THESIS

MOVEMENT ECOLOGY OF MULE DEER IN PARTIALLY MIGRATORY HERDS

Submitted by

Anneke R. M. Hart

Department of Fish, Wildlife, and Conservation Biology

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Master’s Committee:

Advisor: William Kendall

Mat Alldredge
George Wittemyer
Randall Boone

ABSTRACT

MOVEMENT ECOLOGY OF MULE DEER IN PARTIALLY MIGRATORY HERDS

The purpose of animal movement can be broadly partitioned into two categories of factors that either push or pull animals to move (Loe et al. 2009). Animals will move towards resources, such as food or mates, that are necessary to complete their life cycle. Likewise, they will move away from threats, such as predators or inclement weather, to survive. Movement therefore helps augment an animal's ability to access resources and avoid threats because these variables are typically also moving and changing across space and time. There is great diversity across taxa in how animals move. There is huge variation in the distances, regularity, and area over which animals move – certainly across species but often also within species. In all cases, we can expect that the strategy of movement that animals develop will have been shaped by selective processes where animals made choices about how to access resources and avoid threats that subsequently affected their fitness.

In ungulates, a type of movement evolved independently across 17 different lineages (Abraham et al. 2022) that is thought to help them access high-quality forage throughout the annual cycle – i.e., migration. Ungulates that live in mountainous regions can typically maximize their nutrition by spending their winters at low elevation then following the green up as it progresses to higher elevations in the summertime. Selective pressures have shaped herbivore behavior so that they can learn to track food resources as they change in quantity and quality across a landscape. Migratory ungulates typically time their migrations to maximize access to high-quality food resources.

Mule deer (*Odocoileus hemionus*) are unique among ungulates in that they tend to be extremely habitual in their seasonal movements. Like other cervids, they are plastic in terms of timing their movements but exhibit strong fidelity to their seasonal ranges and choice of movement strategy. Mule deer typically establish migratory or resident tactics as adults and stick to that behavior life-long. They also adhere closely to established migration routes and utilize the same extents of seasonal ranges year after year. Mule deer therefore can respond to a seasonally changing environment but are limited in doing so within a fixed spatial extent.

In this work, I examined how migratory strategies of mule deer affect 1) resource selection of irrigated lands and 2) survival of adult females and fawns. The two chapters I produced were unified by an aim to understand the nuances of mule deer movement ecology in two partially migratory herds in south-central Colorado. In my first chapter, I examined how fluctuations in natural forage abundance influence the movements of mule deer in an agricultural system, where irrigation provides enhanced foraging opportunities for ungulates. Mule deer tended to increase their selection for alfalfa when their native forage was poor in quality. In my second chapter, I assessed how migratory strategies influenced survival of fawns and adult female mule deer. I detected apparent tradeoffs in survival of mule deer relative to their migratory strategy. Migrant fawns tended to have higher early survival while residents had higher overwinter survival. Additionally, there was interannual variation in the benefits of migration on survival of adult female deer. My research contributes to a broader understanding of how fluctuations in forage abundance drives mule deer movement and how the movement strategies that deer choose to obtain forage then influences their survival.

Abraham, J. O., N. S. Upham, A. Damian-Serrano, and B. R. Jesmer. 2022. Evolutionary causes and consequences of ungulate migration. *Nature Ecology & Evolution* **6**:998–1006.

Loe, L. E., A. Mysterud, V. Veiberg, and R. Langvatn. 2009. Negative density-dependent emigration of males in an increasing red deer population. *Proceedings of the Royal Society B: Biological Sciences* **276**:2581–2587.

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CHAPTER ONE

Natural Forage Abundance Influences Mule Deer (*Odocoileus hemionus*) Selection for Agriculture

SUMMARY

Ungulates track nutritious forage as the quantity and quality of vegetation changes seasonally across landscapes. Resource tracking at broad scales (i.e., during migrations) is well documented in ungulates; however, this behavior likely also occurs at smaller scales. In agricultural systems, forage availability is not bound to the natural growing season. Irrigation prior to natural spring green-up and after autumn senescence may therefore allow extended foraging opportunities for ungulates. Identifying the patterns and drivers of ungulate crop use is useful to mitigate crop depredation and address other potentially negative impacts of ungulate congregations in agricultural fields. We examined how fluctuations in natural forage abundance influenced mule deer (*Odocoileus hemionus*) selection for hay and alfalfa in two partially migratory mule deer herds in the semi-arid region of south-central Colorado. Mule deer tended to increase their selection for alfalfa in low-precipitation years and within seasons when their natural forage was scarce. Patterns in deer selection for hay relative to fluctuations in the availability of natural forage were less clear. We also found that deer altered their patterns in selection for agriculture at a small scale; resident deer that had agriculture available increased their selection for productive natural vegetation in summer of high-precipitation years. Our results suggest that habitat treatments that promote the growth of high-quality, drought-resistant forage surrounding agricultural fields may help to minimize undesirable deer congregations.

INTRODUCTION

Movements of wild herbivores are strongly influenced by fluctuations in forage availability (van der Graaf et al. 2006, Monteith et al. 2011, Bischof et al. 2012). Agricultural landscapes offer potentially enhanced and extended foraging opportunities for herbivores and can therefore alter wildlife behavior. For example, modifying resource availability can change patterns in animal migrations (Jones et al. 2014). In elk (*Cervus canadensis*), access to agriculture can reduce migratory behavior (Middleton et al. 2013, Barker et al. 2019). Migratory birds, such as Sandhill Cranes (*Antigone canadensis*), often select for forage in grain fields (Pearse 2017, Boggie et al. 2018) to fuel their long-distance movements. Though foraging in agricultural fields may enhance the nutritional condition of some species, this behavior is not without consequence. Annual costs of crop depredation by wildlife are estimated to be around $498 million in the United States (Conover et al. 1995). Also, it is not clear if the benefit of agricultural forage provides a net positive impact on wildlife fitness when other factors are considered. Agricultural fields may sometimes serve as ‘evolutionary traps’ (Schlaepfer et al. 2002) for wildlife (Penteriani et al. 2018, Costa et al. 2021), whereby animals are attracted to these fields for the nutritional benefits but suffer survival or reproductive costs when using these habitats. For example, crops can cause wildlife to congregate at higher densities than typically occur in natural landscapes (Sorensen 2014), which can increase transmission of pathogens (Miller and Conner 2005, Smith et al. 2009), and thereby lower wildlife fitness.

