and white-tailed deer in the Rocky Mountain Arsenal, Colorado, USA.

Limited survival data exists for sympatric adult males in the Great Plains as most studies focus on the survival of adult females (DePerno et al. 2000, Grovenburg et al. 2011), or neonate white-tailed deer and mule deer (Grovenburg et al. 2012, Kern 2019). Similar to studies of adult males, Grovenburg et al. (2011) found that hunting accounted for the majority of mortalities, followed by deer-vehicle collisions for adult female white-tailed deer in Minnesota and South Dakota, USA, with annual survival of 0.76. Deperno et al. (2000) reported annual survival rates of adult female white-tailed deer, which ranged from 0.50 to 0.62 in a three-year study in the Black Hills of South Dakota and Wyoming, USA. Unlike adult males, the greatest proportion of mortalities occurred during spring; with natural causes as the leading source of mortality, followed by harvest, and then accidental causes. The difference in temporal mortality may be due to differing susceptible life history stages between adult male and female deer (e.g., rut versus gestation) and differential harvest.

My study had the unique opportunity to determine periods of mortality for adult males of sympatric populations of non-migratory mule deer and white-tailed deer populations in the western Great Plains, while identifying the influence of rut and hunting on survival between mule deer and white-tailed deer. This information could provide insight into factors currently depressing mule deer abundance. I anticipated weekly cumulative survival would significantly decline after rut; with the 12-day firearm period having the strongest effect on male deer survival of both species. I hypothesized the remaining mortalities would primarily occur during the relatively resource-limited winter months, during a vulnerable life history stage in which mature males are already weakened from rutting lag effects. Lastly, I expected mule deer to have lower annual survival than white-tailed deer as population trajectories are currently declining in Kansas and throughout the Great Plains.

Study Area

I conducted this study at two sites located ~130 km apart in the western third of Kansas during 2018, 2019, and 2020; both sites were composed of private land (Fig. 2.1). The north site (~850 km^2) was in Graham, Norton, Sheridan, and Decatur counties (Fig. 2.2). The south site (~1,370 km^2) was in Scott, Logan, Gove, and Lane counties (Fig. 2.3). Both sites were located in the Central Great Plains and High Plains level III ecoregions (U.S. Environmental Protection Agency [EPA] 2000). Of the eleven physiographic regions in Kansas, all counties included in both study sites were located in the High Plains region; Norton, Graham, Gove, Lane, and Logan counties are also part of the Smoky Hills physiological region (USDA NRCS https://www.nrcs.usda.gov/wps/portal/nrcs/detail/ks/about/?cid=nrcs142p2_033475> Accessed 4/4/21). Elevation in the north site was 666.9 m. Average annual temperatures were 11.89° C, 11.60 ° C, and 12.82 ° C during 2018, 2019, and 2020 respectively. Long-term average annual temperature from 2000-2020 was 12.37° C. Total annual precipitation was relatively wet in 2018 (921.25 mm) and 2019 (744.73 mm), with drought-like conditions in 2020 (369.40 mm) compared to the previous 20 years in which average annual precipitation was 545.32 mm ± 36.58 in the north site (Hill City Municipal Airport, KS, USA; National Oceanic and Atmospheric [NOAA] 2020). Elevation in the south site was 906.5 m. Average annual temperatures were 11.72° C, 11.13° C, and 12.38 ° C during 2018, 2019 and 2020, respectively. Long term annual temperatures from 2000-2020 was 12.02° C at the south site. Total annual precipitation was 666.49 mm, 526.54 mm, and 360.9 mm in 2018, 2019, and 2020, respectively; conditions were dry during 2020 compared to the previous 20 years (2000-2020) when total precipitation averaged 499.45 mm ± 23.22 per year (Scott City, KS, USA; NOAA 2020).

Both study sites were a matrix of cropland and grassland, composed of short- and mixed-grass prairie (U.S. Environmental Protection Agency 2000). The defining difference between both study areas was the presence of the North Fork Solomon River in the north site, which crossed the study area and included floodplain woodlands along riparian areas (Figs. 2.4, 2.5, and 2.6). Most of the south site was east of U.S. Highway 83 and north of State Highway 4 (Figs. 2.7, 2.8, and 2.9). The south site included more draws and elevated "chalk rock" areas relative to the north site.

Available, ground-truthed land cover patch area and distribution were calculated annually by encompassing a 2-km buffer around a 100% minimum convex polygon of the distribution of all deer locations. The north study site included 504 km^2, 857 km^2, and 685 km^2 in 2018, 2019, and 2020, respectively. The south study site encompassed 1,371 km^2, 665 km^2, and 1,023 km^2 in 2018, 2019, and 2020, respectively.

Cover types were defined as Crop, U.S. Department of Agriculture Conservation Reserve Program (CRP), Pasture (i.e., grazed native grassland), Urban (small towns, outbuildings, cemeteries, and other man-made structures), Water, and Woodland (ranging from small pockets of forest, riparian areas, and shelterbelts (Table 2.1). Relative proportion of land cover types varied slightly among years (Table 2.1). However, Crop was the most common land cover type during each year in the north site, with its distribution surrounding Pasture centrally located in the study site (Figs. 2.4, 2.5. and 2.6). Similarly in the south study site, Crop comprised the largest proportion of cover types during all years, with Pasture comprising the second most common land cover type (Figs. 2.7, 2.8, and 2.9).

Corn (*Zea mays*), wheat (*Triticum aestivum*), and milo (*Sorghum bicolor*) dominated agricultural crops (U.S. EPA 2000). Other less abundant crops included sunflowers (*Helianthus* *annus*), alfalfa (*Medicago sativa*), and soybeans (*Glycine max*). Pasture was typically composed of shorter, grazed, native mixed-grass prairie. Prevalent grasses in the mixed-grass prairie included little bluestem (*Schizachyrium scoparium*), sideoats grama (*Bouteloua curtipendula*) and blue grama (*B. gracilis*). Tall thistle (*Cirsium altissimum*), broom snakeweed (*Gutierrezia sarothrae*), Nuttall's sensitive-briar (*Mimosa nuttallii*), and Indian blanket (*Gaillardia pulchella*) were typical forbs; widespread succulents included yucca (*Yucca glauca*) and prickly pear cactus (*Opuntia macrorhiza*). Tracts of CRP included tallgrass prairie species – big bluestem (*Andropogon gerardi*), Indiangrass (*Sorghastrum nutans*), and switchgrass (*Panicum virgatum*) intermixed with forbs such as white prairie clover *(Dalea candida*), Maximillian sunflower (*Helianthus maximiliani*), purple prairie clover (*Dalea purpurea*), and Illinois bundleflower (*Desmanthus illinoensis*; United States Department of Agriculture [USDA], Natural Resources Conservation Service [NRCS] 2020). Woodlands were composed primarily of shelterbelts, small groups of clumped trees intermittently present throughout pastures and the large riparian area in the north site. Prevailing tree species included American elm (*Ulmus americana*), box elder (*Acer negundo*), green ash (*Fraxinus pennsylvanica*), hackberry (*Celtis occidentalis*), black cherry (*Prunus serotina*), eastern cottonwood (*Populus deltoides*), honey locust (*Gleditsia triacanthos*), black locust (*Robinia pseudoacacia*), mulberry (*Morus rubra*), black walnut (*Juglans nigra*), and eastern red cedar (*Juniperus virginiana*). Plum thickets (*Prunus* angustifolia) and smooth sumac (*Rhus glabra*) were common shrubs in both study sites (USDA, NRCS, 2020). Taxonomic authorities were from the Kansas wildlflowers and grasses webpage (www.kswildflower.org) and the Kansas Native Plant Society webpage (www.kansasnativeplantsociety).

Methods

Capture

Adult male capture occurred during February 2018 and 2019, and March 2020 using a commercial helicopter crew (Quicksilver Air Inc., Colorado Springs, CO, USA). They captured and GPS-collared 60 adult male mule deer and white-tailed deer at capture sites in 2018, divided evenly between species and two study sites in western Kansas (i.e., 15 individuals/species/site). Thereafter, in 2019 and 2020, only replacements for the number of male deer that died during the previous year were captured to maintain a sample size of 60 at the start of each field season. The capture crew aerially net gunned, hobbled, and blindfolded captured animals prior to transporting them to a central processing location located at each study site during 2018, 2019 and 2020 (Northrup et al. 2014). No deer were captured ≥8.05 km from the processing location (with the majority being released ≤5 km from capture) to reduce capture myopathy. Restraint from time of capture to release was ≤30 minutes. All captured animals were subjected to a physical exam by on-site veterinarians. For handling safety and control of stressed individuals, males may have been administered chemical sedation in the combined form of Azaperone, Midazolam, and Butorphanol (each drug compound 50 mg/ml, volume of each 0.3 cc with Azaperone and Butorphanol in 1 syringe, and Midazolam in another; IM; Wolfe and Miller 2016). Animals were released at the processing site as previous capture efforts found that animals rapidly returned to capture locations (W. Conway, Texas Tech University, pers. comm.). All deer were captured and handled according to guidelines approved by the American Society of Mammalogists (Sikes et al. 2016), under the Institutional Animal Care and Use Committee at Kansas State University (protocol #3963), and authorized under the Kansas Wildlife, Parks, and Tourism scientific permits (SC-024-2018, SC-015-2019, SC-032-2020). , Morphological measurements (cm) were recorded for all captured deer, including total body length, chest circumference, hind foot, and neck girth. Age determination of captured animals was performed via tooth replacement and wear (Severinghaus 1949). One person aged all captured deer. An index of body condition (1-10) based on the protrusion of the ribs, vertebra and pelvis was assessed and recorded; where 1 represented very poor body fat and 10 represented excellent body fat (modified from Gerhart et al. 1996).

Standard numbered livestock ear tags with contact information were applied to each captured deer using conventional equipment and procedures for identification of individuals. Each deer was fitted with a Vertex Plus-2 radio collar (Vectronics, Berlin, Germany), which contained a very-high-frequency (VHF) beacon, mortality sensor, temperature sensor, 3-axis activity sensor, Iridium Bi-directional option, and a Vectronic timer-controlled drop-off initiated at deployment. Expandable elastic collar inserts were used to account for neck swelling during rut. Each collar was programmed to take a GPS positional fix every two hours, with 12 locations per Iridium message for up to three years (160 weeks). During the 12-day firearm hunting season in late November-early December, all collars recorded a GPS fix 48 times a day (i.e., every half hour). Location and mortality data were obtained remotely with activity data stored on board, location error was estimated to be ~5 m.

Survival

All transmitters were equipped with a mortality detection option that notified me of mortality events, at which time I remotely identified mortality locations. A mortality notification was sent when collars were stationary for three hours. Due to a lack of mortality evidence remaining at the 2018 mortality investigation sites, I reduced collar mortality sensor times from the original eight hours, to six, to ultimately being set to three hours for 2019 and 2020. Once a “mortality mode” notification was received, field personnel immediately located the animal and determined cause of death as one of four categories: “natural” (old age, disease, predation), “anthropogenic” (hunting, suspected poaching, or car strike), or “unknown”. Technicians wore gloves and took pictures during each investigation. Significant hemorrhaging and bite/claw marks were identified to discern between predation events and carcasses being scavenged postmortem. Femur marrow condition assessment (Klein 1964), blood trails, hunter inflicted wounds, predator scat, hair, and matted vegetation were recorded and photographed to assist in determining factors related to each mortality event.

All legally harvested males during archery and the 12-day firearm seasons were directly reported by hunters. Archery seasons occurred from 09-17-18 to 12-31-18, 09-16-19 to 12-31-19 and 09-14-20 to 12-31-20. The 12-day firearm seasons were 11-28-18 to 12-9-18, 12-4-19 to 12-15-19, and 12-02-20 to 12-13-20.

To assess the potential effect of rut on mortality, I defined annual rut periods for each species based on spikes in mean weekly bi-hourly movement rate and mean total sum of movement activity by week across the annual cycle for deer captured in 2018 and 2019 (Chapter 3). Rut occurred during similar weeks both years for each species and site. Rut occurred for mule deer during 11-05-18 to 11-25-18, 11-04-19 to 11-24-19 and 10-29-18 to 11-18-18, 10-28-2019 to 11-16-2019 at the north and south site, respectively. Rut occurred for white-tailed deer during 11-05-18 to 11-25-18, 11-04-19 to 11-24-19 and 10-29-18 to 11-25-18, 10-28-19 to 11-24-19 at the north and south site, respectively.

Assistance in determining the cause and associated factors for mortalities was obtained from the Southeastern Cooperative Wildlife Disease Study at the University of Georgia (SCWDS). Samples of thinly sliced (≥1 cm) organ specimens, including heart (through papillary muscle), lungs, liver, spleen, and kidneys, were collected from any collared male determined to have an unknown cause of death and sent to SCWDS for disease testing to aid in determining cause-specific mortality. Specimen samples were composed of 1-part tissue to ≥10 parts formalin solution to ensure protection from decomposition and autolysis. Stomach lining and body condition were observed, with any abnormalities recorded. In addition, heads of mule deer were sent to SCWDS to test for presence of the *Parelaphostrongylus tenuis* parasite, (i.e., meningeal or brain worm). Retropharyngeal lymph nodes were collected from all collared deer that were harvested or died from unknown or natural causes and opportunistically from other hunter-killed deer with hunter permission, prior to shipping to either SCWDS or the Kansas State University Veterinary Lab for Chronic Wasting Disease (CWD) testing.

Analyses

All statistical analyses were conducted using R (version 3.5.0. R Core Team 2019). A one-way multivariate analysis of variance (MANOVA) was used to test for differences in capture morphometric variables (total body length, hind foot, chest girth, neck circumference, age, and body condition) among species-site groups (i.e., north mule deer [NMD], north white-tailed deer [NWTD], south mule deer [SMD], and south white-tailed deer [SWTD]) for all collared deer. Then I used a one-way analysis of variance (ANOVA; Zar 1996, $\alpha = 0.05$) to test for univariate differences among groups for each morphometric variable following a significant MANOVA ($P < 0.05$). Lastly, I used Tukey HSD to test for differences among groups following a significant ANOVA ($P < 0.05$).

I used Cox proportional hazard models to test categorical effects of study site, year, year x site interaction, age class, and species on the likelihood of mortality (Cox 1972, Allison 1995). I further evaluated the influence of morphometric factors on annual survival (i.e., total body length, chest girth, hind foot length, neck girth). I tested each factor in a model set consisting of 10 single variable and null models. I characterized age class as a categorical variable by assigning individuals to one of three categories (≥3 years, <3 years, and Unknown); no <1 year old males were included in the analysis. Deer collared longer than one year were aged into an older cohort, if applicable, for each year they were alive (e.g., a <3 year-old deer caught in 2018 could become ≥3 year-old during 2019 or 2020 analysis if still living). I used Akaike's Information Criterion adjusted for small sample sizes (AIC_c) to assess relative support for each model (package AIC_cmodavg; Mazerolle 2019) and considered models ≤2.00 ΔAIC_c to be competitive (Burnham and Anderson 2002). I used Akaike weights (w_i) to further assess competing models.

I estimated weekly cumulative survival and annual survival rates with Kaplan-Meier models using the survival package ([survival; v.2.44-1.1, Therneau 2015], Kaplan and Meier 1958, Pojar and Bowden 2004). The starting dates for each year were: 02-15-2018, 02-10-2019, and 03-05-2020. There were no capture myopathies within two weeks of initial capture for collared adult males. I tested one model set with three single variable models: species, site, and age class. I subjected individual survival data to right censoring when there were instances of collar failure or slipped collar. No differences were detected between survival rates when 95% CI of the estimate overlapped. Hazard functions were used to identify the relative most hazardous time of the year for each species and site.

Results

I captured and collared 111 adult male mule deer and white-tailed deer (Table 2.2). I calculated the mean values for morphometric variables recorded during capture for adult males and their associated standard errors for each year of capture and combined years, measurements include total body length neck girth, chest girth, and hind foot length (Tables 2.3, 2.4). Age and mean body condition score were also determined (Tables 2.5, 2.6). Chest girth and hind-foot length were not recorded for the 2018 cohort. Morphometric measurements at capture pooled across years differed among groups ($F_{3, 175} =$ 2.87, P < 0.001, $V^{(s)}$ 0.27). Separately, pooled total body length and chest girth differed among groups (Table 2.4). No other capture morphometric values, including age and body condition score, differed among groups (Table 2.5, 2.6). Across years, south white-tailed deer had the largest mean total body length and south mule deer had the largest mean neck girth (Table 2.4). The majority of deer captured from 2018-2020 were ≥3 years old (Table 2.5). North white-tailed deer had the highest body condition score (5.34) which ranked in the "fair" category, body condition averages from all other groups were consistently in the "poor" category (Table 2.6).

The interaction of site and year (AICc 736.60, $\omega = 0.38$) was the top-ranked model for estimating annual survival based on capture data and other factors thought to be biologically important to adult males (Table 2.7). Site and year was most likely the highest-ranked model because of the significantly lower north site survival during 2020 (0.26 ± 0.09), compared to the previous two years (0.50 ± 0.09, 0.55 ± 0.09) in 2018, and 2019, respectively. The parameter "site" was competitive and within Δ2 AICc. No other biological parameters were competitive.

No differences in annual survival were detected across years between species (mule deer 0.54 ± 0.05, white-tailed deer 0.58 ± 0.05; Table 2.8). Estimated annual survival was 0.56 ± 0.04 (95% CI 0.49-0.64) pooled across species, ages, study sites, and years (2018-2020; Fig. 2.10). Localized periods of high mortality occurred during 2020; compared to 2018 and 2019, survival in the north site (0.26 ± 0.09), during 2020 was drastically lower, specifically for mule deer (0.34

± 0.09) in comparison to white-tailed deer (0.62 ± 0.10) relative to any other species, site, or year combination (Table 2.8).

The greatest percent of adult male mortalities occurred during fall, November (17%) and December (50%), which encompassed the rut period and 12-day firearm seasons (Fig. 2.11). The hazard function for pooled sites and species had the same temporal pattern, identifying the hunting season particularly the 12-day firearm period (weeks 38-44) as the most hazardous time of the year for both sites and species (Fig. 2.12). Of the unknown mortalities, excluding deer suspected of being poached, one third occurred in December, the remaining were scattered throughout the rest of the year, with a slightly greater number of combined mortalities during February-April (33%; Fig. 2.13). There was no obvious temporal trend identifying concentrated periods of natural mortalities (Fig. 2.13). The majority of deer-vehicle collisions occurred in the fall, during or immediately after rut (66%).

Kaplan-Meier cumulative survival results showed that survival of both mule deer and white-tailed deer was affected by harvest season and rut. The annual survival estimate was 0.56 (SE = 0.04, 95% CI 0.49 - 0.64) for adult male white-tailed deer and mule deer combined in western, Kansas, USA, during 2018-2020. The two weeks of firearm season significantly reduced survival by 19.6%, and 12.4% for mule deer and white-tailed deer, respectively. Survival was reduced by 10.6% and 9.8% during rut for mule deer and white-tailed deer, respectively.

Pooled cause-specific mortality results show total mortality (*n* = 76) in addition to 11 censored deer; collars were censored due to premature collar drop offs (*n* = 4), collar failure (*n* = 4), slipped collars deer (*n* = 1), and instances of suspected poaching when only the collar could be located (*n* = 2; Fig. 2.14). Causes of mortality included: legal harvest (50% [firearm = 42%, archery = 8%]), unknown (25%), natural (21%), and deer-vehicle collision (4%; Fig. 2.14). Of the deer that died of natural causes, 50% tested positive for CWD; however, not all natural mortalities were sampled for CWD, so more deer may have actually been CWD positive. Of the unknown mortalities, 16% were suspected poaching incidences (1 north white tailed deer, 1 south white-tailed deer, and 1 south mule deer) where investigations detected cut or otherwise man-made modifications to GPS collars.

In total, 46 CWD samples were collected, of which 37% (*n* = 17) of sampled deer tested positive for the prion indicative of CWD (Fig. 2.14). Site had a greater effect in CWD prevalence than species. The prevalence of CWD detections decreased in magnitude by year between 2018 and 2020 (Fig. 2.14). The majority of positive samples were collected from the north site (88%, *n* = 15). Overall, 54% (*n* = 15/28) and 11% (*n* = 2/18) of samples were positive for CWD in the north and south sites, respectively. Positive CWD tests by species were 38% and 35% for mule deer and white-tailed deer, respectively. No positive incidences of *Parelaphostrongylus tenuis* (i.e. meningeal or brainworm) were detected in sampled mule deer.

Discussion

No differences in species survival were detected across years. Throughout the entire year, the greatest percent of adult male mortalities occurred during fall (67%). Both mule deer and white-tailed deer survival were dramatically affected by harvest season and rut. Although survival differences in species did not occur across years, there was evidence of localized periods of high mortality, particularly for mule deer at the north study site during 2020. There was no obvious single factor responsible for the low survival rates at the north site 2020; however, an increase in mule deer harvest as well as increased disease prevalence may have been additive to natural mortality.

Similar to Whittaker and Lindzey (2001), there was no annual survival difference between species in my study across years. The survival rate for both species of deer in Kansas was considerably lower than the survival rate of a sympatric population in northeast Colorado (0.80-1.0 for mixed male and female mule deer and white-tailed deer, respectively; Whittaker and Lindzey 2001). However, deer in that study were not subjected to hunting, nor were they truly free ranging. As male deer in Kansas of both species are exposed to hunting, it is not surprising that survival rates were lower this study.

The annual survival rate for pooled sites, species, and years in western Kansas (0.56) was lower than the majority of survival rates of other studies of adult male deer (Ditchkoff et al. 2001 [0.68]) and adult female deer (Grovenburg et al. 2011 [0.76]) in the Great Plains. Conversely, some studies in the Great Plains (DePerno et al. 2000 [0.50-0.62]) and others outside but adjacent to the Great Plains that investigated survival of harvestable adult male deer had similar survival rates (Nixon et al. 2001: central and northern Illinois [0.51]; Webb et al. 2007: south Texas [0.49]; Anderson et al. 2015: east central Illinois [0.50]).

Peak mortality occurred during late fall (November and December) when survival rates for adult males were depressed primarily because of the firearms hunting season. This pattern of mortality mirrors the temporal mortality trend found in other studies for free-ranging deer in the Great Plains that were exposed to hunting (Ditchkoff et al. 2001; Grovenburg et al. 2008, 2011). There was no obvious pattern in the temporal mortality of deer that died from natural causes. However, December accounted for a third of the unknown mortalities, some of which may have died from natural causes stemming from rutting lag effects (Clutton-Brock et al. 1982, Ditchkoff et al. 2001). November and December also accounted for the largest percentage of deer-vehicle collisions, which aligned temporally with the peak mortality results of Grovenburg et al. (2008)

who positively associated rut with peak deer-vehicle collisions for white-tailed deer in South Dakota.

Both mule deer and white-tailed deer survival was affected by harvest season and rut. The two weeks of firearm season reduced cumulative weekly survival estimates by 19.6%, and 12.4% for mule deer and white-tailed deer, respectively. Despite no difference in annual survival between species, harvest, particularly the 12-day firearm season, was the greatest cause of mortality for mule deer (64% of total mortality [52% 12-day firearm, 12% archery]), but was not the leading cause of mortality for white-tailed deer (32% of total mortality [29% 12-day firearm, 3% archery]. The leading cause of mortality for white-tailed deer was unknown (38% total mortality).

Harvest represented the leading cause of mortality for pooled deer species (50% [firearm = 42%, archery = 8%]). The percent of mortalities that stemmed from harvest is greater than the percent of adult male white-tailed deer harvest mortalities in southeastern Oklahoma (24%; Ditchkoff et al. 2001). Harvest for deer in my study was closer to that of adult female white-tailed deer in the northern Great Plains (69.9%; Grovenburg et al. 2011). Anderson et al. (2015) also reported a lower percent (26%) of harvested male and female white-tailed deer in east-central Illinois. Similarly, female white-tailed deer in the Black Hills of South Dakota and Wyoming had a lower percent of mortalities due to harvest (22.6%) than male deer in my study (DePerno et al. 2000).