Hay and alfalfa fields offer high-quality forage for cervids, and rank within the top five crops most commonly grown in the western US (Putnam et al. 2000). Hay fields are managed for productivity through seeding, application of fertilizers, and irrigation. In certain seasons, these crops may therefore yield better forage for cervids compared to surrounding natural vegetation.

Managing mule deer (*Odocoileus hemionus*) behavior around agricultural fields may be especially challenging because mule deer tend to be less plastic in their behavior compared to other ungulates (Morrison et al. 2021). Additionally, deer that use agricultural fields during fall tend to congregate on private land, which can create challenges in managing a hunted species (Burke et al. 2018, Gruntorad and Chizinski 2020). Deer also account for a significant portion ($100 million, around 20%) of annual US wildlife crop depredation costs (Conover 2002, Johnson et al. 2014).

To address the issues associated with deer use of agriculture, it is helpful to first identify the patterns and drivers behind this use. Variable use of hay and alfalfa fields by ungulates is likely influenced by disproportionate energy requirements across seasons, fluctuating availability of native and agricultural vegetation, and prevalence of migratory strategies within populations. Garrott et al. (1987) documented that mule deer in western Colorado typically used irrigated hay meadows most heavily in the spring before migrating to summer range and during the fall after returning to winter range. Fall and spring are critical foraging times for ungulates because the sparse vegetation and harsher weather of winter necessitate the acquisition of energy at either end of the winter season (Hurley et al. 2014). Foraging in irrigated hayfields during fall and spring may allow deer to extend their access to succulent vegetation before natural spring green-up and after autumn senescence (Garrott et al. 1987). Winter use of agricultural fields by ungulates has also been documented; however, forage quality in agricultural meadows may be lower than natural vegetation during winter (van Beest et al. 2014) when forbs and grasses will generally be of poorer nutritional quality compared to woody browse (Bartmann 1983). Use of hay and alfalfa fields by deer shortly before summer harvest will conflict most with agricultural production. Both natural and agricultural forage will typically be abundant in summer; however, differences in the quality of irrigated and natural vegetation may be more apparent in arid regions, especially in years of low precipitation.

Studies have documented seasonal variability in ungulate use of agricultural fields, but the effect that annual precipitation has on ungulate use of agriculture has infrequently been considered. This variable is especially important in the United States Intermountain West, where rainfall is minimal and plant productivity is low overall. Increased precipitation provides succulent and nutritious forage for mule deer (Garrott et al. 1987; Schuyler et al. 2019). Precipitation positively affects the productivity of natural vegetation and provides greater availability of water for irrigation. Agricultural fields will typically still be irrigated in dry years, even if the overall availability of water is less, which may result in starker differences in the quality of irrigated versus natural forage in low precipitation years. This difference in quality may affect the frequency with which ungulates choose to forage in crop fields. Although hay and alfalfa fields offer high-quality forage, individuals may only choose to use these fields when they offer better forage than the surrounding native vegetation. Ungulates may select for agricultural forage to meet their metabolic needs but avoid these fields more generally in favor of seeking habitats with better hiding cover (Pierce et al. 2004) and thermal shelter (van Beest et al. 2012) that are farther from human activity (Northrup et al. 2016).

Whether deer alter their patterns of crop use seasonally or inter-annually may also depend on the prevalence of migratory behavior within populations. Migratory ungulates typically move to high elevation ranges in summer (Russell 1932, Bishof et al. 2012, Middleton et al. 2013), therefore crop depredation is most likely the result of resident behavior. Resident strategies in ungulates are associated with higher levels of human-wildlife conflict (Middleton et al. 2013, Robb et al. 2019), and are common in areas where agriculture is available (Robb et al. 2019).

Additionally, migratory and resident deer utilize different mechanisms by which they can alter their use of crops. In fall and spring, migratory deer can alter their selection for agriculture by changing their migration timing, or by varying the frequency of their selection for crops within their seasonal range. Residents can only utilize the latter tactic. Migratory mule deer are capable of altering the timing of their migrations to maximize their access to high-quality forage (Monteith et al. 2011), but overall, deer exhibit minimal plasticity in the spatial extent of the seasonal ranges they utilize (Garrott et al. 1987, Sawyer et al. 2019, Morrison et al. 2021). Therefore, resident mule deer may minimally alter their patterns of selection for agriculture if fidelity to behavior has a stronger bearing on patterns in selection than changes in environmental conditions.

To examine how fluctuations in natural forage abundance influences ungulate use of agriculture, we used resource selection functions (RSFs) to examine patterns in mule deer selection for hay and alfalfa in two partially migratory deer herds in south-central Colorado. Our objectives for this study were to 1) compare mule deer selection for agriculture in years of high and low precipitation 2) identify patterns in deer selection for hay and alfalfa forage across seasons, and 3) examine differences in inter-year and inter-seasonal selection for crops by migrant and resident deer.

METHODS

Study Area

We collected data for this study in two adjacent deer Data Analysis Units (DAUs D-16 and D-34, Fig. 1.1) in the semi-arid region of south-central Colorado. DAUs are intensive CPW big game monitoring areas that encompass the total annual range of specific herds. The annual ranges of these two herds encompass a 12,675 square-kilometer area that includes parts of Teller, Park, Lake, Fremont, Chaffee, Custer, Huerfano, and Pueblo Counties. Fifty-two percent of land within this region is privately owned. Annual precipitation ranges from lows < 15 cm in the valleys and highs > 64 cm at high elevations (Grigg 2020, Vitt 2020). Elevation ranges between 1500 to >4250 meters. Mountains in this region include the Mosquito, Sangre de Cristo, and Wet Mountain Ranges. Mule deer in these herds are partially migratory, and most migrant use of agriculture occurs on their winter range. Vegetation is highly variable across the region but includes alpine tundra, subalpine forests, semidesert shrubland, plains grassland, and pinion-juniper woodlands. Small-scale hay and alfalfa crops and cattle ranching are common land uses in river valleys and along tributaries in this region. Alfalfa and grass hay production are also the 3rd and 4th most common crops by acreage grown in Colorado (Putnam et al. 2000). Flood and sprinkler irrigation are the most common methods used to irrigate fields in south-central Colorado. Duration of field irrigation within a given year depends on water availability and ditch priority, but April-October is typical (Brady Everett, personal communication in Salida, CO). In low precipitation years, landowners with older water rights may call for ditch priority, meaning that landowners with newer water rights must cease irrigating sooner so that those with senior priority may obtain full access to their water allotment (Waskom et al. 2014). Thus, water may become less available in low precipitation years, but typically some irrigated fields will still be available to deer into October. The timing of harvest within the region depends on crop type, irrigation method, and water availability. Sprinkler-irrigated hay and mixed hay/alfalfa are usually cut twice in mid to late June and again in August. Pure alfalfa can be cut 3 times. Flood-irrigated hay is usually cut once in mid to late June. Natural habitat is abundant throughout this system, and agricultural land accounts for a small proportion (~2%) of the cumulative study region. Agricultural fields are typically interspersed among native vegetation, rather than grown in dense monocultures as often occurs in plains systems.

Mule Deer Monitoring

We captured and fitted mule deer with GPS collars at neonate, 6-month, and adult age classes between 2017 and 2021 as part of ongoing survival monitoring occurring in this region. Both male and female deer were captured as fawns, but only females were captured as adults. We retained a sample of 266 individual mule deer that met the criteria for our analyses (see next section). Adult deer were collared using Vectronic Vertex Plus Iridium collars and were monitored for an average of two years excluding mortalities. Adults were captured between late February through March via helicopter. Adults were typically captured annually at 8 locations within the region, though not all deer within this sample had agriculture available in their home ranges. Adult collar fix rates were variable depending on year and season. For most of the year, locations were collected at a 13-hour rate then increased to 3–4-hour intervals during summer to identify parturition. In June and July, we located and captured neonate fawns opportunistically, using vaginal implant transmitters (VITs), and by tracking in on collared, non-VIT female deer. We also captured fawns in winter (November-February) via ground darting and helicopter. Fawns were collared using expandable Vectronic Vertex Globalstar Mini collars and monitored for an average of one year, excluding mortalities and premature collar loss. Fawn collars were programmed to transmit one GPS location per day and stored additional data onboard the collars, collected at 2-hour intervals, that only became available once these collars were retrieved.

Deer Data Processing

We retained deer for our analyses that had both agricultural and native forage available in their home range. Because we aimed to detect changes in deer foraging relative to the quality of available habitat, we filtered our used sample to locations collected during foraging hours and at night (Fig. 1.2). We defined this period as between 2 hours before sunset through 2 hours after sunrise. Deer typically use hay and alfalfa fields during dawn and dusk (Garrott et al. 1987, Rauscher et al. 1995), which is when ungulates tend to forage (Kufeld et al. 1988, Beier and McCullough 1990, Kie et al. 1991). Ungulates often avoid open areas and locations close to human activity during the day (Beier and McCullough 1990, Ager et al. 2003, Godvik et al. 2009, Bonnot et al. 2013). Therefore, we expected general avoidance of crop fields during the daytime. Limiting our sample to locations collected during foraging hours and at night allowed us to retain most of our used sample, which was already coarse in resolution, while eliminating locations collected during periods we expected avoidance of agriculture. We extracted sunrise and sunset times at the center of our study area using the R package Stream Metabolism (Sefick 2023).

We censored individuals from seasonal models if their collars collected fewer than 30 GPS locations during foraging hours in that season. A minimum of 30-50 locations from 20-25 animals is usually sufficient to estimate RSFs for one resource feature (Alldredge and Ratti 1986; Millspaugh et al. 2019). To draw inference on population-level resource selection, which was the goal of our study, sampling many individuals is recommended (Millspaugh et al. 2019). Prioritizing large sample sizes of GPS locations per individual is more important when individual-level inference is the primary objective (Millspaugh et al. 2019). We also censored GPS data from fawns younger than two months. At two months of age, a fawn’s behavior starts to more closely resemble that of an adult (Jackson et al. 1972). Although fawns are still nursing at this age, we assumed their locations would mirror their mother's foraging behavior until they reach independence. We also censored fawns if their maternal doe was included in our sample (n=4), due to lack of independence between their movements.

We removed erroneous deer GPS locations prior to our analyses. We removed any fixes without associated location data (dilution of precision = zero). We retained 3-D GPS locations (GPS unit contacts ≥ 4 satellites) and removed any 2-D GPS locations (GPS unit contacts = 3 satellites) to achieve location accuracy within 100 meters (Lewis et al. 2007). We additionally estimated the speed of deer movements to flag potentially incorrect start/end dates (speed=0) and remove locations if speed exceeded 10.8 km/hour (Ortega 2023).

We identified migratory versus resident deer by calculating net-squared displacement (Bunnefeld et al. 2011) and visually examining deer movements using the program Migration Mapper (Merkle et al. 2022). Deer were defined as migratory if their displacement graph indicated a 'top hat' shape (Bischof et al. 2012) and their seasonal ranges did not overlap (Dusek et al. 1989, Van Deelen et al. 1998). Deer that resided in one area all year (flat displacement curve) or exhibited short distance 'range shifts' where they could easily move back and forth between ranges were considered residents. We also classified any deer not monitored during the migratory period as residents, given that their seasonal home ranges were similar in size to the annual ranges of resident deer.

Land Cover and Environmental Covariates

To capture the fine-scale productivity of natural and agricultural vegetation, we derived the Normalized Difference Vegetation Index (NDVI) for each season between 2017 and 2021 in our study area using Landsat 8 and 9 satellite imagery in R Studio. NDVI is calculated from red and near-infrared light refraction and is correlated with primary productivity (Parker 2003). Values close to zero indicate low plant productivity and values approaching 1.0 indicate high productivity. Landsat 8 and 9 collect imagery every 8 days cumulatively between the two satellites at a 30 x 30-meter resolution. We first removed pixels with cloud or snow contamination. We then calculated NDVI for each pixel using the red (Band 4) and near-infrared (Band 5) bands as NIR-Red/NIR+Red (Tucker 1979). We then calculated the mean, max, and range of NDVI pixels for each season and year between 2017-2021 across our study region. We classified landcover types for each pixel using a National Land Cover Database (NLCD, Dewitz and US Geological Survey 2021) layer from 2019 and removed values classified as water and values < 0 indicating water or snow. We replaced missing NDVI values with the mean for each land cover type for every year and season. We chose this method instead of removing points with missing values from our analyses to retain more of our used sample, given our sample size limitations.