As hypothesized, survival decreased during and following rut for both mule deer and white-tailed deer. This is unsurprising as adult males face their most energetically exhaustive period during rut when they are focused on securing mates and maximizing breeding opportunities rather than on foraging for food or securing security cover (DeYoung 1989, Ditchkoff et al. 2001). Additionally, deer that invest in rutting activities risk potentially becoming more susceptible to natural mortality (Robinette et al, 1957, Clutton-Brock et al. 1982, Ditchkoff et al. 2001). Survival of deer was reduced by 10.6% and 9.8% during rut for mule deer and white-tailed deer, respectively, during 2018 and 2019. Similar to deer in Oklahoma, body length and chest girth, qualities strongly related to success in male dominance hierarchies during rut, were not strongly associated with predicting survival for deer in my study. Causes of mortality during rut were either natural or deer-vehicle collisions as the Kanas firearms season does not include the rut period. Ditchkoff et al. (2001) surmised that the majority of adult male mortalities would occur during or immediately after the breeding season. This was true for deer in my study; however, the overlap of 12-day firearm season with the post-rut period confounds determination of the effect of rut as deer are already dying from rutting lag effects that weakened their body condition making them more vulnerable to natural mortality (Clutton-Brock et al. 1982). Therefore, it was difficult to isolate the definitive influence of rut on natural mortality for deer in my study.

There was evidence of short periods of high localized mortality during the last year of the study. Although there was a pattern of lower survival in the north study site than the south for each year of the study, the top-ranked model for parameters most biologically important for the survival of mule deer and white-tailed deer (site & year) was most likely heavily influenced by the 2020 survival estimates. Survival of mule deer in the north study area during 2020 differed from previous years, with mule deer having drastically lower survival (0.34) compared to the previous two years. As white-tailed deer in the north site did not have a similar decrease in survival, the reduced survival of mule deer was the primary factor in the significantly lower survival for deer in the north study site in 2020 (0.26). When compared to previous years, the abundance of mortalities for north mule deer increased during 2020 in every category of cause specific mortality. In particular, 43% of all north mule deer were harvested during 2020. Additionally, based on contributing reports, incidences of epizootic hemorrhagic disease (EHD) may have increased during 2020 as that summer was much drier than the prior two years, potentially exacerbating the likelihood of EHD transmission, which may have contributed to an increase in natural mortality.

Like much of the western United States, deer in Kansas are currently undergoing diverging species population trends. My objectives were to identify temporal mortality patterns, assess the influences of hunting and rut on adult male survival of both species, and most essentially test for differences in annual and weekly survival rates between species by estimating annual and weekly cumulative survival rates. I hypothesized the residual mortalities after the 12-day firearm season would primarily occur during the relatively resource-limited winter months, during a vulnerable life history stage in which mature males are already weakened from rutting lag effects. This hypothesis was partially supported as a third of unknown mortalities occurred in December; however, natural mortalities showed no major temporal pattern throughout the year. Alternatively, I anticipated weekly cumulative survival would significantly decline after rut due to harvest during the 12-day firearm period for both species. There was evidence in support of the harvest hypothesis as rut and 12-day firearm strongly influenced the survival rate of both species, and harvest was the leading cause of mortality for mule deer, but was not the foremost cause of mortality for white-tailed deer. Most importantly, I expected mule deer to have lower annual survival relative to white-tailed deer as population trajectories are currently declining in Kansas and throughout the Great Plains. Yet, I found no support for differential male survival among the two species and an unknown factor unrelated to male annual survival is inducing the decline of mule deer.

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Management Implications

Although harvest was not the leading cause of mortality for male white-tailed deer, it was the main cause of mortality for male mule deer, and most likely exacerbated the significantly lower north male mule deer survival rates during 2020. One measurable action to increase survival of mule deer, is to decrease the amount of harvested deer. Therefore, to combat the current population trajectory of mule deer abundance, and augment the management and conservation of mule deer in Kansas, I suggest decreasing harvest of male mule deer to directly increase mule deer survival.

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Figures and Tables

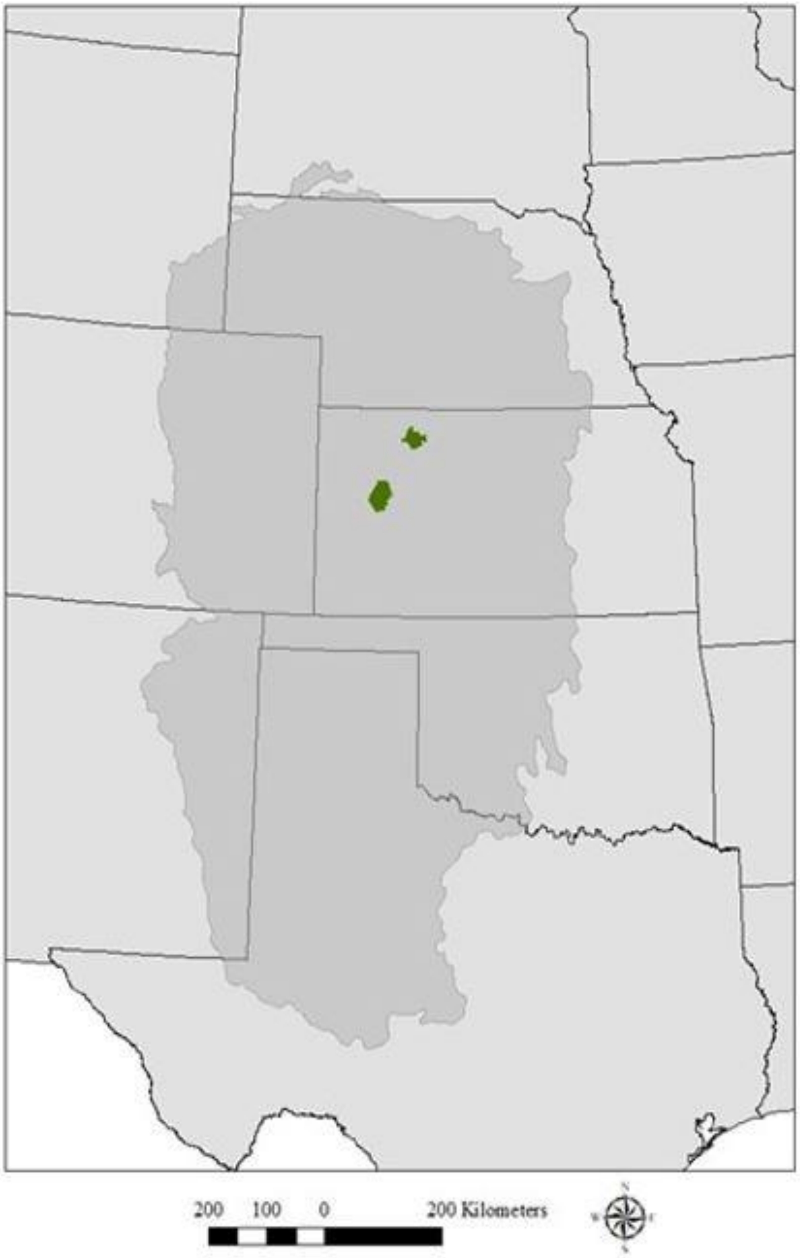

Figure 2.1. The two project study sites for estimating survival of white-tailed deer and mule deer in the western third of Kansas, USA, within the Central Great Plains and High Plains level III ecoregions (U.S. Environmental Protection Agency 2000). The sites were defined as North (top green) and South (bottom green) during 2018 – 2020.

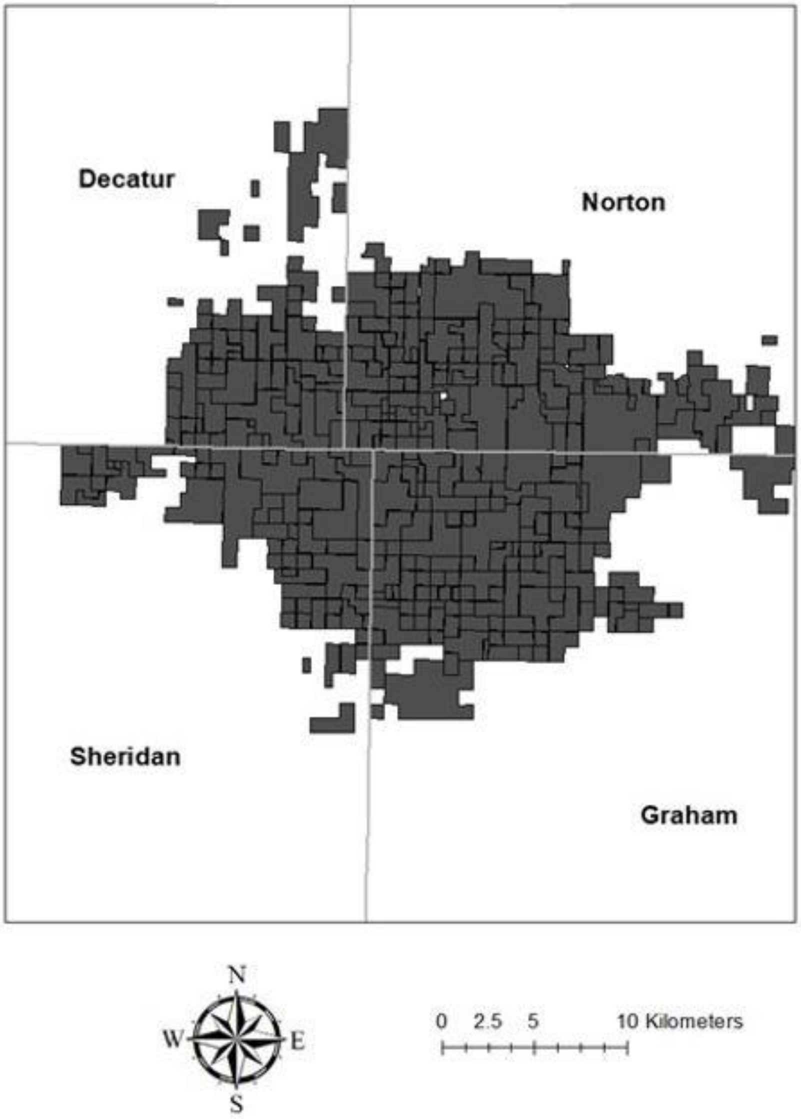

Figure 2.2. The North study site for estimating survival of mule deer and white-tailed deer in western Kansas, USA, during 2018 – 2020, with county lines separating Logan, Gove, Scott and Lane counties. Thinner, smaller lines indicate boundaries of different land use categories.

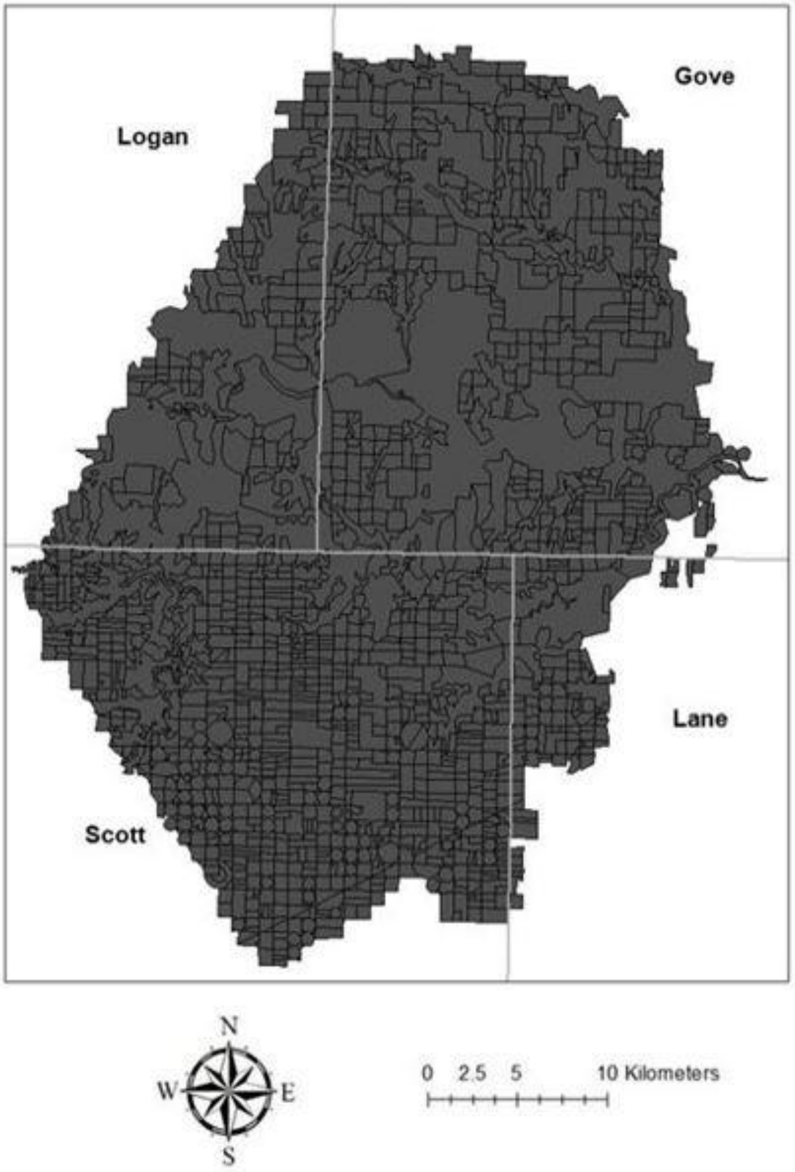

Figure 2.3. The South study site for estimating survival of mule deer and white-tailed deer in western Kansas, USA, during 2018 – 2020, with county lines separating Logan, Gove, Scott and Lane counties. Thinner, smaller lines indicating boundaries of different land cover categories.

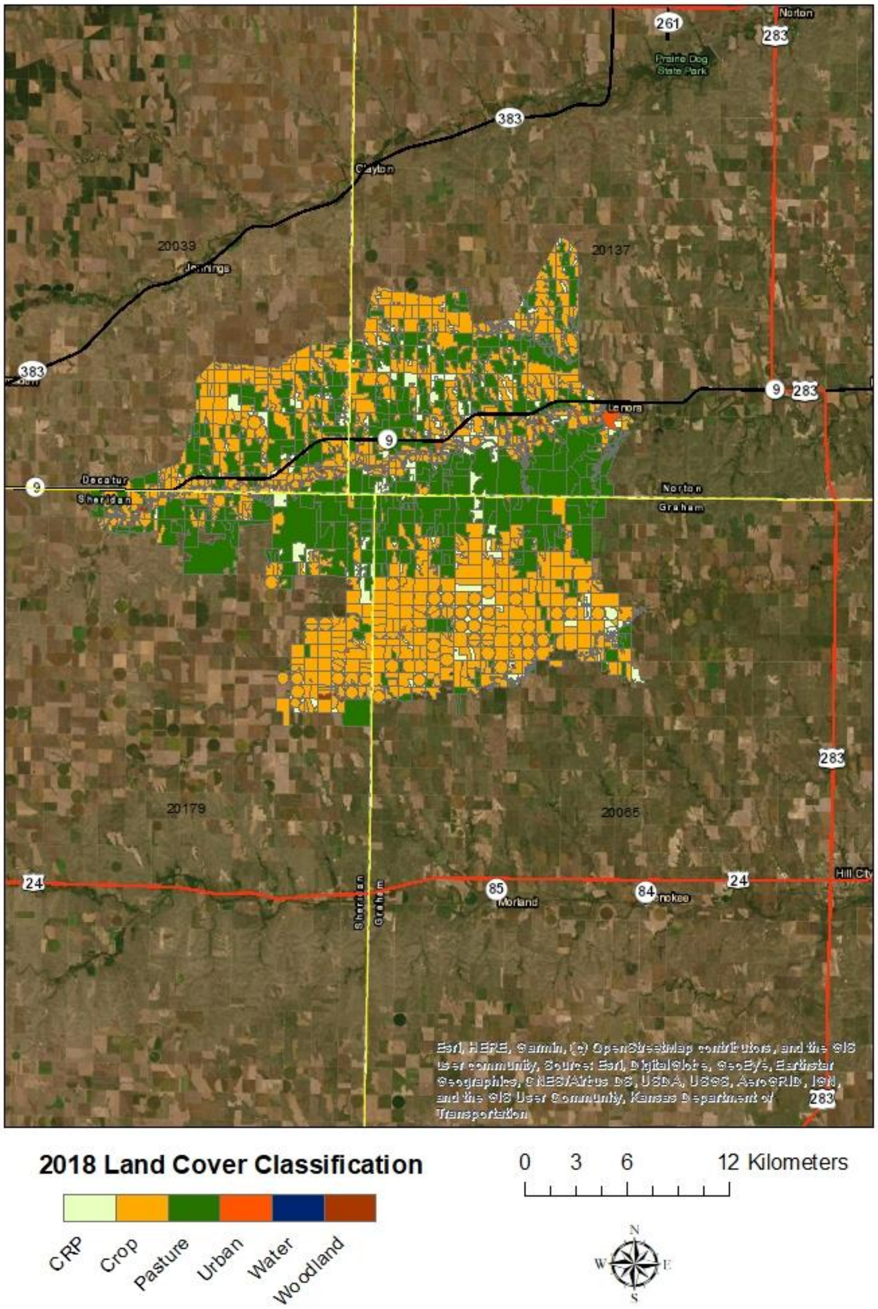

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Figure 2.4. Land cover classifications during 2018 for the North study site (Graham, Norton, Decatur and Sheridan counties) for estimating survival of mule deer and white-tailed deer in western Kansas, USA Land cover classifications included Conservation Reserve Program (CRP), Crop, Pasture, Urban, Water, and Woodland. The primary land cover type was Crop, including corn, milo, and winter wheat, occurring predominantly in the southern portion, and intermixed through the northern half of the site.

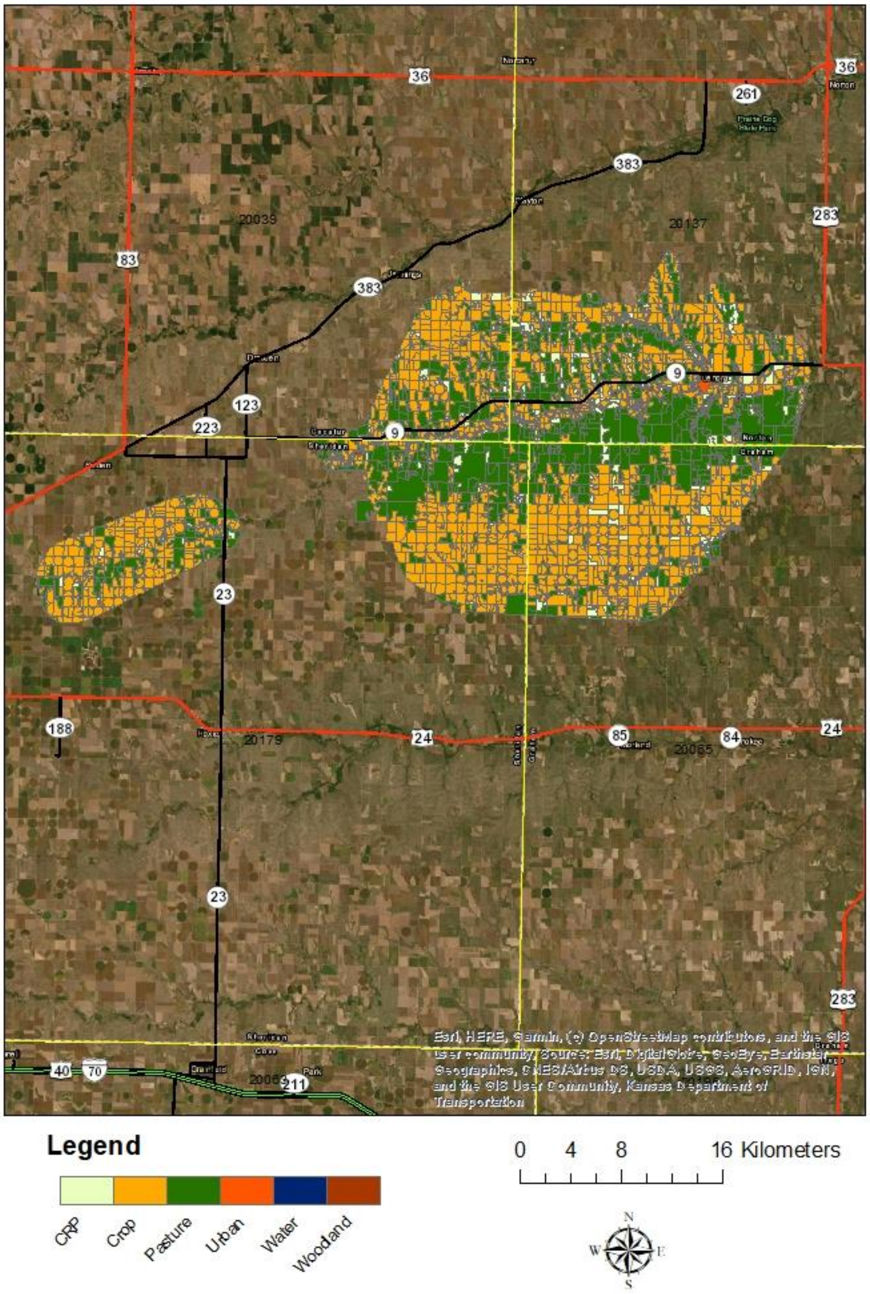

Figure 2.5. Land cover classifications during 2019 for the North study site (Graham, Norton, Decatur and Sheridan counties) for estimating survival of mule deer and white-tailed deer in western Kansas, USA, at a scale greater than other land cover maps to include all deer locations. Land cover classifications included Conservation Reserve Program (CRP), Crop, Pasture, Urban, Water, and Woodland. The primary land cover type was Crop, including corn, milo, and winter wheat, occurring predominantly in the southern portion, and intermixed through the northern half of the site

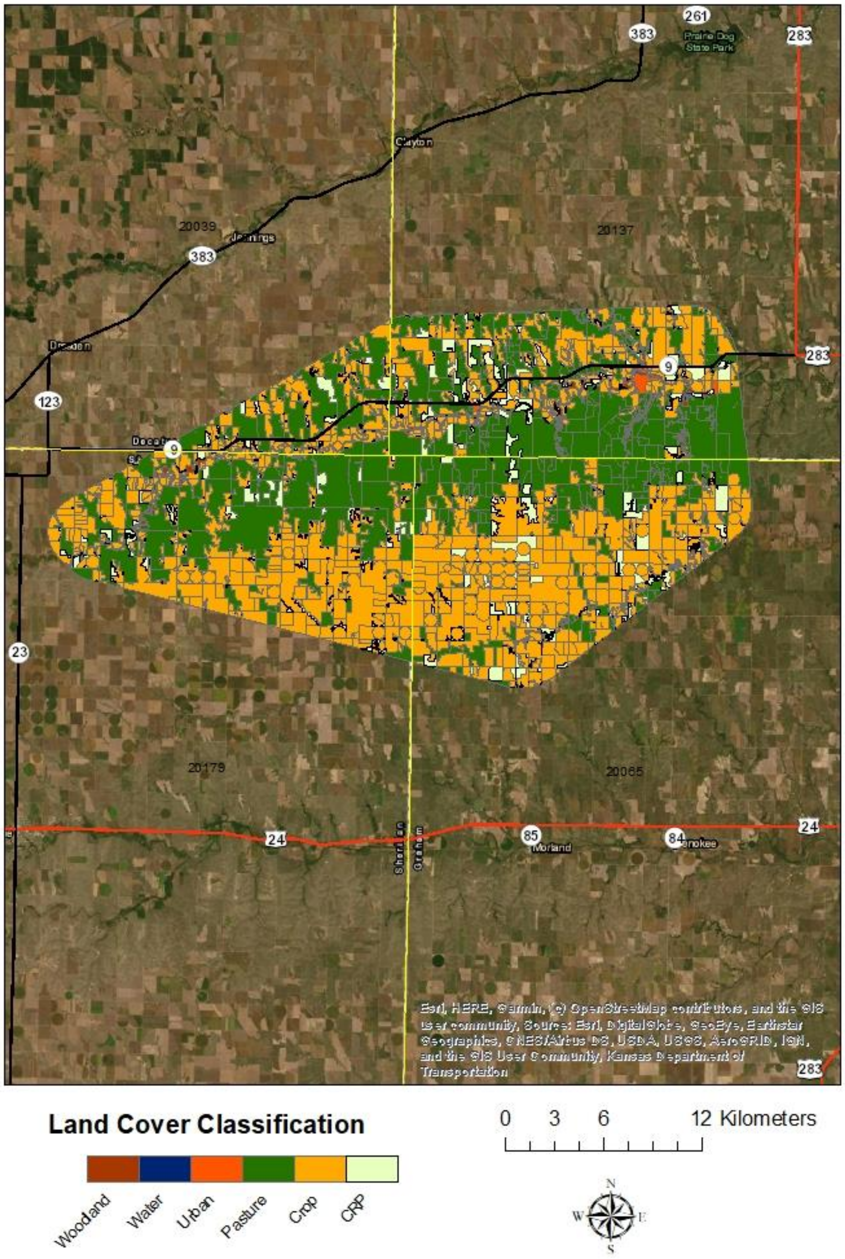

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Figure 2.6. Land cover classifications during 2020 for the North study site (Graham, Norton, Decatur and Sheridan counties) for estimating survival of mule deer and white-tailed deer in western Kansas, USA. Land cover classifications included Conservation Reserve Program (CRP), Crop, Pasture, Urban, Water, and Woodland. The primary land cover type was Crop, including corn, milo, and winter wheat, occurring predominantly in the southern portion, and intermixed through the northern half of the site.