We defined overall year quality by examining the total annual rainfall averaged across the study area. We averaged precipitation for each year using monthly data from DayMet (Thornton et al. 2020). More rainfall occurred within odd years between 2017 and 2021 in our system (Fig. 1.3). We also examined variation in precipitation by season within years (Fig. 1.4). Spring and summer precipitation had the greatest influence on annual variation in precipitation.

Precipitation was lower in fall and winter overall, and there was less variation in precipitation across years within these seasons.

We used two GIS layers created by the Colorado Division of Water Resources for the Arkansas River Valley region (CDWR 2015 and 2020) to identify irrigated agricultural lands across the study area. Only fields that had an associated irrigation structure were included in these data layers. These layers describe field crop type, irrigation method, and whether the irrigation structure diverted water in the year the layer was derived. If the irrigation structure associated with a field did not divert water or the field fell below a peak NDVI threshold, that field was classified as "No Crop." We compared the 2015 and 2020 data layers to reclassify fields into categories of alfalfa, hay/pasture, or unknown crop. We classified fields as unknown crops if they were assigned "No Crop" in both 2015 and 2020. We assigned fields as hay/pasture or alfalfa if they had been classified into these categories in either 2015 or 2020. Fields that switched between hay/pasture and alfalfa were rare, but we classified these as alfalfa if they were grouped into that category in either year. We additionally used NLCD data (Dewitz and US Geological Survey 2021) to identify forested versus open native habitats. We distinguished between these types of natural habitats in our analysis because NDVI values of forested habitats correlate to the quality of the canopy rather than the understory that deer use for forage (Hurley et al. 2014).

Resource Selection Functions

We first examined deer use of agriculture by season to determine an appropriate temporal scale to investigate resource selection. Deer used agricultural fields the least in winter and the most in fall (Fig. 1.5). We chose to examine selection at the scale of 3-month seasons because this scale captured some important within-year variation that may have been lost if models had been simplified to a two-season structure (i.e., notably fall and spring elicit different behavior in relation to agriculture). Seasons were thus structured as Fall (Sep-Nov), Winter (Dec-Feb), Spring (Mar-May), and Summer (June-Aug). We used annual precipitation to categorize our data into high- and low-quality seasons/years (Fig. 1.3). We considered a year to be low quality if precipitation was below the average (46.23 cm) for the 5 years of our study. We categorized winter years as 'low precipitation' when the preceding year was low-precipitation – e.g. 2018 was a low precipitation year, so winter 2018-2019 was classified as low-precipitation.

To address our objectives, we fit population-level resource selection functions in a use-availability framework (Manly et al. 2002) at the scale of individual home ranges (3rd order selection, Johnson 1980) using logistic regression. To draw our sample of available points, we first estimated annual home ranges for each individual by creating 100% minimum convex polygons (Mohr 1947) around all used locations (not limited to foraging hours). Then we randomly sampled points within each home range. We determined an appropriate number of available locations by conducting a sensitivity analysis – i.e. running multiple RSF model iterations using a variable number of available points for each seasonal model until we found the minimum number needed to produce stable coefficient estimates (Northrup et al. 2013). We found that estimates stabilized when our available sample was 25 times the number of used points collected per individual.

We first ran RSF models with our combined dataset to examine the effects of variables we hypothesized would influence selection for agriculture and compared model fit using the Akaike Information Criterion (AIC). We then structured seasonal RSF models using the covariates identified as salient in the top model to address our objectives. This ensured model structure between seasons was the same and comparable. We compared all preliminary models against a null hypothesis (no variation in selection). We separately examined whether landcover status (agriculture, open native vegetation, forest), resource type (alfalfa, hay, unknown crop, open native vegetation, forest), or irrigation method (flood, sprinkler, none) best explained variation in selection and chose to use resource type because it had the lowest AIC (Table 1.1). We also examined whether an interaction between resource type and the (scaled and centered) mean, range, or maximum seasonal NDVI value of patches improved model fit and selected maximum NDVI which had the lowest AIC (Table 1.1).

We then ran 8 generalized linear mixed-effect models separated by season and overall year quality, in which individuals were included as random effects, to identify population-level patterns in selection for agriculture relative to the availability of native forage. All models included an interaction between resource type and seasonal maximum NDVI of patches. We used open vegetation as our reference class for resource type. We included individual deer as a random intercept, which helps to account for uneven sampling of used locations across individuals (Gilles et al. 2006). We verified that the proportions of migrants and residents in each of our separate models were equal, and randomly removed individuals to standardize the proportions where needed (Table 1.2, model sample sizes). Annual home ranges of migratory deer are much larger than that of resident deer, therefore we expected that migrants could have larger coefficients for selection of agriculture in certain seasons, which might bias population-level patterns if sampling was unequal. We ran 16 additional models that were separated by migratory strategy (migrant vs resident) to understand whether detected changes in population-level selection were a product of changes in migration timing or were also influenced by smaller-scale changes in resident behavior.

RESULTS

Selection for Alfalfa

Our models for resource selection of all deer (total population selection) supported our hypothesis that deer selection of alfalfa would differ by season in relation to natural conditions. Specifically, we found an increase in selection for alfalfa in low precipitation years and in seasons when native forage was scarce. Deer strongly selected for alfalfa over natural vegetation in fall of low precipitation years but selected for alfalfa equally to open vegetation in fall of high precipitation years (Fig. 1.6). In fall of low precipitation years, deer selected for alfalfa over open natural vegetation even when those fields were at the mean productivity of all other available vegetation (Fig. 1.7, $\hat{\beta}$ = 1.145, LCL = 0.996, UCL = 1.294). In summer, deer selected for alfalfa equally to open vegetation in low precipitation years at all levels of productivity but chose open vegetation over alfalfa in high precipitation years when both resources were highly productive (Fig. 1.6). In winter and spring of low precipitation years, deer selected for alfalfa over open natural vegetation when these fields were highly productive but did not select for alfalfa when it was equally productive as the other available vegetation (Fig. 1.6, Fig. 1.7). In spring of high precipitation years, deer selected more strongly for alfalfa even when fields were similarly productive to the natural vegetation. In winter of all years, deer strongly avoided alfalfa when it was equally productive as the available vegetation. Alfalfa productivity had a stronger positive effect on selection in low precipitation years across all seasons (Fig. 1.8). This increase was strongest in less productive seasons (fall, spring, and winter). Alfalfa productivity had an especially strong positive effect on selection for alfalfa in winter of low precipitation years (Fig.

1.8, $\hat{\beta}$ = 1.10, LCL = 0.897, UCL = 1.30), when we would expect general scarcity of productive vegetation overall.

We found differences in the selection of alfalfa between resident and migrant deer. Patterns in selection for alfalfa by migrants differed from residents in spring and summer but were similar in fall and winter. Migrants and residents both increased their selection of alfalfa in fall and winter of low precipitation years (Fig. 1.9, Fig. 1.10). Productivity of alfalfa had a strong positive effect on migrant selection in fall of low precipitation years, but minimally influenced resident selection in fall of all years (Fig. 1.11). Still, residents strongly selected for alfalfa in fall of low precipitation years regardless of productivity (Fig. 1.12) and were predicted to select for alfalfa over open vegetation in fall of low precipitation years even at low values of NDVI (Fig. 1.9). Migrants and residents were both predicted to select for alfalfa over open vegetation in winter of low precipitation years when productive fields were available (Fig. 1.9, Fig. 1.10). In spring, residents increased their selection for productive alfalfa in low precipitation years, although they appeared to select similarly for open vegetation when the productivity of both resources was equivalent (Fig. 1.9). In contrast, migrants selected for productive alfalfa over open vegetation in spring regardless of annual precipitation (Fig. 1.10). In summer, residents increased their selection for alfalfa in low precipitation years (Fig. 1.12), though the effect of alfalfa productivity in low precipitation years was similar to that of open vegetation (Fig. 1.11). Still, residents were predicted to select for alfalfa over open natural vegetation in summer of low precipitation years at high levels of productivity. Even more notable was how strongly they preferred productive open natural vegetation over alfalfa in high precipitation years (Fig. 1.9). We were not able to precisely estimate summer selection for alfalfa by migrants (and thus we omitted estimates from Fig. 1.12 due to wide confidence intervals but see Appendix Table A1.1 for full output of RSF Coefficients).

Selection for Hay/Pasture

Deer selected for grass hay less strongly than for alfalfa overall. It was less clear how the availability of native forage affected patterns in deer selection for hay compared to alfalfa. When deer had a choice between foraging in hay and open vegetation patches that were both at average values of productivity, deer selected open vegetation over hay in fall of low precipitation years, spring of high precipitation years, and in winter in all years (Fig. 1.7). Deer selected for hay similarly to open vegetation at average levels of productivity in fall of high precipitation years, spring of low precipitation years, and in summer in all years. Predictive models suggest that deer will select for hay over natural vegetation in fall of low precipitation years when available hay fields are highly productive (Fig. 1.6). Deer were also predicted to slightly increase their selection for hay in winter of high precipitation years when available hay fields are more productive than other available vegetation. Deer selection for hay was similar in high and low precipitation years in spring and summer, but summer selection for hay was notably weaker than selection for open vegetation in high precipitation years.

We again detected some differences in selection for hay between migrant and resident deer. Patterns in fall selection for hay relative to annual precipitation were opposite for migrants and residents; resident deer increased their selection for hay in high precipitation years (Fig. 1.9), while migrants increased their selection for hay in low precipitation years (Fig. 1.10). Resident deer also increased their selection for hay in high precipitation winters (Fig. 1.9), while winter selection for hay was similar for migrants across all years (Fig. 1.10). Annual precipitation minimally affected spring selection for hay by migrants or residents (Fig. 1.9, 1.10). Summer selection for hay was similar for residents in high and low precipitation years. Still, residents selected productive open vegetation over hay at equivalent NDVI values in high-precipitation years, while the inverse was true in low-precipitation years (Fig. 1.9). Migrants selected productive open vegetation over hay in both high and low-precipitation years (Fig. 1.10)

Selection for Unknown Crops

The total population avoided unknown crops relative to open natural vegetation in all seasons when all vegetation was at mean productivity (Fig. 1.7) and patterns in the strength of selection for unknown crops relative to annual precipitation were similar to hay overall. Unknown crop productivity had a similar effect on selection as hay productivity; crop productivity had a strong, positive influence on selection in fall of low precipitation years and in winter of high precipitation years relative to the effect of open vegetation productivity (Fig. 1.8). Although we included the unknown crop category in models we separated by migratory strategy, we struggled to estimate many of the coefficients for migrants because few migrants had unknown crops available to them in their home ranges. Population-level patterns in selection for unknown crops are therefore mostly driven by resident behavior, and this is reflected in the similarity of resident and total population coefficients for unknown crops.

Selection for Forest

Deer generally avoided forest relative to open natural vegetation during foraging hours in all seasons regardless of year quality (Fig. 1.7, Fig. 1.12). Canopy cover (as indexed by NDVI) had a variable effect on deer selection for forest across seasons; in fall and summer of low precipitation years, and in spring, canopy productivity had a slight positive effect on total population selection (Fig. 1.8). In all other seasons, NDVI of forest affected deer selection less or equally to open vegetation. General avoidance of forest by deer suggests that we slightly weakened the effect that agriculture had on selection in certain seasons by separating forest from open vegetation. For example, the strong positive effect of alfalfa that we detected in fall of low precipitation years would have appeared even more strongly positive when comparing it against a reference class that included all non-agricultural resources.