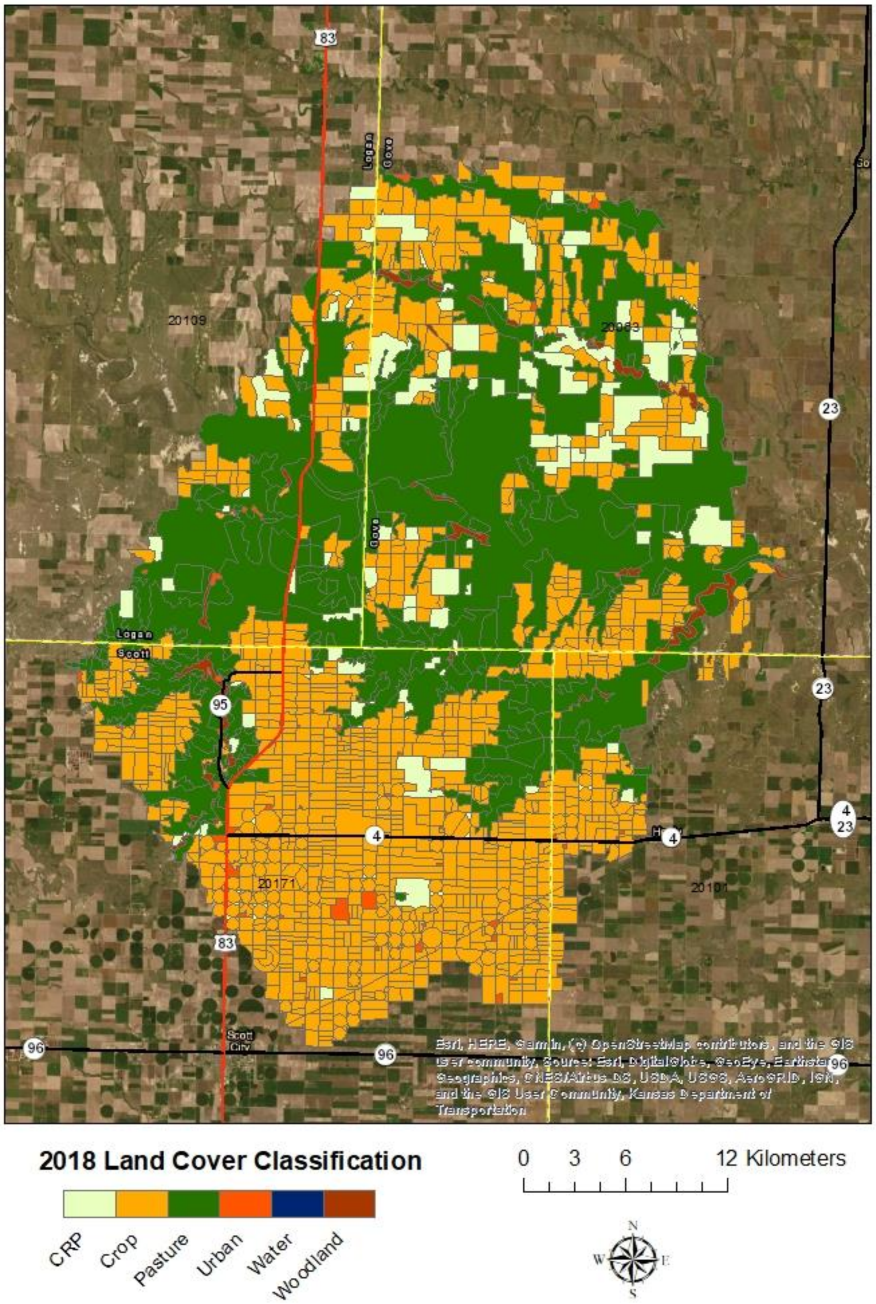

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Figure 2.7. Land cover classifications during 2018 for the South study site (Scott, Gove, Lane and Logan counties) for estimating survival of mule deer and white-tailed deer in western Kansas, USA. Land cover classifications included Conservation Reserve Program (CRP), Crop, Pasture, Urban, Water, and Woodland. The primary land cover type was Crop, which dominated the south half of the study area and was intermixed throughout the rest of the site.

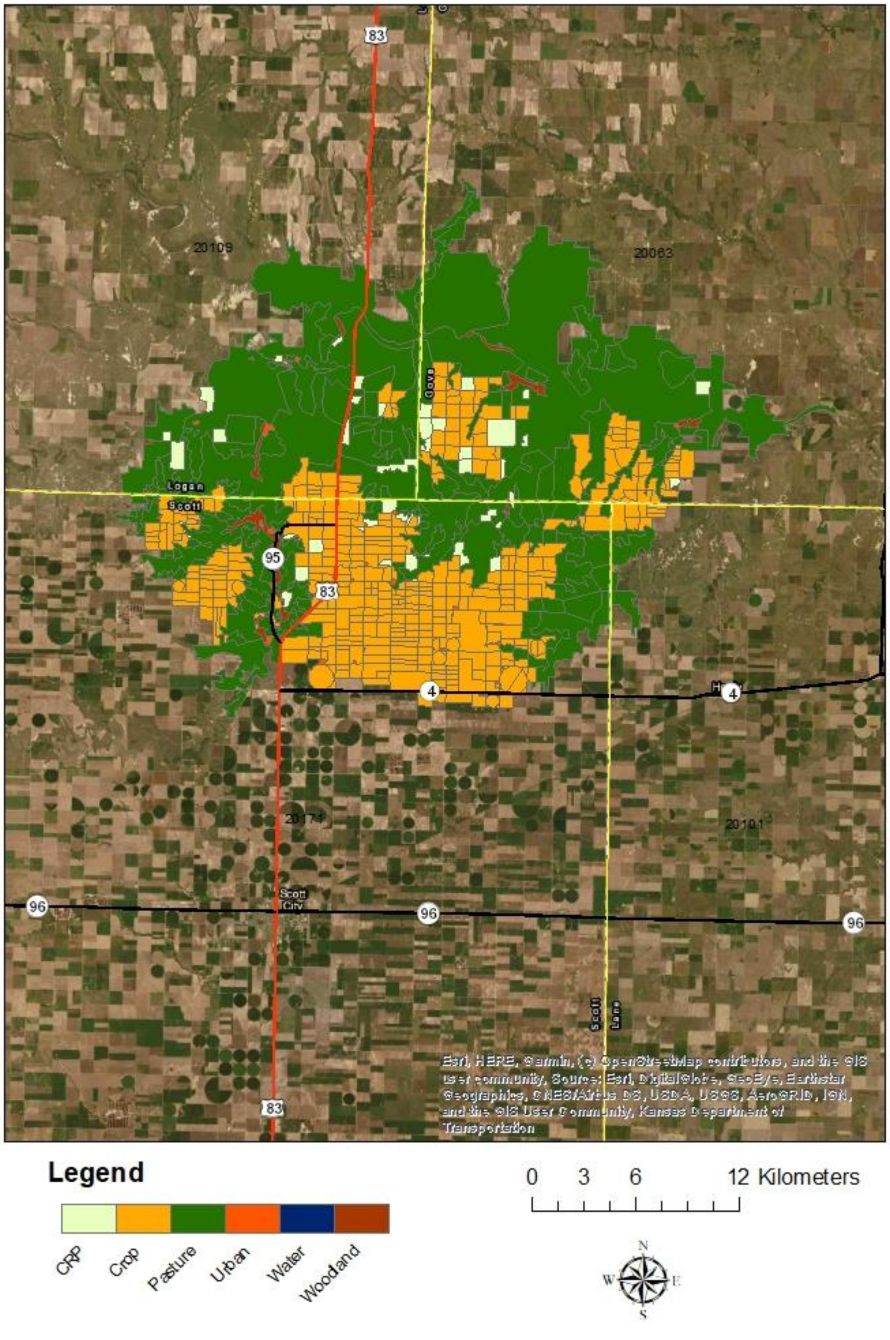

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Figure 2.8. Land cover classifications during 2019 for the South study site (Scott, Gove, Lane and Logan counties) for estimating survival of mule deer and white-tailed deer in western Kansas, USA. Land cover classifications included Conservation Reserve Program (CRP), Crop, Pasture, Urban, Water, and Woodland. The primary land cover type was Crop, which consisted of corn, winter wheat, milo, soybeans, and sunflowers and dominated the south half of the study area, and was blended throughout the rest of the site.

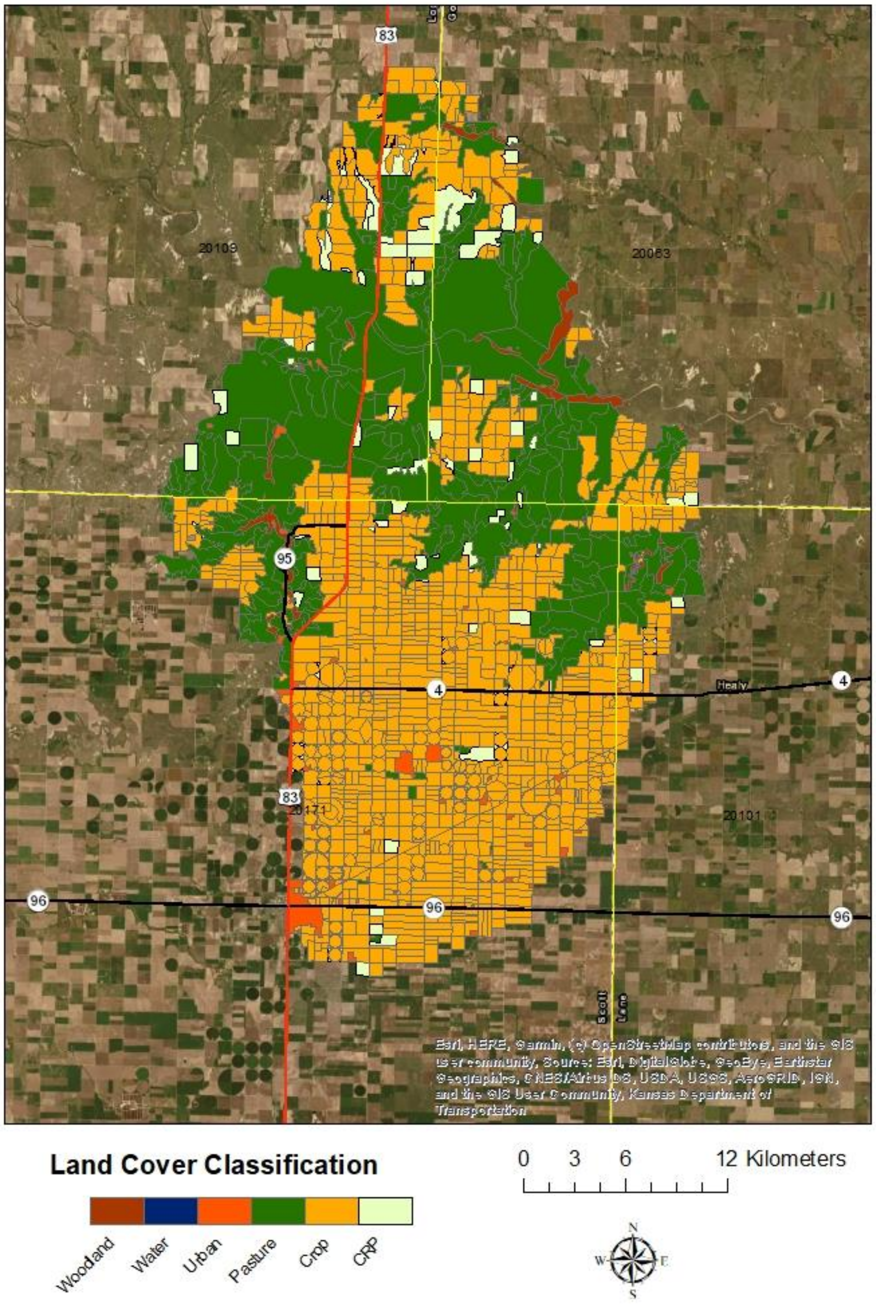

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Figure 2.9. Land cover classifications during 2020 for the South study site (Scott, Gove, Lane and Logan counties) for estimating survival of mule deer and white-tailed deer in western Kansas, USA. Land cover classifications included Conservation Reserve Program (CRP), Crop, Pasture, Urban, Water, and Woodland. The primary land cover type in 2020 was Crop, which occurred primarily throughout the northern tip and southern portion of the site and consisted of corn, winter wheat, milo, soybeans, and sunflowers.

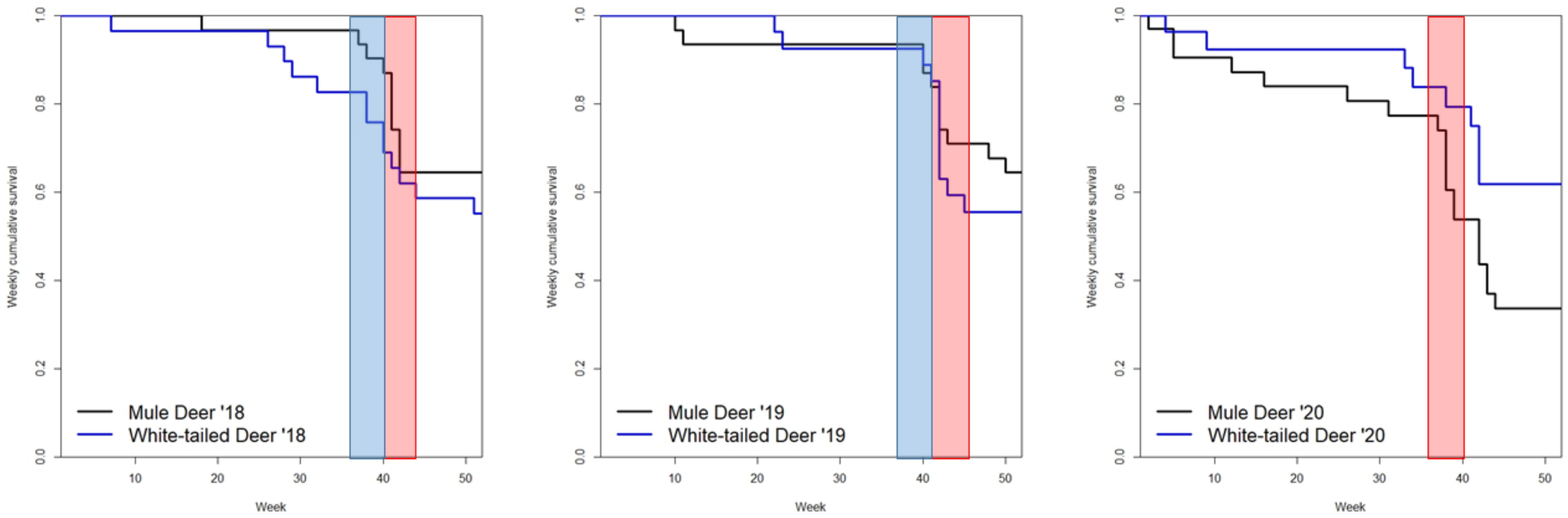


Figure 2.10. Cumulative weekly survival for adult male mule deer and white-tailed deer during 2018, 2019, and 2020. The 12-day firearm (red) occurred during weeks 40-42 in 2018, 42-44 in 2019, and 38-40 in 2020. Rut (blue) took place during weeks ~36-40 in 2018 and ~37-41 during 2019, and had not yet been determined for 2020. Week 1 is the capture date for individual collared deer caught February 15 2018, February 10 2019, and March 5 2020.

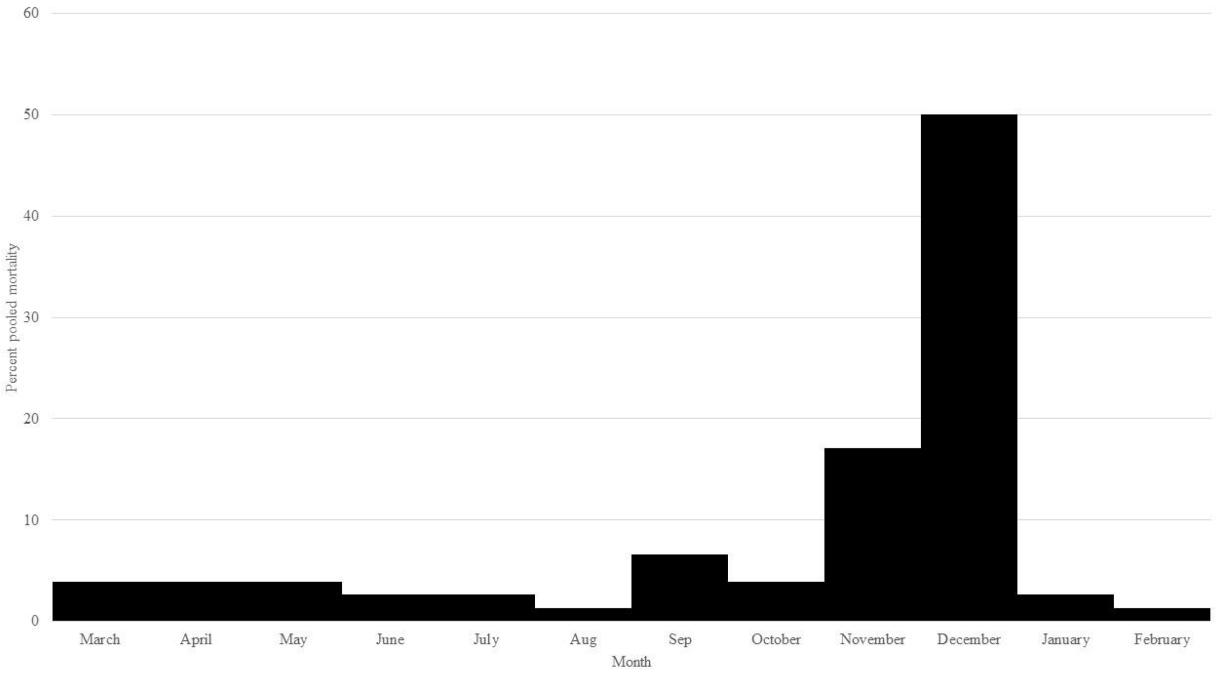


Figure 2.11. Percent of all mortalities including hunter harvest, natural causes, deer vehicle collisions, and unknown causes that occurred throughout the annual cycle during 2018-2020 for mule deer and white-tailed deer in western Kansas, USA.

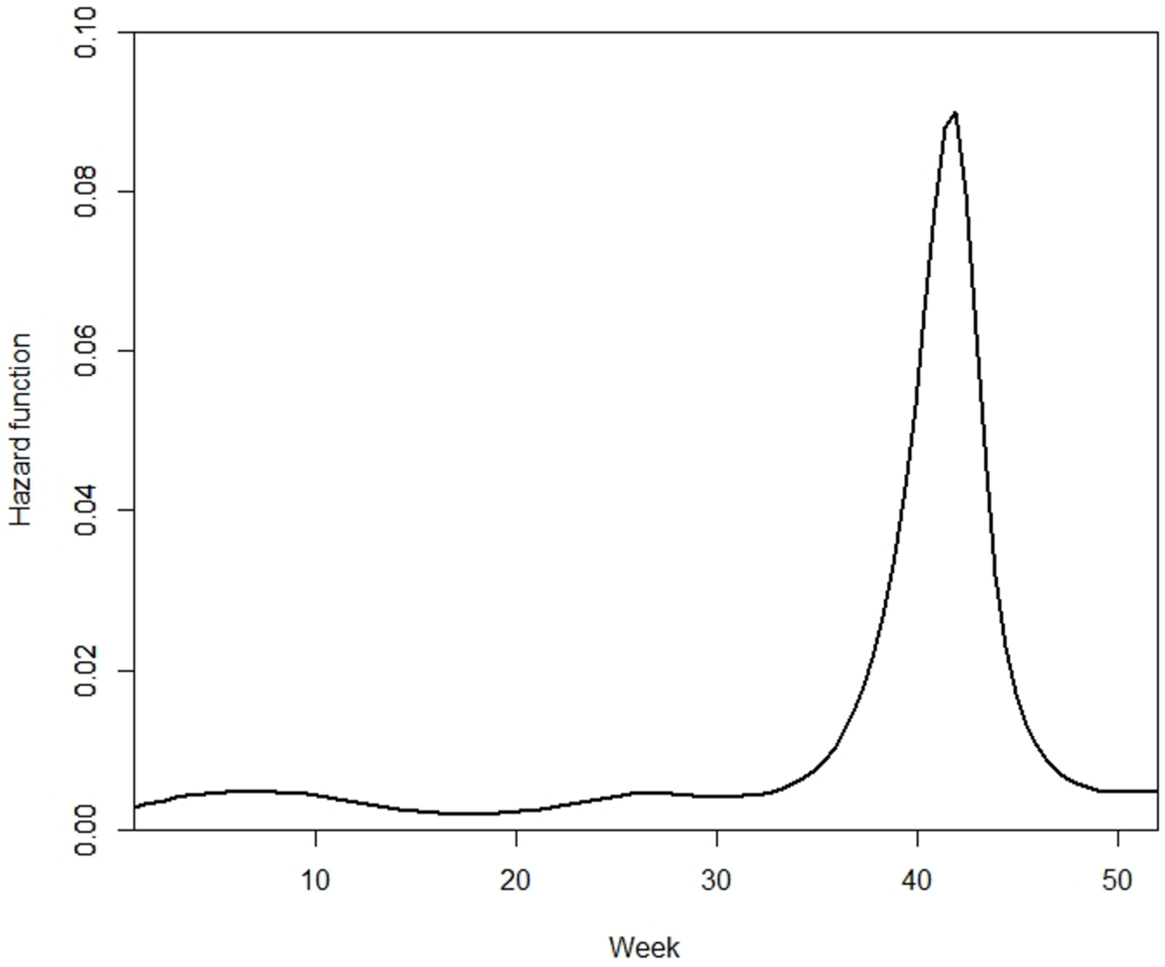


Figure 2.12. Hazard function identifying relative weekly hazard risk for adult male mule deer and white-tailed deer in western Kansas, USA, during 2018 – 2020. Week 1 indicates the week of capture for all collared males. Peak hazard risk of mortality occurred for both species during the firearm hunting season, which occurred in weeks 40-42 in 2018, weeks 42-44 in 2019, and 38-40 in 2020.

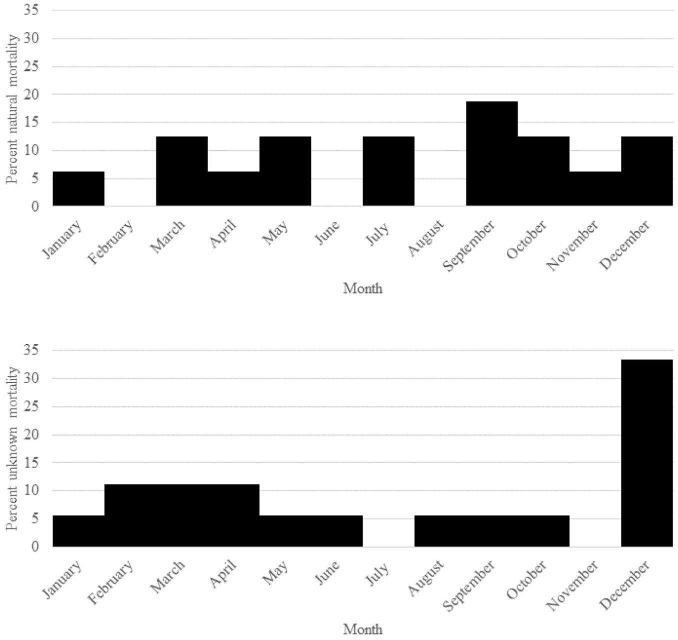
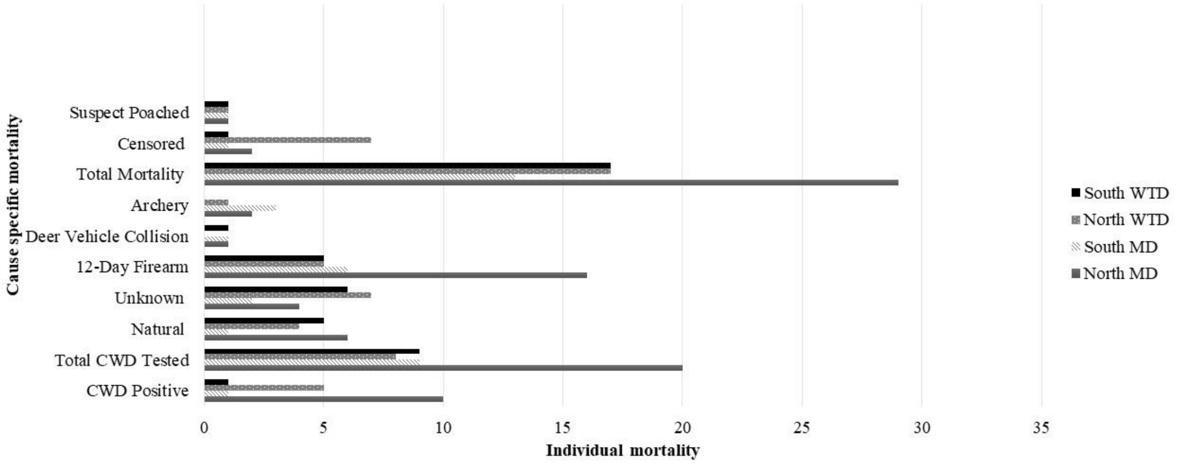


Figure 2.13. Percent natural (top) and unknown (bottom) monthly mortalities throughout the year for both mule deer and white-tailed deer in western Kansas, USA, during 2018 – 2020.