DISCUSSION

Our results suggest that mule deer seek out productive agricultural forage to supplement their native forage when it is poor in quality. We found that total population selection for alfalfa increased in low precipitation years across all seasons when available alfalfa fields were highly productive. We detected an especially strong increase in deer selection for alfalfa in fall and winter of low-precipitation years. Selection for alfalfa was stronger than for open vegetation in fall of low precipitation years, even when available alfalfa fields were minimally productive. This was consistent with our preliminary finding that use of alfalfa was highest in fall overall (Fig. 1.5). Strong selection for productive alfalfa in winter likely does not equate with more intensive use of alfalfa within this season; deer used alfalfa least in winter and avoided alfalfa at mean values of NDVI within all winter seasons. However, this does suggest that deer may congregate at high densities on the few productive alfalfa fields that are available in winter. Results of total population selection for hay relative to the quality of available natural vegetation were harder to interpret overall. While deer did increase their selection for highly productive hay fields in fall of low precipitation years, we did not detect clear patterns across other seasons. We found that deer generally avoided unknown crops relative to other resources in all seasons except during fall in low precipitation years and in winter of high precipitation years if available unknown crops were highly productive. Changes in selection for unknown crops relative to annual precipitation were similar to patterns we found for hay. Most unknown crops were likely either fallow or hay crops, which deer generally avoided compared to alfalfa.

We suspect that the differences in patterns of deer selection for hay versus alfalfa were due to alfalfa fields being more heavily irrigated than hay and because deer prefer forbs over grass. Alfalfa patches tended to have higher NDVI values during the irrigating season (summer and fall) compared to hay (Fig. 1.13). NDVI had a generally positive effect on deer selection, which is consistent with other studies of ungulate resource selection (Morano et al. 2019, Hughey et al. 2021). Therefore, irrigation likely made alfalfa fields more attractive to deer. Additionally, deer typically select for forbs over grass when both are available (Snider and Asplund 1974, Collins and Urness 1983, Torstenson et al. 2006, Schuyler et al. 2021). Grass hayfields often contain forbs, though at lower densities than in alfalfa fields. Our results suggest that patterns in deer selection for hay are likely influenced by whether deer also have access to alfalfa. For example, deer might exhibit similar patterns in selection for hay as alfalfa (i.e., increase their selection for hay in low precipitation years) when only hay is available to them but will likely choose alfalfa over hay in a low precipitation year if both resources are available. This therefore confounds our ability to discern patterns in deer selection for hay in isolation of the effect of alfalfa.

To interpret the increase in selection for alfalfa that we observed across seasons in low precipitation years, we also need to consider the nuances and limitations of using annual precipitation to define high and low forage abundance years. Annual precipitation correlates closely to within-season patterns of precipitation in spring and summer (Fig. 1.3, Fig. 1.4). Annual precipitation is less correlated with fall and winter precipitation, although high precipitation in summer would presumably produce more productive vegetation in the following seasons. The high/low winter categorization thus captures any lagged effects that high or low precipitation in previous seasons has on fall and winter selection. Therefore, patterns of strong selection for alfalfa we detected in fall and winter following a low precipitation year could be a response to an accumulated caloric deficit. Although forage quality tends to be highest in summer, lactation is a major energy tax on adult female deer in summer and fall (Monteith et al. 2014, Bender and Hoenes 2016). Deer that used poor-quality summer habitats may seek out agricultural forage in later seasons to buffer against over-winter energy losses. We did not examine how variable body condition affects selection for alfalfa but expect this may be a factor driving the increases in selection for alfalfa we detected in low precipitation years. In dry regions, deer condition and precipitation are often correlated (Marshal et al. 2008).

We found that resident deer altered their selection within high and low precipitation years. This suggests that mule deer can alter their selection for agriculture at a relatively small scale and that changes in total population selection within high and low precipitation years were not purely a product of migratory deer altering their migration timing. There has been strong support that mule deer are capable of tracking high-quality resources by changing the timing of their migrations (Monteith et al. 2011, Sawyer and Kaufman 2011, Bischof et al. 2012, Lendrum et al. 2013, Merkle et al. 2016, Aikens et al. 2017, Morrison et al. 2021), but weaker evidence for their ability to track resources at smaller spatial scales (Hanley 1982, Langvatn and Hanley 1993, Ortega 2023). Our results support that mule deer are capable of tracking resources that vary in quality at a small scale. Furthermore, we found that in high precipitation years, resident deer increased their selection for open natural vegetation during summer, when most conflict with agricultural production occurs. This suggests that resident deer, who are typically responsible for summer crop depredation, will spend more time foraging in native habitats when they are high in quality. Therefore, habitat treatments that promote the growth of drought-resistant forbs surrounding agricultural fields may help lower rates of crop depredation during the summer season.

We detected changes in selection for agriculture relative to year quality by migrant deer in fall and winter, but selection patterns in spring and summer were consistent across high and low precipitation years. Most migratory deer in our study area utilize native habitats on their summer ranges (Fig. 1.14). We therefore expected minimal changes in summer selection across years. In fall and spring, migratory deer can change their patterns in selection by altering their migration timing or by increasing/decreasing their selection for agriculture within their seasonal ranges. Other studies have found that mule deer migrations are typically more synchronous in spring compared to fall and that spring migrations tend to be closely tied to the timing of spring green-up (Monteith et al. 2011, Lendrum et al. 2013). We found that both fall and spring migrations of deer included in our analyses were fairly asynchronous within years (Fig. 1.15). There was also considerably more variation in the timing of spring migrations across years compared to fall within our study area (Fig. 1.15). This was puzzling to interpret, given that we detected similar patterns in migrant selection for agriculture across years in spring. A possible explanation is that deer may have foraged more intensely on agriculture in years when they migrated earlier to summer range. We found inverse patterns for fall selection. On average, deer returned to their winter ranges around roughly the same time each year but strongly increased their selection for hay and alfalfa in low precipitation years. This suggests that changes in migrant selection within fall of high and low precipitation years were likely due to increased selection after arriving on winter range, rather than due to altering the timing of their arrival.

Differences in selection for agriculture by migrant and resident deer highlight the importance of considering how individual characteristics influence population-level patterns in resource selection. We chose movement strategy as the most important individual characteristic to examine to understand the behavioral mechanisms behind any measured changes in resource selection. However, we acknowledge that other individual traits likely also influence selection for agriculture. For example, sex, age, and reproductive status have been shown to influence ungulate selection (Long et al. 2009, Oehlers et al. 2011, Padié et al. 2015). Additionally, ungulate personality can influence tolerance of human activity (Found 2019) and mediate use of open versus forested habitats (Bonnot et al. 2018). Deer may therefore have variable tolerance of the risks associated with foraging in agricultural fields because of these individual characteristics. Our results suggest that use of agriculture fluctuates for the average deer in our population; however, some deer in our sample may strongly select or avoid agriculture under all conditions and our analyses do not capture this individual variation.