Pooled Mortality 2018-2020	CWD Positive	Total CWD Tested	Natural	Unknown	12-Day Firearm	Deer Vehicle Collision	Archery	Total Mortality	Censored	Suspect Poached
North MD	10	20	6	4	16	1	2	29	2	1
South MD	1	9	1	2	6	1	3	13	1	1
North WTD	5	8	4	7	5	0	1	17	7	1
South WTD	1	9	5	6	5	1	0	17	1	1
Total	**17**	**46**	**16**	**19**	**32**	**3**	**6**	**76**	**11**	**4**

Figure 2.14. Cause-specific mortality, and chronic wasting disease (CWD) results for individual collared male mule deer (MD) and white-tailed deer (WTD) pooled across years (2018, 2019, and 2020) at two study sites: North (Decatur, Graham, Sheridan and Norton counties) and South (Scott, Logan, Lane and Gove counties) study sites in western Kansas, USA.

Table 2.1. Proportion and associated area of land cover types for two study sites (North – Norton, Graham, Decatur, and Sheridan counties and South – Scott, Gove, Logan and Lane counties) where survival of adult male mule deer and white-tailed deer was estimated in western Kansas, USA, during 2018, 2019, and 2020. The North site was dominated by Crop during all years; including corn (*Zea mays*), wheat (*Triticum aestivum*), and milo (*Sorghum bicolor*). The south site land cover composition was also predominately Crop all years. Primarily occurring in the northern portion of the south site. Conservation Reserve Program (CRP) land cover was present in both study sites.

	Land Cover Type					
Study Site & Year	Crop	CRP	Pasture	Urban	Water	Woodland
North 2018	43%	16%	19%	6%	1%	15%
Area (km^2)	243.0	35.0	209.8	3.3	0.129	12.5
North 2019	44%	15%	18%	6%	2%	15%
Area (km^2)	456.8	53.1	322.8	5.2	0.53	19.4
North 2020	39%	23%	16%	4%	4%	14%
Area (km^2)	330.7	53.2	282.5	2.9	0.48	15.6
South 2018	75%	6%	12%	5%	NA	2%
Area (km^2)	621.1	105.6	618.3	9.4	NA	16.2
South 2019	64%	7%	21%	6%	NA	2%
Area (km^2)	202.7	21.1	432.3	2.2	NA	7.0
South 2020	75%	6%	12%	6%	NA	1%
Area (km^2)	543.8	45.3	406.2	13.5	NA	14.8

Table 2.2. Capture totals for mule deer (MD) and white-tailed deer (WTD) at two study sites: North (Norton, Graham, Decatur and Sheridan counties) and South (Scott, Gove, Logan and Lane counties) in western Kansas, USA, during 2018, 2019, and 2020.

Study site/Species	**2018**	**2019**	**2020**	**Total**
North WTD	14	8	7	29
South WTD	16	5	6	27
North MD	16	8	8	32
South MD	14	4	5	23
Total	60	25	26	111

Table 2.3. Average (±SE) capture morphometrics for mule deer (MD) and white-tailed deer (WTD) at two sites: north (N) – Norton, Graham, Decatur and Sheridan and south (S) – Scott, Gove, Logan and Lane counties in western Kansas, USA. Capture morphometrics include mean total body length (TBL), neck girth (Neck), chest girth (Chest) and hind foot length (HF) estimates for both species and study areas in 2018, 2019, and 2020 along with their associated standard errors (SE).

			TBL (cm)	**Neck (cm)**	**Chest (cm)**	**HF (cm)**	***n***
Year	**Site**	**Species**	$\bar{x}$ **± SE**	$\bar{x}$ **± SE**	$\bar{x}$ **± SE**	$\bar{x}$ **± SE**	
2018	S	WTD	207.20±2.22	45.83±0.44	NA	NA	16
2018	N	WTD	206.50±3.06	43.84±0.20	NA	NA	14
2018	S	MD	190.00±3.10	44.57±0.32	NA	NA	14
2018	N	MD	191.53±2.11	43.13±0.87	NA	NA	16
2019	S	WTD	183.30±6.25	48.20±0.33	104.94±2.75	49.87±0.77^{B}	5
2019	N	WTD	174.00±2.72	48.12±0.50	102.43±1.87^{C}	49.18±1.18	8
2019	S	MD	164.50±3.66	49.37±0.32	100.37±0.89	49.25±0.75^{B}	4
2019	N	MD	179.75±3.25	51.06±0.29	106.43±1.03^{C}	51.75±0.73	8
2020	S	WTD	163.16±4.81	47.50±1.72	108.50±1.97	49.33±0.66^{B}	6
2020	N	WTD	180.83±8.97	45.33±2.74	101.83±2.28^{C}	51.00±1.29	7
2020	S	MD	174.75±3.19	57.25±4.15	108.5±1.70	52.5±1.04^{B}	5
2020	N	MD	173.00±4.53	55.00±3.56	110.00±2.70^{C}	50.60±1.22	8

Table 2.4. Comparison of pooled capture measurements (2018-2020) among species-site groups of mule deer (MD) and white-tailed deer (WTD) at two study sites: North (N – Norton, Graham, Decatur and Sheridan counties) and South (S – Scott, Gove, Logan and Lane counties) in western Kansas, USA. Groups consisted of North white-tailed deer (N WTD), South white-tailed deer (S WTD), North mule deer (N MD), and South mule deer (S MD). Capture morphometrics included mean total body length (TBL) (cm), neck girth (cm), chest girth (cm), and hind foot length (HF) (cm) estimates, and associated standard error (SE).

	Group						
	N WTD	**S WTD**	**N MD**	**S MD**	***F***	**DF**	***P***
	$\bar{x}$ **± SE**	$\bar{x}$ **± SE**	$\bar{x}$ **± SE**	$\bar{x}$ **± SE**			
TBL	190.38±3.76$^{A, B}$	192.44±4.17^{A}	183.58±2.20^{B}	182.26±2.96^{B}	4.67	3,175	0.004
Neck	45.58±1.09	46.67±1.01	47.66±1.23	47.85±1.48	0.64	3,175	0.60
Chest	102.10±1.30^{B}	102.14± 1.85^{B}	108.22±1.85^{A}	105.63±1.61$^{A, B}$	5.10	3,175	0.002
HF	49.90±0.82	49.61±0.44	50.88±0.61	50.42±0.62	2.46	3,175	0.06

^{AB}Means followed by the same uppercase superscript do not differ ($P < 0.05$) among groups for each measurement.

Table 2.5. Pooled age classes for collared mule deer (MD) and white-tailed deer (WTD) captured in the north (N: Norton, Graham, Decatur and Sheridan counties) and south (S: Scott, Gove, Logan and Lane counties) study sites in western Kansas, USA, during 2018, 2019, and 2020. No significant differences ($F_{3, 175} =$ 0.10, P =0.96) existed between group (NWTD, SWTD, NMD, and SMD) ages**.** No <1 year old males were included in the analysis.

		Age		
Group	≥3	<3	Unknown	Total
N WTD	13	12	4	29
S WTD	16	8	3	27
N MD	19	10	3	32
S MD	10	11	2	23
Total	58	41	12	111

Table 2.6. Mean body condition score pooled across years and associated standard error for mule deer (MD) and white-tailed deer (WTD) captured at two study sites: North (Norton, Graham, Decatur and Sheridan counties) and South (Scott, Gove, Logan and Lane counties) in western Kansas, USA, during 2018, 2019, and 2020. Mean pooled body conditions recorded at capture ranged from poor (categorized as 3 or 4 on a scale from 1-10) to fair (categorized as 5 or 6 on a scale of 1-10; 10 being highest caliber body score). No significant differences ($F_{3,\ 175} =$ 2.09, P =0.10) were found in body condition between groups (NWTD, SWTD, NMD, and SMD).

Pooled Body Condition Score	**Mean**	**SE**
North WTD	5.34	0.66
South WTD	4.58	0.72
North MD	4.50	0.58
South MD	4.50	0.78

Table 2.7. Cox proportional hazard model selection table for estimation of annual survival for collared deer for male white-tailed deer and mule deer in western Kansas (Norton, Graham, Decatur, Sheridan, Scott, Gove, Lane, and Logan counties), USA, during 2018, 2019, and 2020. Site and year interaction had the lowest Akaike's Information Criterion (AICc) score and was the best fitting model to predict survival based on available capture data from all three years.

Model	**K[a]**	**AICc**	**ΔAICc**	**Deviance**	**AICc *ω***
Site and Year Interaction	5	736.60	0	-363.13	0.38
Site	1	736.78	0.18	-367.38	0.35
Chest	1	739.67	3.07	-368.83	0.08
Age	2	740.40	3.80	-368.17	0.06
Total Body Length	1	740.83	4.23	-369.41	0.05
Neck	1	742.19	5.58	-370.08	0.02
Year	2	742.28	5.67	-369.11	0.02
Hindfoot	1	742.69	6.08	-370.33	0.02
Null	0	742.69	6.08	-371.34	0.02
Species	1	744.55	7.94	-371.26	0.01

[a] K is the number of parameters, AICc is Akaike's Information Criterion, ΔAICc is change of the AICc, and AICc*ω* is the model weight adjusted for small sample sizes

Table 2.8. Annual survival estimates and associated standard errors for pooled years (2018-2020) and individual years, for each site and species (mule deer [MD] and white-tailed deer [WTD]) captured in Norton, Graham, Decatur, Sheridan (North site) and Scott, Gove Lane, and Logan (South site) counties in western Kansas, USA.

	Annual Survival of Adult Male Deer in Western, KS	**Lower 95% CI**	**Upper 95% CI**
All Male Deer 2018-2020	0.56 ± 0.04	0.49	0.64
Site	**Pooled Site Survival Estimate ± SE**	**Lower 95% CI**	**Upper 95% CI**
North	0.45 ± 0.04	0.37	0.54
South	0.66 ± 0.05	0.57	0.76
Site and Year	**Annual Site Survival ± SE**	**Lower 95% CI**	**Upper 95% CI**
North ‘18	0.50 ± 0.09	0.35	0.72
South ‘18	0.70 ± 0.08	0.55	0.89
North ‘19	0.55 ± 0.09	0.40	0.77
South ‘19	0.66 ± 0.08	0.50	0.85
North ‘20	0.26 ± 0.09	0.13	0.52
South ‘20	0.62 ± 0.09	0.47	0.83
Species	**Pooled Annual Species Survival ± SE**	**Lower 95% CI**	**Upper 95% CI**
MD	0.54 ± 0.05	0.45	0.64
WTD	0.58 ± 0.05	0.49	0.69
Species and Year	**Yearly Species Survival ± SE**	**Lower 95% CI**	**Upper 95% CI**
WTD 2018	0.55 ± 0.09	0.40	0.77
MD 2018	0.65 ± 0.09	0.50	0.84
WTD 2019	0.56 ± 0.09	0.39	0.78
MD 2019	0.65 ±0.09	0.50	0.84
WTD 2020	0.62 ± 0.10	0.45	0.86
MD 2020	0.34 ± 0.09	0.20	0.56
Age Class	**Age-Class Survival Estimate**	**95% Lower CI**	**95% Upper CI**
≥ 3 years	0.48 ± 0.05	0.40	0.58

< 3 years	0.71 ± 0.07	0.58	0.85
Unknown	0.61 ± 0.06	0.50	0.74

Chapter 3 - Temporal Movement and Home Range Patterns of Adult Male Mule Deer and White-tailed Deer in Western Kansas

Movement patterns of sympatric white-tailed deer (*Odocoileus virginianus*) and mule deer (*O. hemionus)* populations across the western Great Plains indicate a shift away from their historical occupied range by mule deer and expansion into previously unoccupied range by white-tailed deer (Wallmo 1981, Ballard et al. 2001, Shallow et al. 2015). There is a concern for mule deer populations, which are declining throughout the Great Plains. Mule deer populations are becoming increasingly constrained, and the presence and expanding overlap with white-tailed deer populations may be influencing mule deer decline. In the western Great Plains, movement patterns of sympatric populations are unknown and considered a potential factor influencing landscape occupancy, space use, and habitat selection by both species to the point that movements by white-tailed deer may be contributing to the constriction of mule deer population growth and declining abundance in the region that includes western Kansas, USA. There is a need to understand spatio-temporal movement and home-range patterns between declining mule deer populations and encroaching and expanding white-tailed deer population to inform management strategies (Martinka 1968, Van der Hoek et al. 2002). Knowledge of species home-range area and movements during vulnerable temporal periods for adult male deer, such as during rut and hunting seasons, can help pinpoint susceptible time periods and areas for interactions between white-tailed deer and mule deer populations. Such identification may aid in strategically developing management strategies, including timing of harvest, for adult male mule deer in western Kansas.

Movement rates and home range area can provide explanatory insight into potential limiting factors regulating deer populations. An adult male deer's home range indicates its position in the social hierarchy among other conspecific male deer, and is a reflection of its available resources (e.g., females in estrus during rut, and the quality of available food resources). Deer with access to high quality resources that are plentiful and adequately distributed tend to have smaller home ranges than deer in lower quality areas (Marchinton and Hirth 1984). A deer may travel outside its normal home range or expand its core use area if its immediate needs for survival and reproductive success are not being met. If there is sufficient available food within an animal's home range, then perhaps space or some other resource is limiting population growth. Similarly, deer movements can provide clues to factors regulating demography and population dynamics. Movements and home range area are mediated by stimuli such as hunting pressure (Hygnstrom et al. 2011; Little et al. 2014, 2016; Marantz et al. 2016), rut (Nelson and Mech 1981, Marchinton and Hirth 1984, Beier and McCullough 1990, Tomberlin 2007), and weather conditions (Kernohan et al. 1994). Movements within home ranges are motivated by food or resource availability, location of predators and conspecifics, and landscape heterogeneity and configuration, which influences resource selection (Nelson 1998: Sabine et al. 2002, Phillips et al. 2004, Long et al. 2005, Webb et al. 2009).

Understanding the complexities of deer movements during differing temporal periods can have meaningful implications for management (Rhoads et al. 2013, Little et al. 2014). If hunter observation data are used to help set harvest limits, altered deer movement behavior in which deer change movement patterns to avoid hunters can affect hunter encounter rates, hunter success and cause an over or under estimation of population abundance (Little et al. 2014, Foley et al. 2015, Simoneaux et al. 2016). Misunderstanding temporal movement trends, and over- or under-estimating the species population abundance and distribution may lead to unsuccessful management, and dissatisfied hunters, as well as provide public safety concerns related to deer vehicle collisions (DVCs; Grovenburg et al. 2008) and disease transmission (Walter et al. 2011a).

Many studies focus on how hunting influences movements of female or young male white-tailed deer in the Great Plains, but there is a paucity of information surrounding non-migratory mature males in sympatric populations (Sparrowe and Springer 1970, Grovenburg et al. 2009, Hygnstrom et al. 2011). Harvest seasons have been shown to have mixed effects on deer movement. Sparrowe and Springer (1970) suggested that hunter harvest was the strongest predictor of deer movement regarding male yearling and fawn white-tailed deer in South Dakota, USA. Free ranging white-tailed deer perceive humans as a possible threat or predator and several studies have shown that deer movement is affected by hunter presence (e.g., DeYoung and Miller 2011). Simoneaux et al. (2016) showed deer movements peaked during rut, and hunted adult males moved more than non-hunted males in Louisiana, USA. Little et al. (2014) found that white-tailed deer altered movement to avoid hunters in Oklahoma, USA, during rifle season. Little et al. (2016) reported that hunted adult male white-tailed deer moved faster than adult males who were not hunted, but all deer, including the control non-hunted population decreased total movement over time within the firearm-hunting season in Oklahoma, indicating that all deer perceived a threat on the landscape.

In addition to factors such as landscape composition (Walter et al. 2009), urban sprawl (Walter et al. 2011b), and disturbance (Stephenson 1996), home range area is also shaped by hunting pressure. Marantz et al. (2016) calculated two-day interval micro-ranges for adult male white-tailed deer in south-central Oklahoma, USA. The greatest decrease in micro-range area occurred during the 16-day hunting season. Adult male mule deer in southeastern Colorado, USA, had significantly larger home ranges in the fall compared to the rest of the year, and males in military-related maneuver sectors had larger core ranges (50% harmonic mean transformation [HMT]) than those not exposed to military disturbances (Stephenson et al. 1996). Although military training differs from hunting pressure, males did respond to disturbance by increasing their core use area. The influence of hunting on deer home range area varied by the form of hunting for female white-tailed deer in an overabundant population in Nebraska, USA. Deer were affected little by archery season, but increased home range area 88%-97% during muzzleloader season (Hygnstrom et al. 2011).

Just as harvest exerts an anthropogenic pressure on deer movement, deer are also motivated to alter movements and home ranges based on environmental cues and biological stimuli. Movements by male deer are affected by temporal periods such as season and daily periods (Sparrowe and Springer 1970, Walter et al. 2011b, Simoneaux et al. 2016); but most importantly by the onset of rut (Ozoga and Verme 1985, Foley et al. 2015, Simoneaux et al. 2016). Rut is catalyzed by physiological and behavioral changes a deer undergoes leading up to breeding (Wallmo 1981). Onset of rut is initiated by photoperiod oscillation (Goss 1983), a hormonal shift that leads to a surge in activity, elevated aggression levels, biological cues received from conspecifics, and a marked decrease in food intake as males function as capital breeders during rut and subsequent breeding (Drent and Daan 1908, Houston et al. 2007). It is imprecise to align rut with solely the act of successful mating, as males and females do not share similar breeding duration or capabilities. During the courting phase of rut, bachelor groups dissipate and adult males increase solitary movements and home range area to seek out estrous does, with their greatest movements occurring during the breeding phase of rut, followed by a decrease in movements at the end of rut (Beier and McCullough 1990, Marchinton and Hirth 1984, Tomberlin 2007). Some males may increase their home range area before or during rut, while others may create a fall home range separate from their summer range (Nelson and Mech 1981, Beier and McCullough 1990, Tomberlin 2007). Males rely on energy stored prior to rut (Wallmos 1981, DeYoung 1989, Ditchkoff et al. 2001), and may lose up to 30% of their body mass while engaging in rutting activities (DeYoung 1989, Ditchkoff et al. 2001), which increases their susceptibility to carryover effects following rut (Harrison et al. 2011). This can result in a weakened body condition, and deer that engaged in rutting activities may become more predisposed to natural forms of mortality (Clutton-Brock et al. 1982, Ditchkoff et al. 2001).

The goal of my study was to test for differences in home range and core use areas between species and sites during annual, rut, and 12-day firearm periods. Additionally, I compared total daily and bi-hourly movements between mule deer and white-tailed deer at two study sites in western Kansas, within annual, rut, and 12-day firearm periods. I also compared bi-hourly and total daily distances among seasons to identify seasonal differences in movements. I hypothesized mule deer and white-tailed deer would exhibit differing trends in the area of their home ranges during rut and 12-day firearm because of the current population trajectory of mule deer; I expected mule deer to have significantly smaller home ranges during rut than white-tailed deer; indicating a reduced effort in their attempts to secure breeding opportunities due to low density of females. Furthermore, I hypothesized mule deer would have larger home ranges than white-tailed deer during the 12-day firearm season due to their differing fight or flight responses which stem from their distinct evolutionary escape strategies (Geist 1981). I expected mean total daily and bi-hourly movement rates, and home ranges to increase during the breeding season (i.e., rut; Ozoga and Verme 1985, Foley et al. 2015, Simoneaux et al. 2016). Additionally, I expected movements and ranges to decrease during the 12-day firearm seasons during which deer may perceive a threat on the landscape (Little et al. 2016, Marantz et al. 2016).

Study Area

I conducted this study at two sites located ~130 km apart in the western third of Kansas during 2018, 2019, and 2020; both sites were composed of private land (Fig. 2.1). The north site (~850 km^2) was in Graham, Norton, Sheridan, and Decatur counties (Fig. 2.2). The south site (~1,370 km^2) was in Scott, Logan, Gove, and Lane counties (Fig. 2.3). Both sites were located in the Central Great Plains and High Plains level III ecoregions (U.S. Environmental Protection Agency [EPA] 2000). Of the eleven physiographic regions in Kansas, all counties included in both study sites were located in the High Plains region; Norton, Graham, Gove, Lane, and Logan counties are also part of the Smoky Hills physiological region (USDA NRCS https://www.nrcs.usda.gov/wps/portal/nrcs/detail/ks/about/?cid=nrcs142p2_033475> Accessed 4/4/21). Elevation in the north site was 666.9 m. Average annual temperatures were 11.89° C, 11.60° C, and 12.82° C during 2018, 2019, and 2020 respectively. Long-term average annual temperature from 2000-2020 was 12.37° C. Total annual precipitation was relatively wet in 2018 (921.25 mm), and in 2019 (744.73 mm), with drought like conditions in 2020 (369.40 mm) compared to the previous 20 years in which average annual precipitation was 545.32 mm ± 36.58 in the north site (Hill City Municipal Airport, KS, USA; National Oceanic and Atmospheric [NOAA] 2020). Elevation in the south site was 906.5 m. Average annual temperatures were 11.72° C, 11.13° C, and 12.38° C during 2018, 2019, and 2020, respectively. Long-term annual temperatures from 2000-2020 was 12.02° C at the south site. Total annual precipitation was 666.49 mm, 526.54 mm, and 360.9 mm in 2018, 2019, and 2020, respectively; conditions were dry during 2020 compared to the previous 20 years (2000-2020) when total precipitation averaged 499.45 mm ± 23.22 per year for the south site (Scott City, KS, USA; NOAA 2020).

Both study sites were a matrix of cropland and grassland, composed of short- and mixed-grass prairie (U.S. Environmental Protection Agency 2000). The defining difference between both study areas was the presence of the North Fork Solomon River in the north site, which crossed the study area and included floodplain woodlands along riparian areas (Figs. 2.4, 2.5, and 2.6). Most of the south site was east of U.S. Highway 83 and north of State Highway 4 (Figs. 2.7, 2.8, and 2.9). The south site included more draws and elevated "chalk rock" areas relative to the north site.

Available, ground-truthed land cover patch area and distribution were calculated annually by encompassing a 2-km buffer around a 100% minimum convex polygon of the distribution of all deer locations. The north study site included 504 km^2, 857 km^2, and 685 km^2 in 2018, 2019, and 2020, respectively. The south study site encompassed 1,371 km^2, 665 km^2, and 1,023 km^2 in 2018, 2019, and 2020, respectively.

Cover types were defined as Crop, U.S. Department of Agriculture Conservation Reserve Program (CRP), Pasture (i.e., grazed native grassland), Urban (small towns, outbuildings, cemeteries, and other man-made structures), Water, and Woodland (ranging among small pockets of forest, riparian areas, and shelterbelts; Table 2.1). Relative proportion of land cover types varied slightly among years (Table 2.1). However, Crop was the most common land cover type during each year in the north site, with its distribution surrounding Pasture centrally located in the study site (Figs. 2.4, 2.5. and 2.6). Similarly in the south study site, Crop comprised the largest proportion of cover types during all years, with Pasture comprising the second most common land cover type (Figs. 2.7, 2.8, and 2.9).

Corn (*Zea mays*), wheat (*Triticum aestivum*), and milo (*Sorghum bicolor*) dominated agricultural crops (U.S. EPA 2000). Other less abundant crops included annual sunflower (*Helianthus annuus*), alfalfa (*Medicago sativa*), and soybeans (*Glycine max*). Pasture was typically composed of shorter, grazed, native mixed-grass prairie. Prevalent grasses in the mixed-grass prairie included little bluestem (*Schizachyrium scoparium*), sideoats grama (*Bouteloua curtipendula*) and blue grama (*B. gracilis*). Tall thistle (*Cirsium altissimum*), broom snakeweed (*Gutierrezia sarothrae*), Nuttall's sensitive-briar (*Mimosa nuttallii*), and Indian blanket (*Gaillardia pulchella*) were typical forbs, and widespread succulents included yucca (*Yucca glauca*) and prickly pear cactus (*Opuntia macrorhiza*). Tracts of CRP included tallgrass prairie species; big bluestem (*Andropogon gerardi*), Indiangrass (*Sorghastrum nutans*), and switchgrass (*Panicum virgatum*) intermixed with forbs such as white prairie clover *(Dalea candida*), Maximillian sunflower (*Helianthus maximiliani*), purple prairie clover (*Dalea purpurea*), and Illinois bundleflower (*Desmanthus illinoensis*; United States Department of Agriculture [USDA], Natural Resources Conservation Service [NRCS] 2020). Woodlands were composed primarily of shelterbelts, small groups of clumped trees intermittently strewn throughout pastures and the large riparian area in the north site. Prevailing tree species included American elm (*Ulmus americana*), box elder (*Acer negundo*), green ash (*Fraxinus pennsylvanica*), hackberry (*Celtis occidentalis*), black cherry (*Prunus serotina*), eastern cottonwood (*Populus deltoides*), honey locust (*Gleditsia triacanthos*), black locust (*Robinia pseudoacacia*), mulberry (*Morus rubra*), black walnut (*Juglans nigra*), and eastern red cedar (*Juniperus virginiana*). Plum thickets (*Prunus angustifolia*) and smooth sumac (*Rhus glabra*) were common shrubs in both study sites (USDA, NRCS 2020). Taxonomic authorities were from the Kansas wildlflowers and grasses webpage (www.kswildflower.org) and the Kansas Native Plant Society webpage (www.kansasnativeplantsociety).

Methods

Capture

Adult male capture occurred during February 2018 and 2019 using a commercial helicopter crew (Quicksilver Air Inc., Colorado Springs, CO, USA). They captured and GPS-collared 60 adult male mule deer and white-tailed deer at capture site in 2018, divided evenly between species and two study sites in western Kansas (i.e., 15 individuals/species/site). Thereafter, in 2019 only replacements for the number of male deer that died during the previous year were captured to maintain a sample size of 60 at the start of each field season (i.e., March). The capture crew aerially net gunned, hobbled, and blindfolded captured animals prior to transporting them to a central processing location located at each study site in 2019 (Northrup et al. 2014). No deer were captured ≥8.05 km from the processing location (with the majority being released ≤5 km from capture) to reduce capture myopathy. Restraint from time of capture to release was ≤30 minutes. All captured animals were subjected to a physical exam by on-site veterinarians. For handling safety and control of stressed individuals, males may have been administered chemical sedation in the combined form of Azaperone, Midazolam, and Butorphanol (each drug compound 50 mg/ml, volume of each 0.3 cc with Azaperone and Butorphanol in 1 syringe, and Midazolam in the other; IM; Wolfe and Miller 2016). Animals were released at the processing site as previous capture efforts found that animals rapidly returned to capture locations (W. Conway, Texas Tech University, pers. comm.). All deer were captured and handled according to guidelines approved by the American Society of Mammalogists (Sikes et al. 2016), under the Institutional Animal Care and Use Committee at Kansas State University (protocol #3963), and authorized under the Kansas Wildlife, Parks, and Tourism scientific permits (SC-024-2018, SC-015-2019, SC-032-2020).

Standard numbered livestock ear tags with contact information were applied to each captured deer using conventional equipment and procedures for identification of individuals. Each deer was fitted with a Vertex Plus-2 collar (Vectronics, Berlin, Germany), which contained a very-high-frequency (VHF) beacon, mortality sensor, temperature sensor, 3-axis activity sensor, Iridium Bi-directional option, and a Vectronic timer-controlled drop-off initiated at deployment. Expandable elastic collar inserts were used to account for neck swelling during rut. Each collar was programmed to take a GPS positional fix every two hours, with 12 locations per Iridium message for up to three years (160 weeks). During the 12-day firearm hunting season in late November-early December, all collars recorded a GPS fix 48 times a day (i.e., every half hour). Location and mortality data were obtained remotely with activity data stored on board, location error was estimated to be ~5 m.

Movement

I used GPS Plus X (v.10.4.8, Vectronic) software to remotely monitor male locations and associated movements throughout the annual, rut, and 12-day firearm periods. All legally harvested males during archery and 12-day firearm seasons were directly reported by hunters. Archery seasons took place from 09-17-18 to 12-31-18, and 09-16-19 to 12-31-19. The 12-day firearm seasons were 11-28-18 to 12-9-18, and 12-4-19 to 12-15-19.

Bi-hourly movement (m/2h) was derived as the distance between individual successive locations (distance between each set of fixes) for individual males. Daily movement (m) was determined by calculating sum of the distances between successive bi-hourly locations traveled by an individual deer in 24 hours.

To assess the potential effect of rut on total daily movement and bi-hourly movement, I defined annual rut periods for each species based on spikes in mean weekly bi-hourly movement rate and mean total sum of movement activity by week across the annual cycle for deer captured in 2018 and 2019. I used these derived time periods to determine home range and core use area sizes during rut. Rut occurred during similar weeks both years for each species and site. Rut occurred for mule deer during 11-05-18 to 11-25-18, 11-04-19 to 11-24-19 and 10-29-18 to 11-18-18, 10-28-2019 to 11-16-2019 at the north and south site, respectively. Rut occurred for white-tailed deer during 11-05-18 to 11-25-18, 11-04-19 to 11-24-19 and 10-29-18 to 11-25-18, 10-28-19 to 11-24-19 at the north and south site, respectively.

Analyses

I analyzed the influence of hunting pressure (12-day firearm period) and rut on home range area, relative to the rest of the year, as predictors of home range and core use area size for both species and sites. I used a two-way multivariate analysis of variance (MANOVA) to simultaneously test the effects of study site, species, and subsequent interaction between study site and species on 50% core use and 95% home range areas within the annual, rut, and 12-day firearm season periods. The symbol V(s) was used as the test statistic to denote Pillai-Barlett trace (V = tr (HT-1) in all MANOVA analyses (Pillai 1955, Muller 1998). Then I used a two-factor analysis of variance (ANOVA) to test univariate effects of the categorical variables on 50% core use and 95% home range areas following detection of significant MANOVA differences ($\alpha = 0.05$). All analyses were conducted in R (version 3.6.1, R Core Team 2020).

I analyzed the influence of hunting pressure (12-day firearm period) and rut as predictors of deer movement (bi-hourly and daily movement sum) for all groups (north mule deer [NMD], north white-tailed deer [NWTD], south mule deer [SMD] and south white-tailed deer [SWTD]). A one-way MANOVA was used to test for differences in total daily distance and bi-hourly movement distances among groups within the annual, rut, and 12-day firearm season periods.

Following a significant MANOVA ($P < 0.05$), I used an ANOVA (Zar 1996; $\alpha = 0.05$) to test for differences among groups for each response variable (total daily movement and bi-hourly movement). Lastly, I used Tukey HSD tests for pair-wise comparison of group factors following significant ($P < 0.05$) ANOVA results.

To evaluate general patterns in male deer movements, I used a one-way MANOVA to test for differences (total daily movement and bi-hourly movement as response variables) among different time periods (annual, rut, and 12-day firearm) comparing deer movements and space use among time periods regardless of species or site. Following a significant MANOVA ($P < 0.05$), I used a one-way ANOVA to test each single variable for differences among time periods. Finally, I used a Tukey HSD test to test for differences among time periods (annual, rut, and 12-day firearm season) following a significant ($P < 0.05$) ANOVA.

Results

The interaction between site and species was not significant ($F_{1, 107} = 0.55$, $P = 0.58$, V(s) = 0.01) for home range (95%) or core use area (50%) space use during the annual season. However, measures of space use (95% home range and 50% core use areas) differed between species ($F_{1, 107} = 3.84$, $P < 0.02$, V(s) = 0.07) and site ($F_{1, 107} = 25.71$, $P < 0.001$, V(s) = 0.33) during the annual season (Tables 3.1, 3.2). Annually, mule deer had larger home ranges and core use areas than white-tailed deer and deer in the south site had larger home ranges and core use areas than deer in the north site (Tables 3.1, 3.2). Within the rut season, there was not a significant effect for the interaction between site and species ($F_{1, 92} = 2.35$, $P = 0.10$, V (s) = 0.05), or a significant effect of species ($F_{1, 92} = 0.39$, $P = 0.68$, V (s) = 0.01). However, site was an effect on the combined dependent variables; 95% home range extent and 50% core use area

($F_{1, 92}$ = 10.0, $P < 0.001$, V (s) = 0.18). Both the home range and core use areas were larger in the south site compared to the north site during rut. None of the independent variables tested during 12-day firearm including: the interaction of site and species ($F_{1, 78}$ = 1.26, P = 0.29, V(s) = 0.03), species ($F_{1, 78}$ = 0.52, P = 0.60, V(s) = 0.01), or site ($F_{1, 78}$ = 2.71, P = 0.07, V(s) = 0.07) yielded any significant differences for home range or core use areas. Although white-tailed deer had larger home ranges and core areas than mule deer, and south deer had larger ranges than north deer during the firearm seasons, neither comparison between species or sites was statistically different (Tables 3.1, 3.2).

Movements differed ($F_{3, 412209}$ = 3743.6, $P < 0.001$, V (s) = 0.05) among groups within the annual season (Tables 3.3, 3.4). Bi-hourly movement and total daily distances differed among groups (Table 3.3, 3.4). White-tailed deer in the north had the slowest bi-hourly and least total annual movement out of all groups, while white-tailed deer in the south had the fastest bi-hourly speeds and greatest total daily movements. Both groups in the north study site had slower bi-hourly movements and shorter daily movements than groups in the south study site (Tables 3.3, 3.4).

Bi-hourly and total daily movement differed among groups during rut ($F_{3, 25469}$ = 103.01, $P < 0.001$, V (s) = 0.02; Tables 3.3, 3.4). Bi-hourly movement differed between north and south groups, and also differed between species in the north site. However, bi-hourly movement did not differ between south white-tailed deer and south mule deer (Table 3.3). All groups differed in total daily distance during rut (Table 3.4). During rut, north mule deer had the slowest bi-hourly movement and least amount of total daily movement; white-tailed deer in the south had the fastest bi-hourly movement and greatest amount of total daily movement (Table 3.3, 3.4). South groups had faster bi-hourly movements and greater total daily distances than north groups during rut. (Tables 3.3, 3.4).

Within the 12-day firearm season period, bi-hourly movement and total daily movement differed among groups ($F_{3,\,11765}$, = 115.50, $P < 0.001$, V (s) = 0.06; Tables 3.3, 3.4). Again, north group bi-hourly movement differed from south groups and bi-hourly movement differed between species in the north site. However, there were no differences between mule deer and white-tailed deer bi-hourly movement in the south site (Table 3.3). All 4 groups differed in terms of their total daily distance during the 12-day firearm season (Table 3.4). During 12-day firearm season, mule deer groups had the slowest bi-hourly movements, as well as the shortest daily movements compared to white-tailed deer groups; north mule deer having the slowest bi-hourly movements and shortest total daily movements of all four groups (Tables 3.3, 3.4). Though, unlike in the other time periods (annual and rut), north white-tailed deer had the fastest bi-hourly movement, and the greatest total daily movements of the 4 groups rather than south white-tailed deer. (Tables 3.3, 3.4).

Bi-hourly movement ($F_{2,\,449452} = 3692.7$, $P < 0.001$) and total daily movement ($F_{2,\,449452} = 19244$, $P < 0.001$) differed among time periods (annual, rut, 12-day firearm) without regard to species or site ($F_{2,\,449452} = 9227.1$, $P < 0.001$, V(s) = 0.079) (Tables 3.3, 3.4). Deer had the fastest bi-hourly and greatest daily movements during the rut period, followed by the 12-day firearm period, with the slowest bi-hourly and least amount of total daily movements occurring during the annual period (Table 3.5). All deer had significantly faster bi-hourly speeds and increased total daily movements during rut compared to their annual speeds and daily movements. On average, all deer at least doubled their total daily movements during rut.

On average, deer home range area was influenced by rut and 12-day firearm season (Table 3.6). White-tailed deer home range area increased (25%) during rut compared to their annual home range area, but home range area did not increase during rut for mule deer. Mule deer maintained their largest home range sizes during the annual period. However, both species increased their core use area sizes during rut; white-tailed deer (61%) and mule deer (27%) compared to their annual core use area. Mule deer and white-tailed deer decreased their home range (MD: 82%, WTD: 71%) and core use (MD: 86%, WTD: 74%) area during 12-day firearm season compared to their home range area during rut. Both species had the smallest home range and core areas during the hunting season. Home range (annual: 62%, rut: 45%, 12-day firearm: 44%) and core areas (annual: 61%, rut: 38%, 12-day firearm: 47%) were larger in the south site compared to the north site in each time period. Similarly, deer movements were affected by rut and 12-day firearm season. Total daily movements increased >50% during rut for all groups: north mule deer (61%), south mule deer (60%), north white-tailed deer (73%), and south white-tailed deer increased movements (51%) during rut compared to their annual daily movements. Movements during 12-day firearm season were less than during rut, but greater than during the annual period. Compared to their rutting movements; total daily movement during the 12-day firearm period decreased by 35%, 33%, 5%, and 32% for north mule deer, south mule deer, north white-tailed deer, and south white-tailed deer, respectively.

Discussion

To maximize strategic management of mule deer in western Kansas, it is crucial to understand and quantify the temporal effects of vulnerable time periods such as 12-day firearm season and rut on deer movements and home range distributions. Home range areas and movement trends can provide clues to understanding interspecific relationships and interactions with conspecifics, insight into a deer's access to high quality resources, and reveal knowledge of how species respond to hunting pressure. These movement insights can provide inference to unravel the interspecific relationships between white-tailed deer and mule deer, for which white-tailed deer may be exerting dominance over waning mule deer populations. Home range and core use areas differed between species annually as a whole but did not differ during rut or 12-day firearm season. Annually, mule deer had larger home ranges and core use areas than white-tailed deer. Movements differed among groups (NMD, NWTD, SMD, SWTD) during all three time periods (annual, rut, and 12-day firearm). During rut and 12-day firearm season, mule deer groups had slower bi-hourly movements and shorter total daily movements than white-tailed deer groups; north mule deer had slower bi-hourly movements and shorter total daily movements than all other groups. Bi-hourly movement rate and total daily distance differed among seasonal time periods without regard to species or site. Deer home ranges and movements were influenced by rut. Post-rut confounded the effects of 12-day firearm season on deer movement and home ranges. White-tailed deer home range and mule deer core use area increased during rut; home range and core use areas decreased for all deer during 12-day firearm season which overlapped with the post-rut recovery period. All deer increased their bi-hourly movements and total daily movements during rut, followed by decreased movements during 12-day firearm season. The marked decrease in home range extent during the 12-day firearm season, and the reduction in movements could have been influenced by the proximity of the successive 12-day firearm season relative to the end of rut. It has been reported that home ranges increase during rut (Beier and McCullough 1990, Tomberlin 2007) and that movement rates decline after the rutting period subsides (Beier and McCullough 1990, Marchinton and Hirth 1984), although the presence of hunters on the landscape may have been a contributing factor; movements most likely decreased during the 12-day firearm season because of the coinciding timing of post-rut; a biological time when males are known to reduce activity while recovering from the physiological demands of rut.

Annually mule deer had larger home ranges and core use areas than white-tailed deer. Deer with access to high quality resources that are plentiful and adequately distributed tend to have smaller home ranges than deer in lower quality areas (Marchinton and Hirth 1984). Although annual species survival did not differ among 2018-2020, mule deer during 2020 had significantly lower survival than white-tailed deer (Chapter 2). A possible explanation for mule deer exhibiting larger annual home ranges than white-tailed deer is that white-tailed deer are out competing mule deer for access to available areas of high-quality resources. Although it has been reported that segregation due to large-scale topography typically precludes the competition for food (Martinka 1968, Krausman 1978), both species can share the same spatial niche (Wiggers and Beasom 1986, Whittaker and Lindzey 2004, Brunjes et al. 2006) and have similar diets (Anthony and Smith 1977, Krausman 1978).

A contrary explanation could be related to differing species population level resource selection. Annually, the top model which best predicted home range selection at the herd level showed that mule deer selected for steeper slopes (Chapter 4). Conversely, land cover characteristics was the top model for white-tailed deer population level selection. In the north site, white-tailed deer selected highest for land cover categories such as woodland and CRP. In the south site, where there is less available woodland cover (Table 2.1), white-tailed deer selected for CRP (Chapter 4). These differences in resource selection could explain why mule deer annual home ranges were larger; if steeper slopes were distributed in larger areas across the landscape that could be why mule deer consistently exhibited trends of having larger annual home range and core use areas than white-tailed deer. Kie et al. (2002) reported mule deer home range locations were influenced by the selection of habitat features, which existed across the span of much larger areas than the home range alone. This pattern is in accordance with the literature of studies within the western Great Plains, where, in areas of sympatry, mule deer typically inhabit ranges in higher, drier elevations, compared to white-tailed deer that typically select for riparian areas (Kramer 1973, Teer 1996). Other studies reported that mule deer segregate spatially and topographically from white-tailed deer (Martinka 1968, Krausman 1978, Lingle 2002). This pattern of topographical segregation is also true for deer in my study (Chapter 4).

The significant effect of species on home range area in my study was unlike other studies in the Great Plains. Additionally, the sample size of similar studies in the Great Plains was considerably lower than the sample size for deer in my study, which may have allowed me to calculate more accurate home range sizes. Walter et al. (2011) reported no difference between species fixed kernel estimator annual home ranges for adult mule deer (n = 11, 10 km^2) and white-tailed deer (n = 22, 7 km^2) in western Nebraska. Fixed kernel home ranges were also similar between adult mule deer (n = 7, 8.8 km^2) and white-tailed deer (n = 7, 7.4 km^2) in west-central Texas (Brunjes et al. 2009). Annual home range area for mule deer in southeast Colorado was similar to those estimated in my study (minimum convex polygon; military maneuver site: n = 8: 28.89 km^2, nonmaneuver site: n = 7: 41.67 km^2). Annual home range areas for mule deer (n = 55: 24.89 km^2) and white-tailed deer (n = 56: 19.68 km^2) were larger for deer in my study than those in Nebraska and Texas, but similar to mule deer in Colorado. This could be partially explained by home ranges in my south site (29.25 km^2) being significantly larger than those in north site (15.43 km^2), which were closer in area to those found in Nebraska and Texas. The larger south site home range could be explained by the lack of woodland cover compared to the north site (Table 2.1). Long et al. (2005) found that in areas with scarce tree cover, deer may be forced to move longer distances to find appropriate habitat patches.

Movements differed among species-site groups during all three time periods (annual, rut, and 12-day firearm). During rut and 12-day firearm season, mule deer groups had slower bi-hourly movements and shorter total daily movements than white-tailed deer groups. North mule deer had significantly slower bi-hourly movements and shorter total daily movements than all other groups, while north white-tailed deer had the fastest bi-hourly movements, and the greatest amount of total daily movements. Differences in movement speed and total daily movement between species could be due to the species having evolved dissimilar predator escape strategies (Geist 1981, Lingle 2002). Mule deer are slower than white-tailed deer and rarely able to successfully outrun predators (Lingle 1992, 1998). So, instead of immediately running, mule deer will often form defensive groups to ward off predators (Lingle 2001, Linge and Pellis 2002). Mule deer have been observed and appeared to be almost circling the predator while attempting to always keep the threat within view (Geist 1981). Conversely, white-tailed deer normally flee when pursued by predators, escaping through use of speed (Lingle and Pellis 2002). If mule deer and white-tailed deer respond to hunters in the same way they do to predators as suggested by DeYoung and Miller (2011), it could be an explanation for the increased speed and greater movements of white-tailed deer compared to mule deer during the hunting season.

Although there were no significant differences in annual species survival, if white-tailed deer are displaying faster bi-hourly rates and increased movements as their biological fight or flight response during the hunting season, compared to mule deer, such a difference in predator escape strategy could be contributing towards increased mortality of mule deer during 12-day firearm season (Chapter 2). Compared to white-tailed deer, mule deer, particularly north mule deer, were the most heavily affected species by the 12-day firearm period; they were also the slowest group with the least amount of movements (Chapter 2, Table 2.14). This finding is in alignment with Whitman et al. (2018) who found increased mortality rates for deer who moved slower than conspecifics during the fall hunting season.

Movements significantly differed among time periods without regard to species or site. All collared deer in my study exhibited increased movements during rut compared to their annual movements, similar to other studies of white-tailed deer within the Great Plains (Webb et al. 2010). Other studies measuring movements of adult males during rut found males increased movements to enhance their female encounter rates and augment their likelihood of reproductive success (Foley et al. 2015, Simoneaux et al. 2016). Deer in my study (averaged white-tailed deer total daily movement at both sites during rut: 7,692 m) had similar movements to Webb et al. (2010) who reported that white-tailed deer male movements were greater during rut (7,363 ± 364 m) than after rut (6,156 ± 260 m), in Oklahoma. This is expected, and in accordance with literature that reports adult males increase solitary movements to seek out estrous does during rut, with their greatest movements occurring during the breeding phase of rut, followed by a decrease in movements at the culmination of rut (Beier and McCullough 1990, Marchinton and Hirth 1984, Tomberlin 2007).

Although white-tailed deer increased their home range area during rut, a trend characteristic of adult males (Beier and McCullough 1990, Tomberlin 2007), mule deer did not. Despite not increasing their home range area, mule deer did increase their core use area during rut. It is possible that mule deer did not increase their home range during rut because it was already sufficiently large enough to provide available estrus females. Or potentially since mule deer herds more likely consist of mixed males and females during winter (Lingle 2003) compared to white-tailed deer who are more solitary and engage in “tending-bond” mating systems (Hirth 1977); mule deer might be exhibiting more harem style mating systems during rut which do not require them to travel as far in search of mates. Deer do not use the entirety of their annual home range equally, the core use area (50% of the deer’s home range use; Favreau 2005) may only represent 12-17% of the entire home range (Campbell et al. 2004, Tomberlin 2007). If the same is true for a mule deer’s home range during rut, perhaps expanding the bounds of their core range is all that is needed to find enough females to meet their mating requirements. Mule deer in my study could be exhibiting a similar mating strategy such as white-tailed deer in south Texas, in which Foley et al. (2015) reported that most males only used a small portion (26-34%) of their home range during rut, and returned to the same sites to search for estrus does. This differs from Brown’s (1974) dominant floater hypothesis in which males continuously traverse large portions of their home range to seek out estrus does and return to their original location within 8-30 h (Tomberlin 2007). Conceivably, the lack of home range expansion during rut could be a contributing factor for mule deer decline; by not participating as intensively in rutting activities, male mule deer may be missing out on finding and securing breeding opportunities. This lack of breeding effort may be beneficial to the individual if by not participating in rut increases their survival. If males exert less energy into participating in rutting activities, this reduced effort may shield them from forms of natural mortality that would be caused by rutting carry over effects (Clutton-Brock et al. 1982, Ditchkoff et al. 2001). Rut was not the only influence of deer movement and home range area. Both bi-hourly and total daily movement significantly decreased and home ranges were smaller during the 12-day firearm hunting season for all deer. Speculatively, similar to other studies in the Great Plains, deer in my study may have perceived hunters as a threat on the landscape, and altered their movements and home range sizes to avoid detection (Little et al. 2014, 2016; Marantz et al. 2016). However, adult male movements are known to decline after the rutting period ends (Beier and McCullough 1990, Marchinton and Hirth 1984), and the timing of the 12-day firearm season, which overlapped with post-rut; a time when males are weakened from exerted movements and lack of food in their search for estrus females, was most likely the primary cause of the marked decrease in movement and range size during the 12-day firearm season.