Because we can almost always expect that there will be variation in patterns of selection across individuals, recent publications have suggested that fitting random slopes for individuals should be standard practice for estimating resource selection functions (Muff et al. 2020).

Furthermore, even when population-level inference is the primary objective of a study, intercept-only models can sometimes produce biased estimates and overly high confidence in results (Muff et al. 2020). Therefore, we should be cautious in assuming that differences in selection across seasons and within high and low precipitation years are truly different based on our estimated confidence intervals. We tried fitting random slopes in addition to random intercepts; however, we chose to abandon this approach due to issues with model convergence. We suggest that the dominant patterns in our results, such as strong selection for alfalfa in fall and in winter at high levels of productivity, still bear weight, even though we suspect there may be considerable variation in selection across individuals that our study does not capture.

Additionally, we were not able to examine the full scope of influence that other factors of environment have on resource selection of mule deer outside of agricultural systems, such as distance to cover, distance to water, fine-scale vegetation types, or elevation (Kufeld et al. 1988, Nicholson et al. 1997, Pierce et al. 2004). While these variables have been shown to influence general selection of mule deer in other systems, including these covariates would have considerably complicated our models and thus hindered our ability to interpret our results. Given that we already had a limited sample of used points per individual, we chose to prioritize including the variables most important to our question of interest. While including these variables could provide nuance to patterns in deer selection for agriculture, we do not think including them would change the overarching patterns in selection that we detected. Our results are intended to compare selection for agriculture across seasons and within seasons in high and low precipitation years but should not be interpreted as a comprehensive model of resource selection for this system.

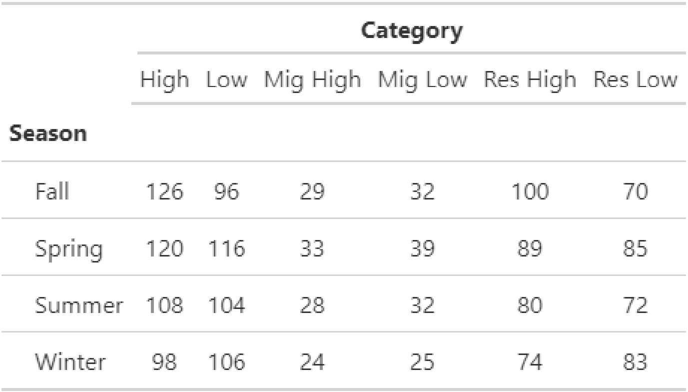
Our results are best interpreted in the context of our study system, and use of these results for prediction in other areas should be limited to areas where hay and alfalfa are the primary crops available to mule deer. Carrollo et al. (2017) examined mule deer selection for agriculture in southwestern Colorado and found that deer selected strongly for sunflower crops in a high precipitation year but preferred alfalfa during a low precipitation year. Therefore, in systems where other desirable crops are available to mule deer, increased precipitation may result in crop switching rather than increased selection for non-agricultural forage. Additionally, we reiterate that in south-central Colorado, natural vegetation is abundantly available in areas where hay and alfalfa are produced. Our results may therefore not apply to areas of dense agricultural production where natural vegetation is scarce. Use of a resource tends to be equal to its availability at extremely high and low levels of availability (Holbrook et al. 2019). Therefore, in systems of extremely high or low densities of agriculture, deer are unlikely to exhibit changes in their selection in high and low precipitation years.

TABLES AND FIGURES

Table 1.1 Results of AIC model selection examining possible covariate structures that influence mule deer selection for agriculture in the D-16 and D-34 mule deer herds in south-central Colorado.

Model	AICc	ΔAICc	DF	logLik
Resource Type * Max NDVI	1937182	0	11	-968580
Resource Type * Mean NDVI	1937201	19.65	11	-968590
Resource Type + Mean NDVI	1937305	123.36	7	-968646
Resource Type + Max NDVI	1937313	131.16	7	-968649
Resource Type * Range NDVI	1942493	5311.56	11	-971236
Resource Type + Range NDVI	1942799	5617.73	7	-971393
Max NDVI	1945918	8736.2	3	-972956
Mean NDVI	1946584	9402.31	3	-973289
Resource Type	1946851	9669.47	6	-973420
Landcover Status	1948763	11581.4	4	-974378
Range NDVI	1949336	12154.04	3	-974665
Irrigation Method	1953486	16304.34	4	-976739
Null	1954425	17243.54	2	-977211

Table 1.2 Model sample sizes of south-central Colorado mule deer in the D-16 and D-34 mule deer herds for resource selection models categorized by season, movement strategy, and precipitation. ‘High’ and ‘Low’ refer to high vs low precipitation years. ‘Mig’ and ‘Res’ refer to migrant versus resident deer. We resampled a total of 266 individual deer for seasonal models. Migrant and resident models do not total to combined models due to eliminating individuals to standardize the proportion of migrants and residents across models.