Mule deer are currently contracting from their historical ranges across the Great Plains. In areas of sympatry such as western Kansas, mule deer populations are constricted and have diverging population and distribution trends from white-tailed deer. I hypothesized that mule deer and white-tailed deer would exhibit differing trends in the area of their home ranges during rut and 12-day firearm because of the current population trajectory of mule deer; I expected mule deer to have significantly smaller home ranges during rut than white-tailed deer; indicating a reduced attempt in their effort to secure breeding opportunities. Although mule deer did not have larger home ranges during rut compared to their annual home ranges, their core areas did increase and the area of their rut home ranges did not significantly differ from those of white-tailed deer. Furthermore, I hypothesized mule deer would have larger home ranges during the 12-day firearm season due to their differing evolutionary escape strategies (Geist 1981). This was incorrect as mule deer and white-tailed deer home range area did not differ during 12-day firearm season, although their total daily and bi hourly movements differed suggesting their fight or flight responses and evolutionary escape strategies differed as well. Annual home range area did differ between species; with mule deer having larger home ranges, which could be related to a lack of available high-quality resources for mule deer (Marchinton and Hirth 1984); potentially contributing to their decline, as mule deer in 2020 had significantly lower survival rates than white-tailed deer. I hypothesized mean total daily and bi-hourly movement rates, and home ranges would increase during the breeding season (i.e., rut; Ozoga and Verme 1985, Foley et al. 2015, Simoneaux et al. 2016); concurrently both mule deer and white-tailed deer displayed these trends in my study. Additionally, I hypothesized movements and ranges would decrease during the 12-day firearm seasons in which deer may perceive a threat on the landscape (Little et al. 2014, 2016; Marantz et al. 2016). Deer in western Kansas, did decrease movements and home range areas relative to rut, but their movements were still greater when compared to their baseline annual movements. Movements stalled and ranges decreased during post-rut, a time when males reduce activity to recover from the energetic and nutritional demands of rut. The overlap of the successive 12-day firearm season with post-rut confounds the ability to isolate the effect hunting had on deer movement and range size. Mule deer displayed the slowest bi-hourly movement and the least amount of daily movement during the hunting season, which could also be adversely affecting their population decline (Whitman et al. 2018).

Management Implications

Deer movement patterns and home ranges in western Kansas are affected by rut and the succeeding 12-day firearm season. The leading cause of mortality for adult male mule deer is harvest. Because rutting lag effects have been reported to potentially increase forms of natural mortality (Clutton-Brock et al. 1982, Ditchkoff et al. 2001), I suggest delaying the start of 12-day firearm season for adult male mule deer for at least two weeks after rut ends. Ideally, beginning the season no earlier than ~December 10 may offer rutting male mule deer a chance to recover and improve their weakened body condition before exposing them to hunter harvest.

Furthermore, managers and private landowners should take into consideration the average home range size that a male mule deer requires during differing temporal periods; the mean annual home range size for mule deer in this study was 24.89 ± 0.01 km^2, 24.47 ± 1.74 km^2 during rut, and 10.19 ± 1.03 km^2 during the 12-day firearm season.

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Figures and Tables

Table 3.1. Comparison of pooled 2018 and 2019 mean Biased Random Bridge 95% isopleth home ranges (km^2) and associated standard error (SE) of species and site, during the annual period (capture date to capture date), 12-day firearm season, and rut periods for collared mule and white-tailed deer in the North (Decatur, Sheridan, Norton, Graham counties) and South study sites (Scott, Logan, Lane, and Gove counties) in western Kansas, USA.

Period	$\bar{x}$ **± SE**	***F***	**DF**	***P***
Annual				
Species*		6.91	1,107	0.01
Mule Deer	24.89 ± 0.01			
White-tailed	19.68 ± 1.80			
Site*		51.79	1,107	<0.001
North	15.34 ± 1.15			
South	29.25 ± 1.69			
Rut				
Species		0.09	1,92	0.76
Mule Deer	24.47 ± 1.74			
White-tailed	25.30 ± 2.50			
Site*		15.98	1,92	<0.001
North	18.77 ± 1.97			
South	29.75 ± 1.88			
12-Day Firearm				
Species		0.89	1,78	0.35
Mule Deer	10.19 ± 1.03			
White-tailed	12.11 ± 2.04			
Site*		5.42	1,78	0.02
North	8.53 ± 1.15			
South	13.40 ± 1.63			

*Means significantly differ ($P < 0.05$).

Table 3.2. Comparison of pooled 2018 and 2019 mean Biased Random Bridge 50% isopleth home ranges (km^2) and associated standard error (SE) of species and site, during the annual period (capture date to capture date), 12-day firearm season, and rut periods for collared mule and white-tailed deer in the North (Decatur, Sheridan, Norton, Graham counties) and South study sites (Scott, Logan, Lane, and Gove counties) in western Kansas, USA.

Period	$\bar{x}$ **± SE**	***F***	**DF**	***P***
Annual				
Species*		7.42	1,107	0.007
Mule Deer	3.75 ± 0.26			
White-tailed	2.81 ± 0.30			
Site*		35.51	1,107	<0.001
North	2.29 ± 0.20			
South	4.28 ± 0.29			
Rut				
Species		0.35	1,92	0.56
Mule Deer	4.91 ± 0.37			
White-tailed	5.29 ± 0.58			
Site*		8.65	1,92	0.004
North	4.03 ± 0.46			
South	5.93 ± 0.42			
12-Day Firearm				
Species		1.04	1,78	0.31
Mule Deer	1.96 ± 0.23			
White-tailed	2.42 ± 0.48			
Site*		4.63	1,78	0.03
North	1.64 ± 0.26			
South	2.65 ± 0.36			

*Means significantly differ ($P < 0.05$).

Table 3.3. Comparison of mean bi-hourly movement rates and associated standard error (SE) among groups, pooled by years (2018 and 2019) for the annual period, rut, and 12-day firearm season periods for mule deer (MD) and white-tailed deer (WTD) in two study sites (North [N] and South [S]) in western Kansas, USA.

Period	$\bar{x}$ ± **SE**	***F***	**DF**	***P***
Annual		1417.60	3, 412209	<0.001
N MD	286.84 ± 1.33^{C}			
S MD	351.88 ± 1.68^{B}			
N WTD	279.98 ± 1.48^{D}			
S WTD	406.63 ± 1.82^{A}			
Rut		40.23	3,25469	<0.001
N MD	537.79 ± 8.31^{D}			
S MD	645.98 ± 11.41^{B}			
N WTD	599.72 ± 12.40^{C}			
S WTD	678.92 ± 9.04^{A}			
Firearm Season		44.0	3,11765	<0.001
N MD	392.67 ± 11.23^{D}			
S MD	465.94 ± 11.42^{C}			
N WTD	569.06 ± 14.95^{A}			
S WTD	500.63 ± 14.95^{B}			

^{ABCD}Means followed by the same uppercase superscript do not differ ($P < 0.05$).

Table 3.4. Comparison of mean total movement (m) in a 24-hour period and associated standard error (SE) among groups, pooled by years (2018 and 2019) for the annual period, rut period (varies by species and site) and 12-day firearm season for mule deer (MD) and white-tailed deer (WTD) and study site (North [N] and South [S]) in western Kansas, USA.

Period	$\bar{x}$ **± SE**	***F***	**DF**	***P***
Annual		7697.00	3,412209	<0.001
N MD	3432.16 ± 7.02^{A}			
S MD	4213.90 ± 8.65^{B}			
N WTD	3356.31 ± 7.86^{C}			
S WTD	4874.55 ± 8.89^{D}			
Rut		208.52	3,25469	<0.001
N MD	6451.94 ± 45.83^{A}			
S MD	7789.41 ± 60.60^{B}			
N WTD	7204.11 ± 70.71^{C}			
S WTD	8180.10 ± 47.50^{D}			
12-Day Firearm		238	3,11765	<0.001
N MD	4528.30 ± 42.06^{A}			
S MD	5598.31 ± 52.76^{B}			
N WTD	6850.97 ± 94.04^{C}			
S WTD	5926.92 ± 59.73^{D}			

^{ABCD}Means followed by the same uppercase superscript do not differ ($P < 0.05$).

Table 3.5. Mean bi-hourly distance and mean total movement (m) in a 24-hour period with associated standard error (SE) for all deer, without regard to site or species, during the annual period (capture date to capture date), 12-day firearm season, and rut periods for collared mule and white-tailed deer in the North (Decatur, Sheridan, Norton, Graham counties) and South study sites (Scott, Logan, Lane, and Gove counties) in western Kansas, USA.

Seasons	**Bi-hourly Distance**	**Total Daily Distance**
Annual	334.79 ± 0.81^{C}	4010.47 ± 4.22^{C}
Rut	620.25 ± 5.04^{A}	7463.54 ± 27.44^{A}
12-Day Firearm	476.16 ± 6.59^{B}	5650.99 ± 31.73^{B}

^{ABC}Means followed by the same uppercase superscript do not differ ($P < 0.05$).

Table 3.6 Pooled 2018 and 2019 mean Biased Random Bridge 95% and 50% isopleth home ranges (km^2) and associated standard error (SE) for each group (north mule deer [NMD], north white-tailed deer [NWTD], south mule deer [SMD] and south white-tailed deer [SWTD]) during the annual period (capture date to capture date), 12-day firearm season, and rut periods for collared mule and white-tailed deer in the North (Decatur, Sheridan, Norton, Graham counties) and South study sites (Scott, Logan, Lane, and Gove counties) in western Kansas, USA.

Period			**Annual km^2**	
N MD	95% HR	Mean ± SE	Min.	Max.
		18.47 ± 1.39	6.57	33.8
	50% Core	2.91 ± 0.28	1.17	7.00
S MD	95% HR	32.03 ± 2.34	15.93	65.62
	50% Core	4.68 ± 0.39	1.37	9.44
N WTD	95% HR	11.58 ± 1.64	0.77	32.16
	50% Core	1.54 ± 0.21	0.13	3.61
S WTD	95% HR	26.66 ± 2.37	8.08	51.4
	50% Core	3.9 ± 0.43	1.02	9.23
Home Range and Core Use Area Pooled by Year (2018-2019)			**Rut km^2**	
N MD	95% HR	18.07 ± 1.84	1.68	40.83
	50% Core	3.97 ± 0.48	1.51	11.69
S MD	95% HR	31.36 ± 2.42	10.92	57
	50% Core	5.92 ± 0.5	2.22	12.03
N WTD	95% HR	20.08 ±4 .58	5.28	72.19
	50% Core	4.12 ± 1.01	1.15	16.4
S WTD	95% HR	28.19 ± 2.86	6.27	66.8
	50% Core	5.93 ± 0.69	0.88	13.5

Home Range and Core Use Area		**12-Day Firearm km^2**		
Pooled by Year (2018-2019)				
N MD	95% HR	8.48 ± 0.99	0.77	20.38
	50% Core	1.54 ± 0.2	0.11	4.88
S MD	95% HR	12.27 ± 1.89	3.36	20.79
	50% Core	2.46 ± 0.44	0.58	9.09
N WTD	95% HR	8.59 ± 2.86	0.55	41
	50% Core	1.82 ± 0.68	0.09	9.89
S WTD	95% HR	14.7 ± 2.76	3.44	44.34
	50% Core	2.86 ± 0.59	0.58	9.89

Chapter 4 - Temporal space use, and herd level resource selection at the second order scale, of male mule deer and white-tailed deer in western Kansas

Mule deer (Odocoileus hemionus) and white-tailed deer (O. virginianus) across the western Great Plains are displaying disparate population trends, potentially because of increased interspecific competition intensified by a lack of large-scale topographical separation that is common in other areas of sympatry (Martinka 1968, Brunjes et al. 2006). While mule deer population distribution is decreasing and potentially contracting westward (Ballard et al. 2001, Shallow et al. 2015), concomitant white-tailed deer populations are growing and expanding within the western Great Plains (Martinka 1968, Baker 1984, Van der Hoek et al. 2002). Despite evolutionary adaptations where these species segregate within sympatric ranges and partition resources in a way that benefits their dissimilar predator escape strategies (Geist 1981, Lingle 2002), mule deer and white-tailed deer may compete for limited resources if populations are using similar niches (Martinka 1968, Anthony and Smith 1977, Krausman 1978, Wiggers and Beasom 1986, Wood et al. 1989). Relationships among landscape features and their spatial configuration in shaping the distribution and ranges of deer in sympatric populations is understudied (Kie et al. 2002). In western Kansas, USA, sympatric deer populations share, and likely compete for, food, cover, and space given the lack of opportunity to geographically segregate. There is a potential for one or more of shared resources to be limiting and exacerbating underlining factors contributing to mule deer decline. Relating and comparing resource selection and space use between sympatric populations of mule deer and white-tailed deer in western Kansas may help elucidate important ecological relationships underlying population trends.

Changes in land cover and use may also be a driving force behind the declining abundance and occupied range of mule deer in the western Great Plains. Because mule deer and white-tailed deer share the same resources in western Kansas, there is speculation that white-tailed deer who are theorized to be aggressors, and may be displaying interference competition against mule deer, may also have a competitive advantage in acquiring high-quality resources because alterations in land cover (i.e., increased woody areas) are more beneficial to white-tailed deer. Such conditions drive the hypothesis that white-tailed deer are competitively dominant over mule deer because white-tailed deer are commonly associated with areas of woody cover (Mackie 1981, Mackie et al. 1998). Mule deer may not be as adaptable to changing land use practices as their competitor, the habitat generalist white-tailed deer (Grovenburg et al. 2009). Increasing woody encroachment resulting from long-term fire suppression and other large landscape-scale changes has led to shifts in available habitat in favor of edge species, such as white-tailed deer rather than mule deer (Williamson and Hirth 1985). White-tailed deer have adapted to fragmented landscapes throughout the Great Plains, finding food and shelter almost everywhere (Sparrowe and Springer 1970) - including areas of woody cover, agricultural areas, suburban/urban development, and river bottoms (Mackie 1981). In turn, white-tailed deer have expanded their range westward in the Great Plains invading space never before occupied by the species, potentially inhibiting mule deer from obtaining necessary resources (VerCauteren and Hygnstrom 2011).

In addition to white-tailed deer’s strategic use of wooded areas to benefit their security cover, their use of tall grass CRP species may also be benefitting their survival, and also aiding in their expanding distribution. Higgins (1987) hypothesized that CRP grasslands provide a necessary resource in heavily cultivated farmlands with limited cover; such as the south study site. If white-tailed deer are using tall grass CRP species to fulfill and enhance their escape, screening and loafing cover; CRP may aid in white-tailed deer increasing their range in areas where they were historically limited to riparian zones.

It has been reported that in areas of geographic overlap, mule deer and white-tailed deer often occupy areas of differing environmental characteristics (Lingle 2002, Brunjes 2006). Mule deer in the Great Plains select for open ranges, often in rugged terrain, high in elevation with steep slopes; unlike white-tailed deer that select for areas with mild terrain, often in lower elevation riparian areas with abundant tree cover (Severson 1981, Lingle 2002, Avey 2003). If the two species display alternative trends in temporal space use at vulnerable times of the year (rut, hunting season) and also differ in their resource-selection at the herd level, unearthing these patterns may provide explanatory insight into which important environmental features are currently underrepresented on the landscape. Knowledge of macro-habitat features (e.g., slope, elevation, aspect, topographic roughness) and categorical landcover (e.g., crop, CRP, pasture, woodland) selected by mule deer during critical time periods in western Kansas, will inform management strategies for increasing mule deer abundance.

There have been several studies identifying space use and resource selection by deer in the Great Plains, but none specifically with the intent of identifying herd-level selection, and space use during vulnerable time periods of the year for sympatric adult male mule deer and white-tailed deer with the intent of improving mule deer population growth. Walter et al. (2011) used discrete-choice models to compare seasonal differences in resource selection by male mule deer and white-tailed deer using land cover data in western Nebraska, USA. They found land cover and juxtaposition of crops and woodland cover influenced the selection of resources by male mule deer during winter, but showed little selection for any class of land cover during summer. Resource selection by male white-tailed deer was most related to proximity to woodland cover during summer and winter; this relationship was most pronounced during winter. Among other effects, land cover influenced the selection of resources by male white-tailed deer during both seasons. Whittaker and Lindzey (2004) studied confined sympatric mule deer and white-tailed deer spatial and resource use trends on Rocky Mountain Arsenal, in northeast Colorado, USA. They reported distribution and resource use at three different spatiotemporal scales: annually, seasonally, and site specific levels of diet composition. Annually, neither species used the study area uniformly, nor were there differences between annual species utilization distributions. Significant differences between species distributions did occur seasonally. Seasonal home range segregation allowed the species to eat similar foods without exposing them to interspecific interactions. Mule deer used areas predominantly based on forage availability and based ancillary selection on the amount of available cover during winter, whereas white-tailed deer used resources based on the level of security and thermoregulatory cover available. Seasonal differences in home range composition were more distinct in the winter, and no interspecific differences were found during the fall. Diet composition (forbs, grasses, and browse) was similar between species. No difference between species for selection of individual plant species occurred; diets were most similar during winter (70.41% similar) compared to spring (39.41%). Brunjes et al. (2006) evaluated the role of vegetation and topography on habitat use by sympatric deer in west-central Texas, USA, at the second-and third-order scale. Resources selected varied for males of both species based on spatial scale evaluated. Male mule deer used steeper slopes and higher elevations with less visual cover than white-tailed deer. Differences in use and selection occurred at the core area scale. Interspecific overlap occurred in the home range suggesting a temporal factor may govern resource partitioning at different spatial scales, or suggests competition may also be structuring resource use decisions by deer. Brunjes et al. (2009) reported interspecific home-range overlap was less common than intraspecific overlap; indicating habitat partitioning may have occurred on a temporal scale, or at a finer spatial scale than can be detected from home range analyses for sympatric species in west-central Texas. Core-area interspecific overlap; which indicates a greater potential for competition than home range overlap (Wauters and Dhondt 1985), only occurred once and was less common than home range interspecific overlap for male mule deer and white-tailed deer (Brunjest et al. 2009).

Further analysis is needed to explore the temporal space use relationships and herd level-selection between free-ranging populations of sympatric mule deer and white-tailed deer in the Great Plains to better understand factors that may be driving the decline of mule deer populations. My objectives were to examine temporal space use at the landscape scale, and population-level resource selection of macro habitat by adult male mule deer and white-tailed deer in western Kansas during three time periods (annually, rut, and 12-day firearm season). I hypothesized that temporal space use would vary throughout the year, with mule deer and white-tailed deer using and selecting for land cover categories strategically during the 12-day firearm season to increase security cover (i.e., increased usage of woodland and CRP). Further, white-tailed deer would use woodlands at the greatest proportion during the hunting season, and use woodlands more than mule deer (Severson 1981). Concurrently, I hypothesized mule deer would differentially select for macro-habitat features such as: topographic roughness, slope and elevation (Geist 1981, Kramer 1972, Severson 1981, Lingle 2002, Avey 2003); areas which separate them topographically from white-tailed deer who often select for lower elevation riparian areas with increased cover (Martinka 1968, Krausman 1978, Severson 1981).

Study Area

I conducted this study at two sites located ~130 km apart in the western third of Kansas during 2018, 2019, and 2020; both sites were composed of private land (Fig. 2.1). The north site (~850 km^2) was in Graham, Norton, Sheridan, and Decatur counties (Fig. 2.2). The south site (~1,370 km^2) was in Scott, Logan, Gove, and Lane counties (Fig. 2.3). Both sites were located in the Central Great Plains and High Plains level III ecoregions (U.S. Environmental Protection Agency [EPA] 2000). Of the eleven physiographic regions in Kansas, all counties included in both study sites were located in the High Plains region; Norton, Graham, Gove, Lane, and Logan counties are also part of the Smoky Hills physiological region (USDA NRCS https://www.nrcs.usda.gov/wps/portal/nrcs/detail/ks/about/?cid=nrcs142p2_033475> Accessed 4/4/21). Elevation in the north site was 666.9 m. Average annual temperatures were 11.89° C, and 11.60° C, during 2018, and 2019, respectively. Long-term average annual temperature from 2000-2020 was 12.37° C. Total annual precipitation was relatively wet in 2018 (921.25 mm) and 2019 (744.73 mm), compared to the previous 20 years in which average annual precipitation was 545.32 mm ± 36.58 in the north site (Hill City Municipal Airport, KS, USA; National Oceanic and Atmospheric [NOAA] 2020). Elevation in the south site was 906.5 m. Average annual temperatures were 11.72° C, and 11.13° C, during 2018, and 2019, respectively. Long-term annual temperature from 2000-2020 was 12.02° C at the south site. Total annual precipitation was 666.49 mm, and 526.54 mm, in 2018, and 2019, respectively; compared to the previous 20 years (2000-2020) when total precipitation averaged 499.45 mm ± 23.22 per year (Scott City, KS, USA; NOAA 2020).

Both study sites were a matrix of cropland and grassland, composed of short- and mixed-grass prairie (U.S. Environmental Protection Agency 2000). The defining difference between both study areas was the presence of the North Fork Solomon River in the north site, which crossed the study area and included floodplain woodlands along riparian areas (Figs. 2.4, 2.5, and 2.6). Most of the south site was east of U.S. Highway 83 and north of State Highway 4 (Figs. 2.7, 2.8, and 2.9). The south site included more draws and elevated “chalk rock” areas relative to the north site.

Available, ground-truthed land cover patch area and distribution were calculated annually by encompassing a 2-km buffer around a 100% minimum convex polygon of the distribution of all deer locations. The north study site included 504 km^2, 857 km^2, and 685 km^2 in 2018, 2019, and 2020, respectively. The south study site encompassed 1,371 km^2, 665 km^2, and 1,023 km^2 in 2018, 2019, and 2020, respectively.

Cover types were defined as Crop, U.S. Department of Agriculture Conservation Reserve Program (CRP), Pasture (i.e., grazed native grassland), Urban (small towns, outbuildings, cemeteries, and other man-made structures), Water, and Woodland (ranging from small pockets of forest, riparian areas, and shelterbelts (Table 2.1). Relative proportion of land cover types varied slightly among years (Table 2.1). However, Crop was the most common land cover type during each year in the north site, with its distribution surrounding Pasture centrally located in the study site (Figs. 2.4, 2.5. and 2.6). Similarly in the south study site, Crop comprised the largest proportion of cover types during all years, with Pasture comprising the second most common land cover type (Figs. 2.7, 2.8, and 2.9).

Corn (*Zea mays*), wheat (*Triticum aestivum*), and milo (*Sorghum bicolor*) dominated agricultural crops (U.S. EPA 2000). Other less abundant crops included sunflowers

(*Helianthus annus*), alfalfa (*Medicago sativa*), and soybeans (*Glycine max*). Pasture was typically composed of shorter, grazed, native mixed-grass prairie. Prevalent grasses in the mixed-grass prairie included little bluestem (*Schizachyrium scoparium*), sideoats grama (*Bouteloua curtipendula*), and blue grama (*B. gracilis*). Tall thistle (*Cirsium altissimum*), broom snakeweed (*Gutierrezia sarothrae*), Nuttall's sensitive-briar (*Mimosa nuttallii*), and Indian blanket (*Gaillardia pulchella*) were typical forbs; widespread succulents included yucca (*Yucca glauca*) and prickly pear cactus (*Opuntia macrorhiza*). Tracts of CRP included tallgrass prairie species – big bluestem (*Andropogon gerardi*), Indiangrass (*Sorghastrum nutans*), and switchgrass (*Panicum virgatum*) intermixed with forbs such as white prairie clover *(Dalea candida*), Maximillian sunflower (*Helianthus maximiliani*), purple prairie clover (*Dalea purpurea*), and Illinois bundleflower (*Desmanthus illinoensis*; United States Department of Agriculture [USDA], Natural Resources Conservation Service [NRCS] 2020). Woodlands were composed primarily of shelterbelts, small groups of clumped trees intermittently present throughout pastures and the large riparian area in the north site. Prevailing tree species included American elm (*Ulmus americana*), box elder (*Acer negundo*), green ash (*Fraxinus pennsylvanica*), hackberry (*Celtis occidentalis*), black cherry (*Prunus serotina*), eastern cottonwood (*Populus deltoides*), honey locust (*Gleditsia triacanthos*), black locust (*Robinia pseudoacacia*), mulberry (*Morus rubra*), black walnut (*Juglans nigra*), and eastern red cedar (*Juniperus virginiana*). Plum thickets (*Prunus angustifolia*) and smooth sumac (*Rhus glabra*) were common shrubs in both study sites (USDA, NRCS, 2020). Taxonomic authorities were from the Kansas wildlflowers and grasses webpage (www.kswildflower.org) and the Kansas Native Plant Society webpage (www.kansasnativeplantsociety).

Methods

Capture

Adult male capture occurred during February of 2018 and 2019, using a commercial helicopter crew; Quicksilver Air Inc. (Colorado Springs, CO, USA). They captured and GPS-collared 60 adult male mule deer and white-tailed deer in 2018, divided evenly between species and two study sites in western Kansas (i.e., 15 individuals/species/site). Thereafter, in 2019 only replacements for the number of male deer that died during the previous year were captured to maintain a sample size of 60 at the start of each field season. They captured male deer using net guns, followed by hobbling and blindfolding them prior to attaching radio collars at the capture site in 2018. In 2019, captured male deer were transported to a central processing location located at each study site to attach radio collars (Northrup et al. 2014). No deer were captured ≥8.05 km from the processing location (with the majority being released ≤5 km from capture) to reduce capture myopathy. Restraint from time of capture to release was ≤30 minutes. All captured animals were subjected to a physical exam by on-site veterinarians. For handling safety and control of stressed individuals during transport in 2019, males may have been administered chemical sedation in the combined form of Azaperone, Midazolam, and Butorphanol (each drug compound 50 mg/ml, volume of each 0.3 cc with Azaperone and Butorphanol in 1 syringe, and Midazolam in the other; IM; Wolfe and Miller 2016). Animals were released at the processing site as previous capture efforts found that animals rapidly returned to capture locations (W. Conway, Texas Tech University, pers. comm.). All deer were captured and handled according to guidelines approved by the American Society of Mammalogists (Sikes et al. 2016), under the Institutional Animal Care and Use Committee at Kansas State University (protocol #3963), and authorized under the Kansas Wildlife, Parks, and Tourism scientific permits (SC-024-2018, SC-015-2019).

Standard numbered livestock ear tags with contact information were applied to each captured deer using conventional equipment and procedures for future identification. Each deer was fitted with a Vertex Plus-2 collar (Vectronics, Berlin, Germany), which contained a very-high-frequency (VHF) beacon, mortality sensor, temperature sensor, and 3-axis activity sensor, as well as Iridium Bi-directional option and a Vectronic timer-controlled drop-off initiated at deployment. Expandable elastic collar inserts were used on male collars to account for neck swelling during rut. Each male collar was programmed to take a GPS positional fix every two hours, with 12 locations per Iridium message for up to three years (160 weeks). Location and mortality data were obtained remotely with activity data stored on board, location error was estimated to be ~5 m.

Landcover Data

To evaluate use at the landscape scale, I plotted the proportion of deer points for all groups (north mule deer, south mule deer, north white-tailed deer, and south white-tailed deer) to identify temporal space use of different land cover categories during the annual period, rut periods, and 12-day firearm seasons. The annual periods were demarcated from March 11 - March 10, 2018 - 2020. Rut occurred during 11-05-18 to 11-25-18, 11-04-19 to 11-24-19 and 10-29-18 to 11-18-18, 10-28-2019 to 11-24-2019 at the north and south site, respectively, for mule deer. Rut occurred during 11-05-18 to 11-25-18, 11-04-19 to 11-24-19 and 10-29-18 to 11-25-18, 10-28-19 to 11-24-19 at the north and south site, respectively, for white-tailed deer. The 12-day firearm seasons were 11-28-18 to 12-9-18, and 12-4-19 to 12-15-19 (Table 2.2).

To evaluate differences in species' second order of selection at the population scale (i.e., the home range of the social group, or herd; Johnson 1980), I defined area of land cover types available for resource selection analysis by creating seasonal (annual, rut, and 12-day firearm) minimum convex polygons (MCP) using the Geospatial Modeling Environment tool in ArcGIS (Beyer 2012). Seasonal MCPs were configured around the combined deer herd locations (based off of Vectronic GPS locations for each group of deer). I buffered the MCPs by the average sum of daily distance of each of the four groups of deer (north mule deer, south mule deer, north white-tailed deer, and south white-tailed deer) for that respective period. The buffered MCP demarcated the "available" area for each study site. The Vectronic GPS locations collected throughout the study site for each season represented the "used" points. I then generated the same number of random points as the combined total of actual deer "use" locations for each of the four groups during each season, constrained by the respective "available" buffer for each group at the population scale to assess second-order resource selection.

To evaluate landcover selection, I created a ground-truthed map in a geographic information system (GIS; ArcMap v.10.6, ESRI, Redlands, CA) to represent land cover for both study sites. I classified land cover into one of five categories: pasture, cropland, woodland, CRP, and urban. In addition, I used an 800-m resolution USGS digital elevation model (DEM) raster (specific to the counties in both study sites) in conjunction with the "spatial analyst" and "surface" tools in ArcGIS to estimate pixel values for the raster surface of percent slope and aspect. Spatial tool information was accessed from the ESRI ArcGIS Pro database (https://pro.arcgis.com/en/pro-app/latest/tool-reference/spatial-analyst/an-overview-of-the-spatial-analyst-toolbox.htm). Slope was defined as the steepness of each cell on the ArcGIS raster surface. The lower the slope value, the flatter the terrain; the higher the slope value, the steeper the terrain (Eberly 1999, Hofmann et al. 2001, Ligas and Banasik 2011). Aspect identified the compass direction that the downhill slope faced for each location from each cell of the raster surface. The definition for aspect was obtained from the ESRI ArcGIS pro database (https://pro.arcgis.com/en/pro-app/latest/tool-reference/spatial-analyst/aspect.htm). Then topographic roughness was calculated using the same DEM raster and the 2.0 Geomorphometry and Gradient Metrics Toolbox in ArcGIS (Evans et al. 2014). Topographic roughness represented the roughness in a continuous raster within a specified window (Blaszczynski 1997, Riley et al. 1999). Continuous raster data (aspect, slope, elevation, and topographic roughness) was appended to each individual adult male's used and available random point within the home range of the social group, in the "used and random deer points" polygon shapefile, using the "extract multi-values to points" tool in ArcGIS. Landscape information from the map (i.e., landcover categorical data) was extracted by selecting the "used and random deer points" layer (that included the previously appended raster data). Then I used the "overlay" and "identify" tools in ArcGIS to append information to the respective landcover map (for the correct year of data (i.e. groundtruthed map for 2018 or 2019). Once all landcover and continuous raster data had been appended to the deer "used" and "random/available" points, I combined both years of data (2018 and 2019) before beginning the analyses.

Analyses

Prior to analysis, I tested all predictor variables (slope, elevation, topographical roughness, aspect, and landcover [categories included: crop, CRP, pasture, and woodland]) for multicollinearity; correlated variables ($r > |0.70|$) were not included in the same model. Slope and topographical roughness were correlated for every group other than annual south white-tailed deer. Therefore, they were tested separately with the other predictor variables in one of two model suites (i.e., slope + aspect + elevation + landcover or topographic roughness +aspect + elevation + landcover). They were not included in the same model candidate set for any group besides annual south white-tailed deer. I standardized all continuous variables using a z-score to place all continuous predictor variables (aspect, elevation, slope, topographic roughness) on the same scale to allow for direct comparison of coefficients. There were too few urban values to be accurately included in the model candidate set without causing artificial inflation, so urban was removed from all candidate sets that ranked the single variable landcover model as the top model. I created two a priori model suites that included only single variable models to assess resource selection by mule deer and white-tailed deer (for each site and season [annual, rut, 12-day firearm]). I then used fixed-effects logistic regression to model second-order resource selection by comparing observed “use” with predicted selection using the lme4 package in Program R (R Development Core Team 2019, Bates 2015). I tested model suites for each season by species and site group to determine which continuous and categorical macrohabitat characteristics best predicted space use by each species’ social group.

I used Akaike’s Information Criterion adjusted for small sample sizes (AICc) to assess support for models in each model suite (package AICcmodavg; Mazerolle 2019). I considered models ≤ 2.00 ΔAICc to be competitive (Burnham and Anderson 2002). Akaike weights (ωi) was used to further assess competing models. Then models were removed post hoc if the 95% confidence intervals of parameter estimates overlapped zero for any covariate in that particular model. Variables that significantly influenced space use ($P < 0.05$) were those with coefficients with 95% confidence intervals that did not overlap zero. I used the slope of regression models as a measure of predictive ability of logistic models (Howlin et al. 2004), and calculated probability of use plots for top-ranked continuous models. I used selection ratios from each species’ top ranked model to determine the strength of selection between land cover variables (Keating and Cherry 2004).

Results

Space use (deer location relative to land cover type) at the landscape scale varied temporally by site and species (Figure 4.1). Patterns of use between both sites were similar for crop and CRP usage. Crop usage decreased during 12-day firearm, and became most critical during the 12-day hunting season; comparatively to other seasons for all groups except south white-tailed deer. Simultaneously, use of CRP also increased for both species during the 12-day firearm seasons except for mule deer in the north site and south white-tailed deer. North deer woodland usage increased from rut into the 12-day firearm season, and woodlands were more important for white-tailed deer than mule deer. Pasture use was high during every season for every group, except north white-tailed deer. Urban and water use were negligible (<0.03 m) for both species.

Population-level selection of macro habitat differed between species. There was only one top model that held weight for each group and respective season. There were no competitive models within 2 ΔAICc units in either model suite, for any group or season (Table 4.1). The top model for north mule deer was slope, during all three seasons (annual $\beta = 0.43 \pm 0.005$; rut $\beta = 0.57 \pm 0.02$; 12-day firearm $\beta = 0.65 \pm 0.03$; Figures 4.2, 4.3, 4.4; Table 4.1). North mule deer selected for the steepest slopes during the annual and rut time periods. The top model for mule deer in the south varied by time of year (Table 4.1). Similar to north mule deer, slope was the top-ranked model that best predicted home range selection during the annual period ($\beta = 0.56 \pm 0.006$) for south mule deer (Figure 4.2). Elevation, was the top model for south mule deer during rut ($\beta = 0.43 \pm 0.02$) and during 12-day firearm ($\beta = 0.51 \pm 0.03$) (Figures 4.3, 4.4). South mule deer exhibited a positive linear relationship with elevation and selected for higher elevations (Figures 4.3, 4.4).

Landcover was the top ranked single variable model which best predicted population level selection for adult white-tailed deer during all seasons (Table 4.1). Annually, north white-tailed deer selected for woodland, crop, CRP, and avoided pasture (Figure 4.5). Strongest selection occurred for woodlands ($\beta = 3.57 \pm 0.03$) followed by CRP ($\beta = 2.21 \pm 0.02$). During rut and 12-day firearm, north white-tailed deer similarly selected for woodland, crop, and CRP, and against pasture (Figures 4.6, 4.7). Woodlands, followed by CRP, were the two land cover categories that exhibited the strongest selection during rut ($\beta = 2.51 \pm 0.13$, $\beta = 2.11 \pm 0.08$, respectively) and during 12-day firearm ($\beta = 2.82 \pm 0.19$, $\beta = 2.68 \pm 0.13$, respectively). Annually, south white-tailed deer selected for CRP, crop, pasture, and against woodland (Figure 4.5). They selected strongest for CRP ($\beta = 1.46 \pm 0.02$). During rut, south white-tailed deer selected for CRP, crop, pasture, and against woodland, selecting the most for CRP ($\beta = 1.78 \pm 0.06$; Figure 4.6). In the 12-day firearm season, white-tailed deer again strongly selected for CRP ($\beta = 1.42 \pm 0.09$) and showed minimal selection for crop ($\beta = 0.08 \pm 0.06$), while selecting against pasture (Figure 4.7). Woodlands was removed from the south white-tailed deer 12-day firearm candidate set to prevent artificial inflation.

Discussion

Space use at the landscape scale varied temporally by site and species. Patterns between both sites were similar for crop and CRP usage; crop usage decreased during 12-day firearm for both species including all groups except south white-tailed deer; while CRP usage shifted, and out of all seasons, became most critical during the 12-day hunting season for south mule deer and north white-tailed deer. Woodland use increased from the rut period into the hunting season, and was most vital for white-tailed deer. Population-level selection of macro habitat differed between species. Slope and elevation were the top models most important for herd-level home range selection by mule deer, during all three time periods. Landcover was the top-ranked model predicting herd home range selection by white-tailed deer in all time periods (annually, rut, and 12-day firearm). White-tailed deer exhibited the strongest selection for woodlands followed by CRP in the north site, and for CRP in the south site.

Crop use at the landscape scale decreased during the 12-day firearm season for mule deer in both sites and north white-tailed deer. Simultaneously, CRP use increased from rut into the hunting season, and became more important for south mule deer and north white-tailed deer. This finding indicates deer may be shifting use away from crop and towards tall CRP grasslands during the hunting season, which could be harder for hunters to access, and may provide a form of vertical structure that acts as security cover and shields deer from hunter view. Higgins (1987) hypothesized that CRP grasslands provide a necessary resource in heavily cultivated farmlands with limited cover; such as the south study site. Female white-tailed deer in the northern Great Plains selected for CRP bedding sites during a mild winter (Grovenburg et al. 2010a). Similarly, white-tailed deer fawns selected for bedding sites in tall CRP grasslands, which provided both concealment from predators and a layer of thermoregulatory protection (Grovenburg et al. 2010b). Although there are no studies in the Great Plains that specifically explored whether adult males use CRP as a form of security cover during the hunting season, it is safe to assume they may be making similar judgements to avoid hunter detection by using CRP fields.

Woodland usage at the landscape scale also increased from rut into the hunting season for north mule deer and white-tailed deer at both sites. This is in accordance with the literature that reports white-tailed deer typically use riparian areas and other areas with dense screening cover (Martinka 1968, Krausman 1978, Severson 1981). During the cooler months, deer use woodland areas for thermal insulation and to curtail energy costs (Verme 1965, Dusek 1980, Swenson et al. 1983). Whittaker and Lindzey (2004) suggested that home ranges of white-tailed deer were based on perceived level of security and available thermal cover. Similarly, Kilgo et al. (1998) reported white-tailed deer in Florida, USA, adapted their behavior to avoid hunters by avoiding open areas and selecting certain landscape features, such as areas of mature pine forests. Deer in my study may have also been using woodlands for security cover, with added protection from cooler temperatures during the hunting season. While south mule deer did not increase their woodland usage from rut to the 12-day firearm season, north mule deer did. This may have been because there is more available tree cover in the north site. Mule deer may use woodlands in a similar way as white-tailed deer in areas with abundant woodland cover to evade hunter detection and minimize thermoregulatory costs.

Slope and elevation were factors in the top-ranked models most important for herd-level home range selection by mule deer during all three time periods. Similar studies in the Great Plains reported that in sympatric areas mule deer used higher elevations (>870 m) and steeper slopes than white-tailed deer (e.g., Brunjes et al. 2006). By selecting for slope and elevation during the 12-day firearm season, in the north and south sites, respectively, mule deer may be making selections to enhance their predator escape strategies and increase their survival. Geist (1981) suggested the differing escape strategies of mule deer and white-tailed deer may contribute to interspecific selection of differing habitat features. Seton (1929) found that mule deer could escape dogs in rugged, uneven terrain but not in open plains. Mule deer carefully watch predators from far distances and move in open spaces far more frequently then white-tailed deer, selecting for areas of rough and broken terrain that are an advantage to them but a disadvantage to predators, vertically bounding away from danger in areas of difficult footfall (Geist 1981). By using a higher elevation vantage point, mule deer might better observe hunters at a greater distance who they perceive as predators. By using steeper slopes, they are showcasing their evolutionary adaptations that have better suited them to stott and bound in rocky areas, which are difficult for predators to follow, rather than rely on speed as white-tailed deer do.

Landcover was the top-ranked model predicting herd-level home-range selection for white-tailed deer in all time periods (annually, rut, and 12-day firearm). White-tailed deer exhibited the strongest selection for woodlands followed by CRP in the north site, and selected strongest for CRP in the south site. In the north site, both annually and at vulnerable times for adult male deer (rut and 12-day firearm season) white-tailed deer characteristically selected woodlands, as predicted based on other studies that explored white-tailed deer habitat relationships (Martinka 1968, Krausman 1978, Severson 1981). Walter et al. (2011) also tested seasonal resource selection patterns by male mule deer and white-tailed deer in Nebraska. They reported that landcover influenced selection of resources by white-tailed deer during both winter and summer; selection was most influenced to proximity of woodland cover, particularly during the winter. Similarly, Whittaker and Lindzey (2004) reported that mule deer and white-tailed deer had significant differences in their seasonal species distributions, and patterns were most distinct in the winter. White-tailed deer selected areas based on security and thermoregulatory cover, with greater proportions of riparian trees in their home ranges during all seasons.

Despite landcover being the top ranked model for white-tailed deer in the north, white-tailed deer selected for CRP and against woodlands annually and during rut in the south site.

This is similar to female white-tailed deer in South Dakota, which selected for CRP and against wetland forests during a mild winter (Grovenburg et al. 2010a). In my study, this could be occurring if CRP is perceived as a higher quality resource in terms of security cover, and potentially perennial forage depending on the time of the year (spring and summer). Swenson et al. (1983) reported that deer showed variation in wintering strategy based upon cover and food resources available within their home range. It is possible that the limited amount of woodland available in the south site was not of sufficient quality in terms of offering concealment or security cover (i.e., primarily shelterbelts in close proximity to people), and deer at the population level avoided those woodlands in a response to avoid humans. It is also possible that available woodlands were not managed in a way that is advantageous for white-tailed deer; potentially being too dense, or thick to offer early seral stage nutritious forage, or conversely, being too sparse as to offer satisfactory security or thermal cover.

Mule deer and white-tailed deer space use at the landscape scale, and population-level selection varied temporally in western Kansas. Space use at the landscape scale indicated that deer of both species may both be using similar patterns to avoid detection by hunters by increasing use of either CRP or woodlands during the 12-day firearm season. It is possible that whatever factors are driving mule deer decline could be exacerbated by interspecific competition, but results of my study showed that both species are most likely partitioning resources in a way that benefits their evolutionary adaptations. By each species selecting for different macrohabitat features during all three time periods (annually, rut, and 12-day firearm), it appears that resource partitioning may be occurring on a temporal scale, similar to Brunjes et al. (2009). It would also appear that deer at the population level are selecting for macrohabitat features that separate them topographically as well; as mule deer selected for higher elevations than white-tailed deer, similar to reports from other studies of deer in the Great Plains. Although the magnitude of topographical features that separate mule deer and white-tailed deer in other areas may not be as prominent in Kansas, the elevational gradient seems to be sufficient to allow for mule deer to select higher elevations, and for white-tailed deer to select other available features (i.e., woodland) that they deem more beneficial to their fitness.

Mule deer populations and distributions in the western Great Plains are declining. My objectives were to examine temporal space use at the landscape scale, and population-level resource selection of macrohabitat by adult male mule deer and white-tailed deer in western Kansas during three time periods (annually, rut, and 12-day firearm season). I hypothesized that temporal space use would vary throughout the year, with mule deer and white-tailed deer using and selecting for land cover categories strategically during the 12-day firearm season to increase security cover (i.e., increased usage of woodland and CRP), and white-tailed deer would use woodlands at the greatest proportion during the hunting season, using woodlands more than mule deer. Temporal space use did vary throughout the year by site and species, and both species did use space strategically during the hunting season. White-tailed deer did use woodlands more than mule deer; however, they did not use woodlands during 12-day firearm more than during the annual period. Concurrently, I hypothesized mule deer would select for macro habitat features such as topographic roughness, slope and elevation. There was evidence supporting this hypothesis as mule deer in western Kansas, did select for slope and elevation during all time periods; these selections differed from those of white-tailed deer which arguably made population level selections based primarily off of thermal and security cover, similar to male white-tailed deer in Colorado (Whittaker and Lindzey 2004).

Management Implications

At the population scale, mule deer in western Kansas select for steep slopes and high elevations. As these macrohabitat features cannot be actively managed, I suggest concentrating management efforts on strategic solutions that could help boost mule deer survival; actions which provide thermal cover, forage, and concealment from predators and hunters. Woodlands already present on the landscape, are important to mule deer during critical time periods (12-day firearm season), by using selective tree harvest, and managing woodlands in a way which promotes early seral stage understory growth, it will provide mule deer with nutritious forage which will help males obtain necessary energy reserves for rut, and aid in combatting rut carry over effects. Additionally, well managed woodlands would provide mule deer with browse through the winter; a time when forage availability is limited. By increasing and promoting CRP to private landowners, mule deer will have added security cover during the hunting season. Lastly, crop use was high during all time periods for both species, encouraging landowners to leave waste grain and late season standing corn may assist in bolstering mule deer survival for males that survived the 12-day firearm season.

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Figures and Tables

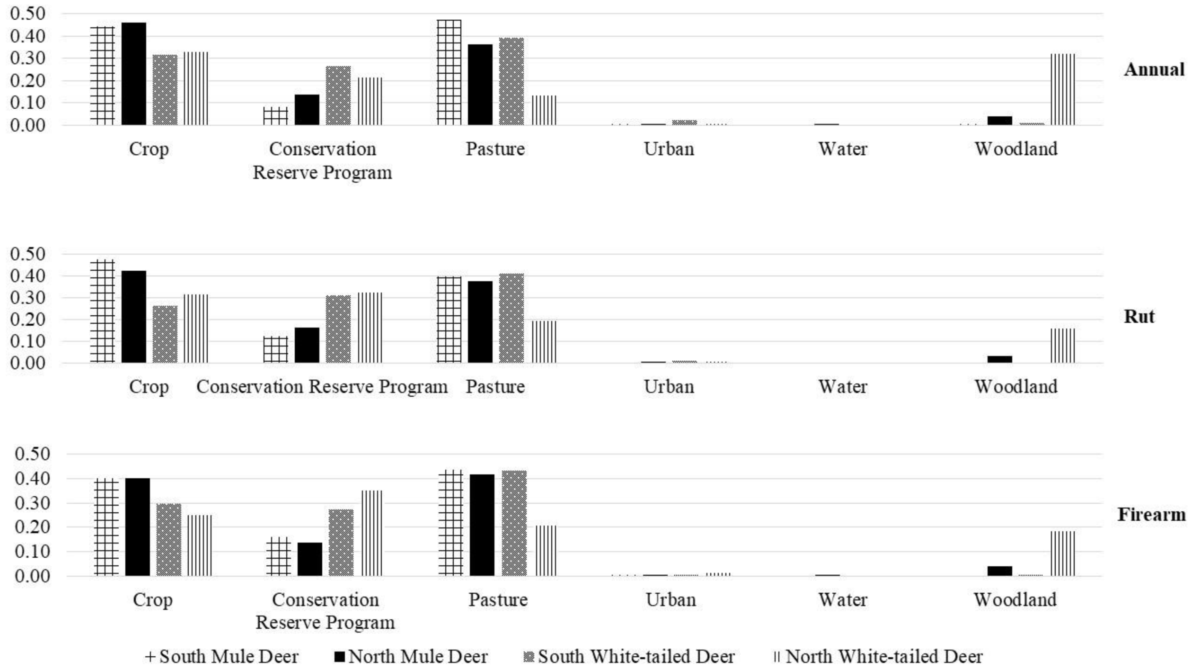

Figure 4.1. Landscape level use (deer location [proportion of GPS points] relative to landcover type) during the annual, rut, and 12-day firearm season, for combined study years (2018, 2019) for adult male white-tailed deer, and mule deer at two study sites; the north site (Norton, Graham, Sheridan, Decatur counties) and the south site (Gove, Scott, Logan, and Lane counties) in western Kansas, USA.

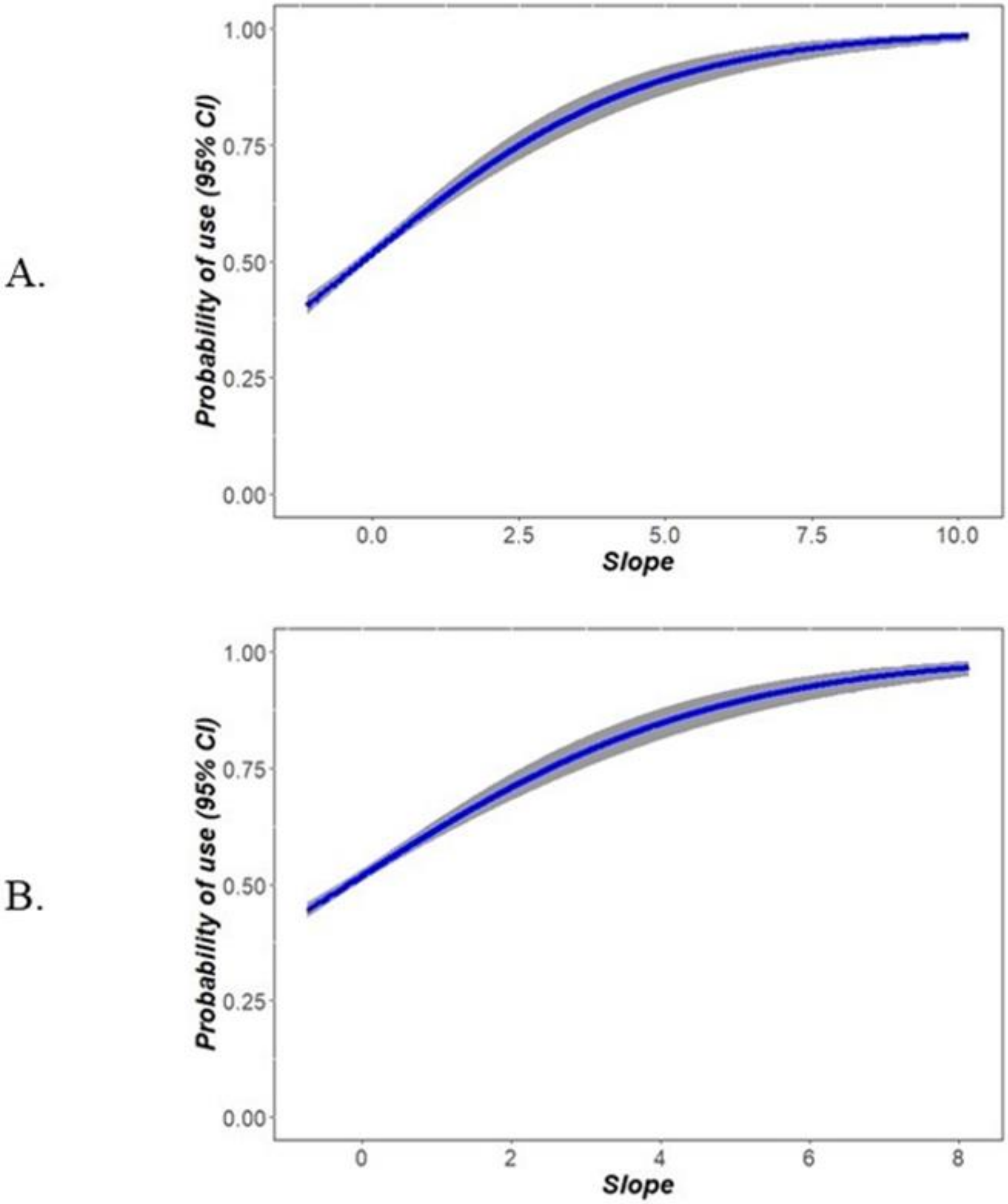

Figure 4.2. Z-transformed annual probability of use for slope by adult male mule deer in the north site (A.) that included Graham, Sheridan, Decatur, and Norton counties, and the south site (B.) that included Gove, Scott, Logan and Lane counties in western Kansas, USA, during 2018 and 2019. Prior to transformation slope values ranged from (0-41º) in the north site and, (0-45º) in the south site.

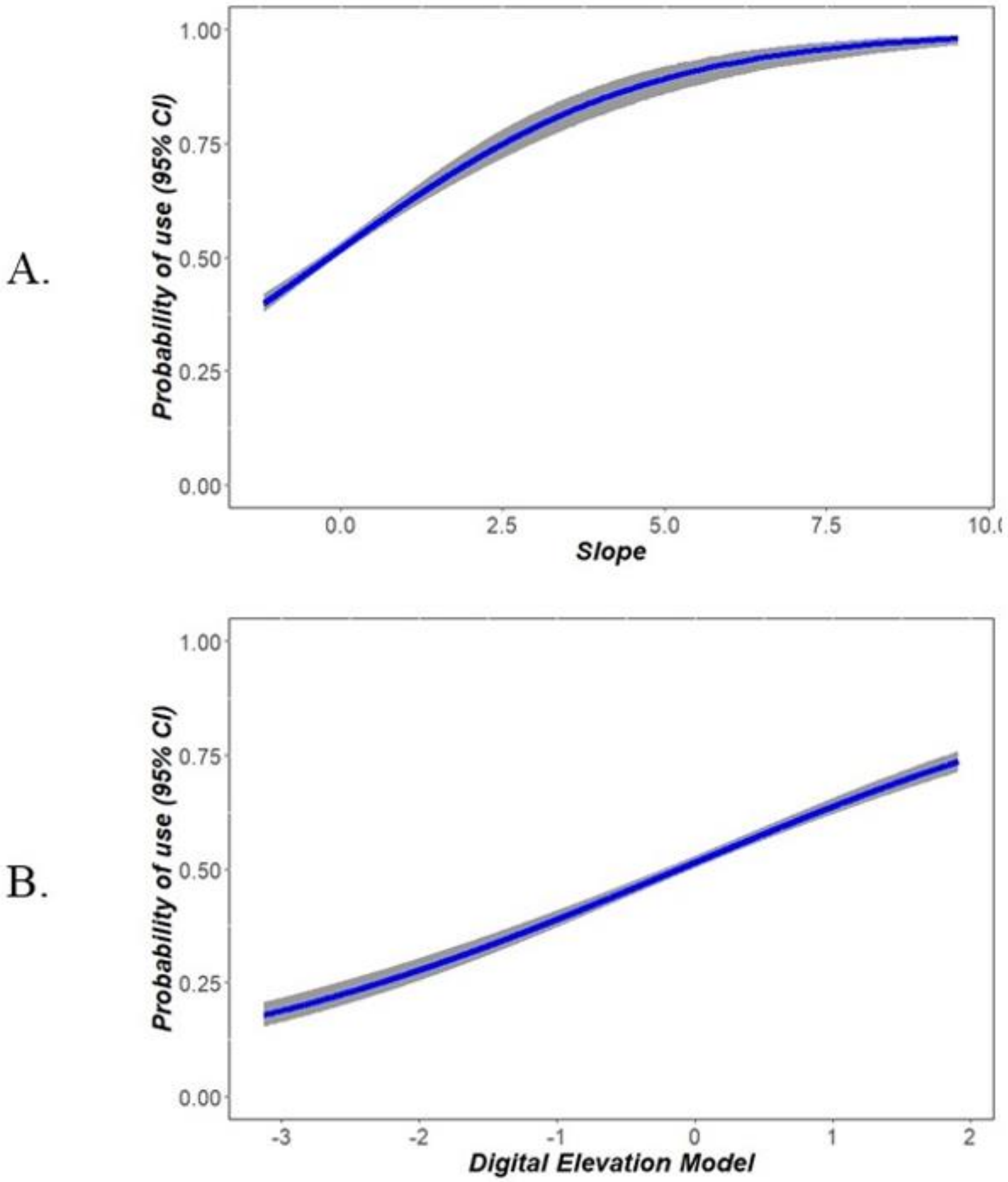

Figure 4.3. Z-transformed probability of use of slope by mule deer during the rut season in the north site (A.) that included Graham, Sheridan, Decatur, and Norton counties, and z-transformed probability of use of elevation of mule deer in the south site (B.) that included Gove, Scott, Logan, and Lane counties in western Kansas, USA, during 2018 and 2019. Prior to transformation, slope values in the north site ranged from (0-37º) and elevation values ranged from (762-941 m) in the south site.

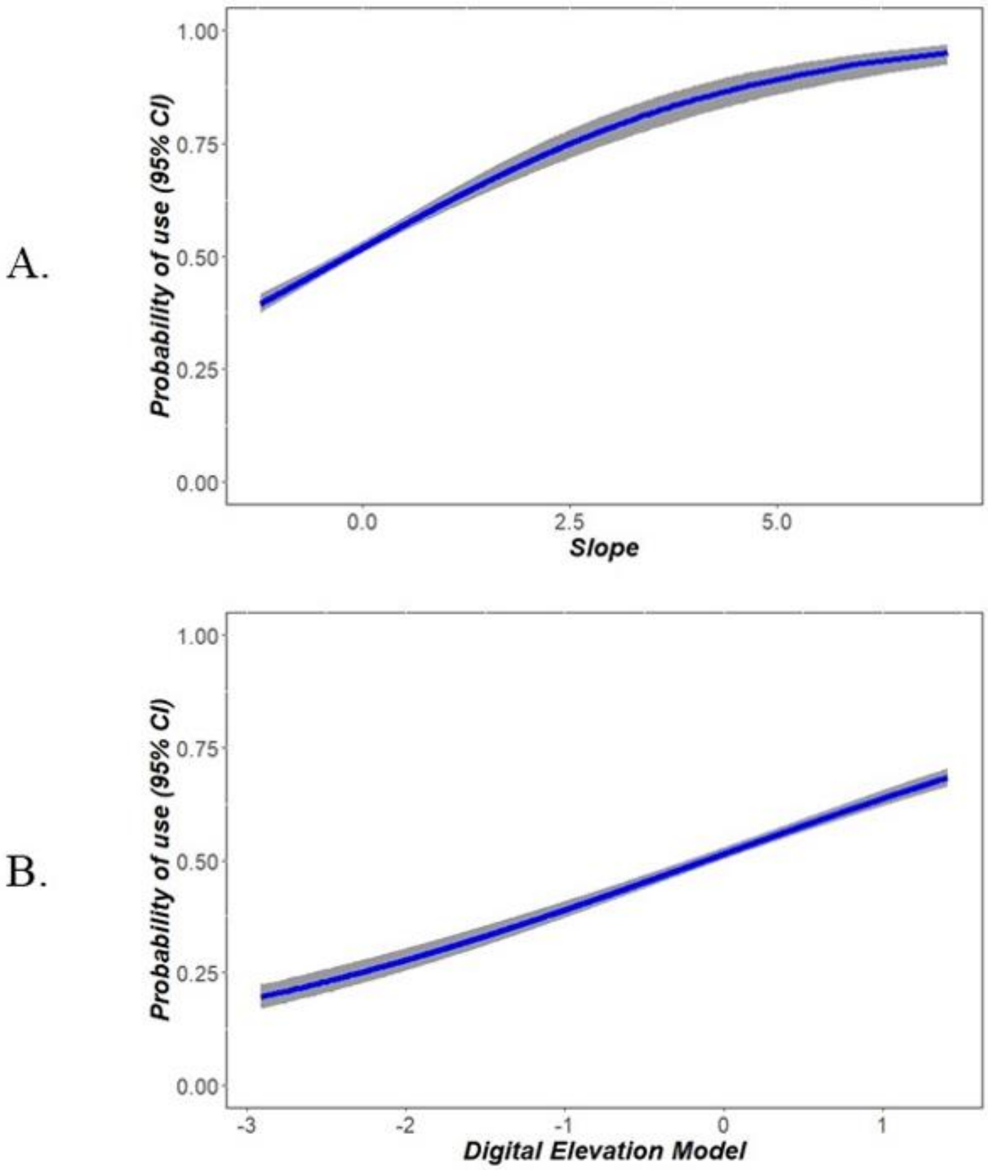

Figure 4.4. Z-transformed probability of use of slope by mule deer during the 12-day firearm season in the north site (A.) that included Graham, Sheridan, Decatur, and Norton counties, and z-transformed probability of use of elevation of mule deer in the south site (B.) that included Gove, Scott, Logan, and Lane counties in western Kansas, USA, during 2018 and 2019. Prior to transformation slope values in the north site ranged from (0-30º) and elevation ranged from (764-921 m) in the south site.

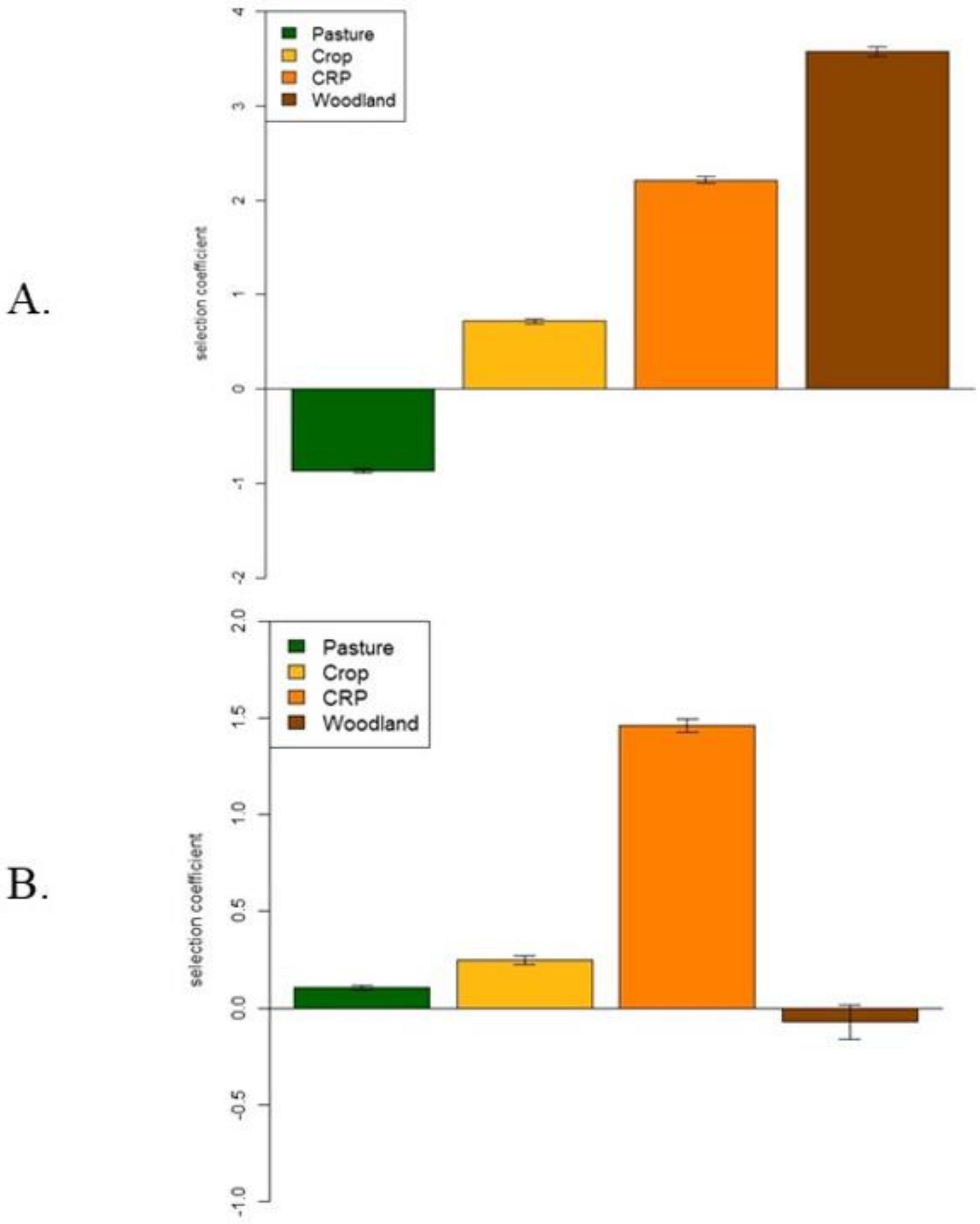

Figure 4.5. Annual selection strength of land cover types (pasture, crop, CRP, and woodland) in white-tailed deer home ranges at the herd level in the north site (A.) that included: Graham, Sheridan, Decatur, and Norton counties and south site (B.) that included: Gove, Scott, Logan, and Lane counties, in western Kansas, USA, during 2018 and 2019.

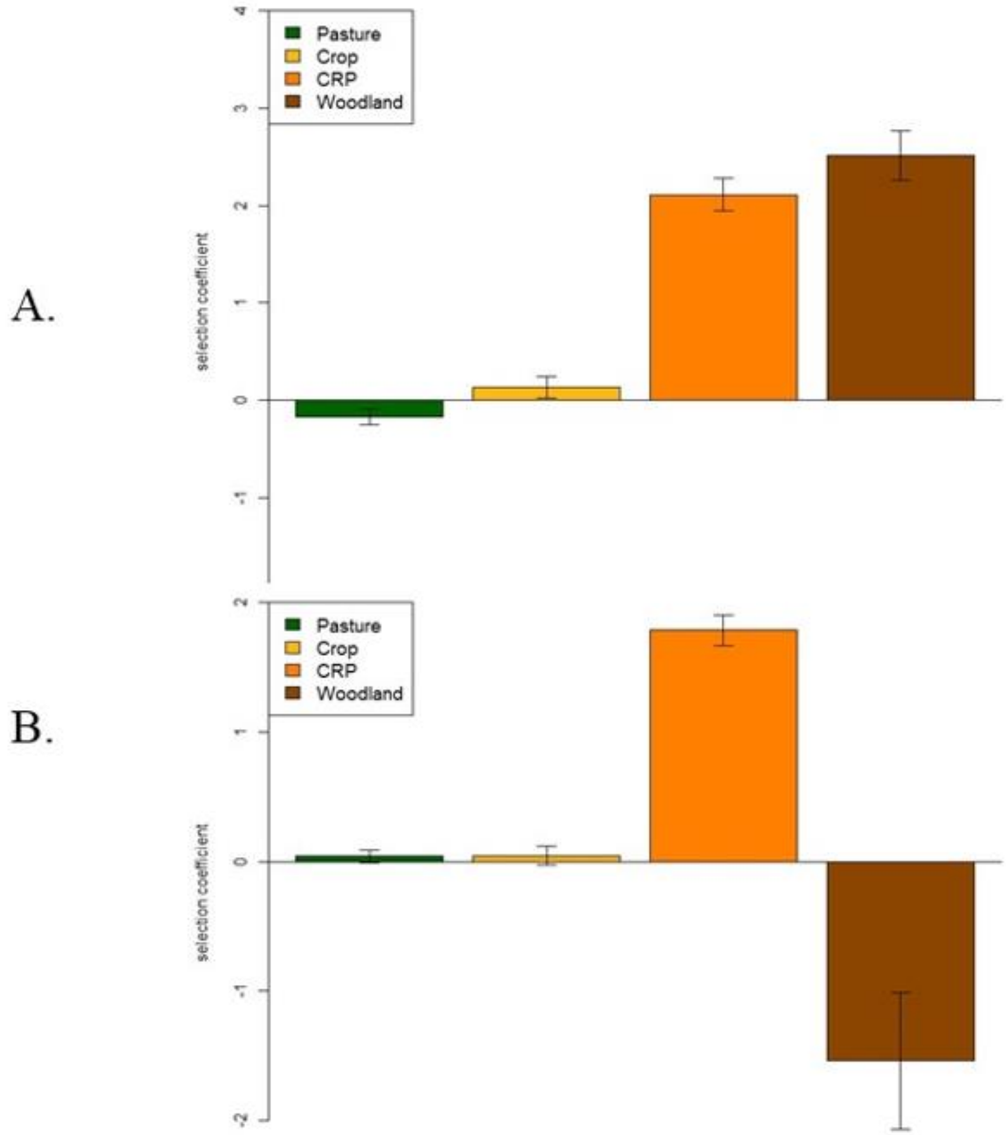

Figure 4.6. Selection strength of land cover types (pasture, crop, CRP, and woodland) during rut in white-tailed deer home ranges at the herd level in the north site (A.) that included: Graham, Sheridan, Decatur, and Norton counties and south site (B.) that included: Gove, Scott, Logan, and Lane counties, in western Kansas, USA, during 2018 and 2019.

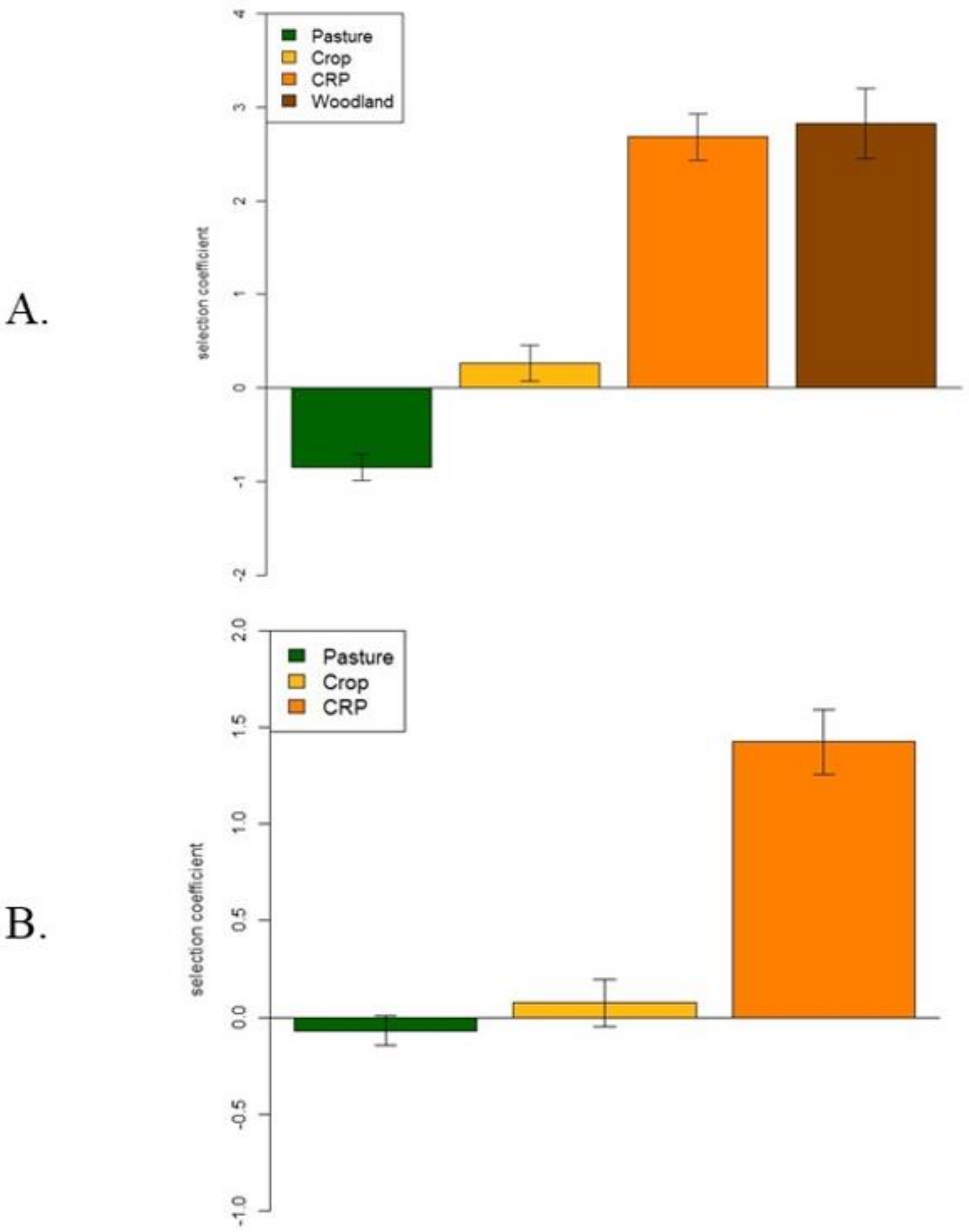

Figure 4.7. Selection strength of land cover types (pasture, crop, CRP, and woodland) during 12-day firearm season in white-tailed deer home ranges at the herd level in the north site (A.) that included: Graham, Sheridan, Decatur, and Norton counties and south site (B.) that included: Gove, Scott, Logan, and Lane counties, in western Kansas, USA, during 2018 and 2019.

Table 4.1. Top-ranked model results for adult male mule deer and white-tailed deer from respective model suites tested separately including single variable models relevant for predicting home range selection at the population scale: (elevation, aspect, slope, topographical roughness, and land cover) for every season (annual, rut, and 12-day firearm), for both species of deer at the north (Sheridan, Decatur, Graham, Norton counties) and south (Scott, Gove, Lane, and Logan counties) study sites in western, Kansas, USA, during 2018 and 2019. There were no competing models <2 ΔAICc from any top-ranked model.

Season & Group	**Top Model**[a]	**AICc**[b]	**ΔAICc**[c]	**ω**[d]	**K**[e]	**LL**[f]
Annual						
North Mule	Slope	268947.1	0	1	2	-134471.60
South Mule	Slope	232735.7	0	1	2	-116365.80
North White-tailed	Landcover	164346.8	0	1	4*	-82169.40
South White-tailed	Landcover	234148.7	0	1	4*	-117070.40
Rut						
North Mule	Slope	21388.4	0	1	2	-10692.20
South Mule	Elevation	18668.2	0	1	2	-9332.089
North White-tailed	Landcover	8837.5	0	1	4*	-4414.75
South White-tailed	Landcover	18683.3	0	1	4*	-9337.63
12-Day Firearm						
North Mule	Slope	8141.9	0	1	2	-4068.94
South Mule	Elevation	7535.5	0	1	2	-3765.74
North White-tailed	Landcover	3281.1	0	1	4*	-1636.56
South White-tailed	Landcover	7109.7	0	1	3**	-3551.85

[a] Highest ranked model out of previous candidate set (elevation, aspect, slope, topographic roughness, and land cover type)

[b]. Akaike's Information Criterion corrected for small sample size (Burnham and Anderson 2002)

[c.] Difference in AICc relative to minimum AIC

[d] Model weight

[e] Number of parameters

[f] Log likelihood

*Urban category removed out of top ranked landcover models to prevent artificial inflation

**Urban and woodland categories removed out of landcover model to prevent artificial inflation