	Category					
	High	Low	Mig High	Mig Low	Res High	Res Low
Season						
Fall	126	96	29	32	100	70
Spring	120	116	33	39	89	85
Summer	108	104	28	32	80	72
Winter	98	106	24	25	74	83

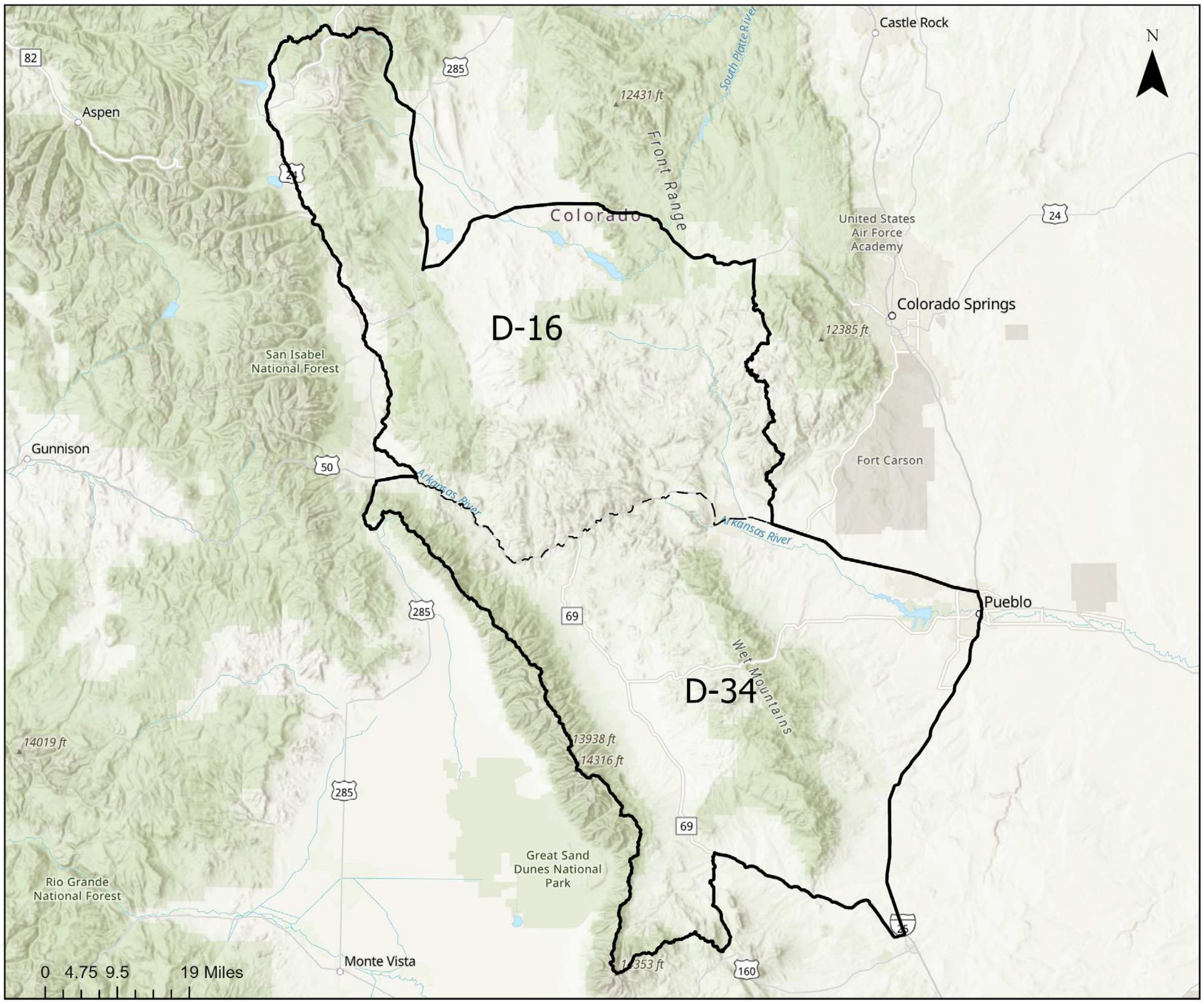


Figure 1.1 Mule deer data analysis units (DAU) D-16 and D-34 located in south-central Colorado.

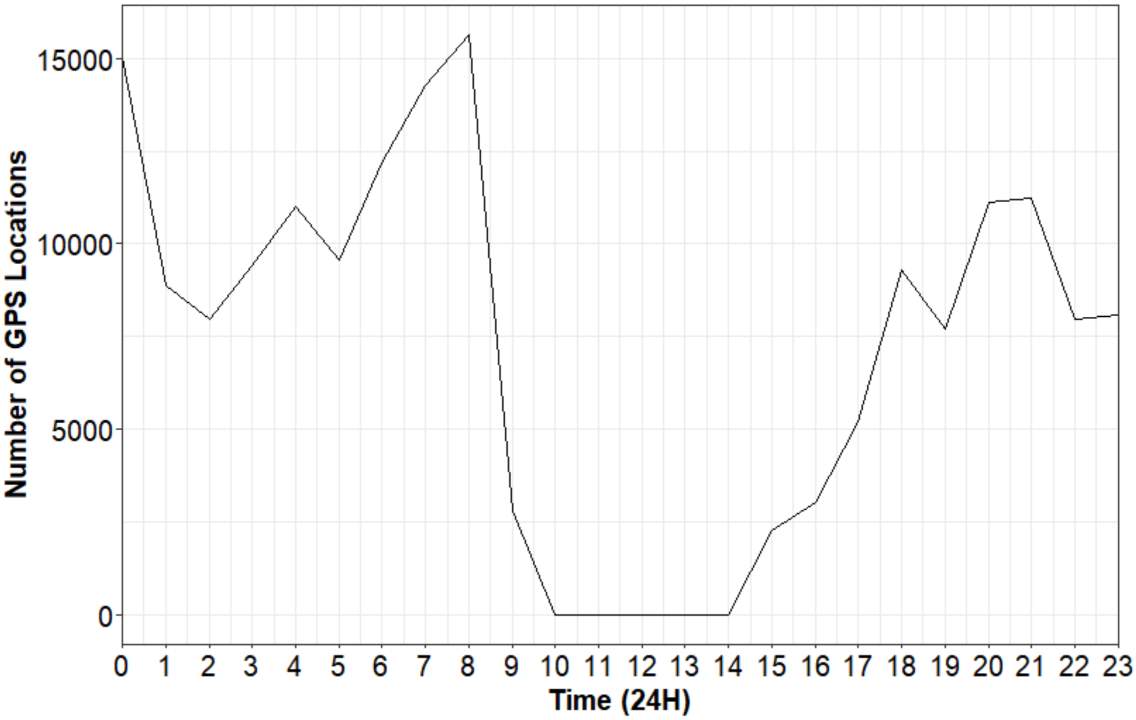


Figure 1.2 Sampling of GPS locations for all south-central Colorado mule deer in the D-16 and D-34 herds included in our analysis across a 24-hour period after filtering locations to only include points taken between 2 hours after sunset through 2 hours after sunrise.

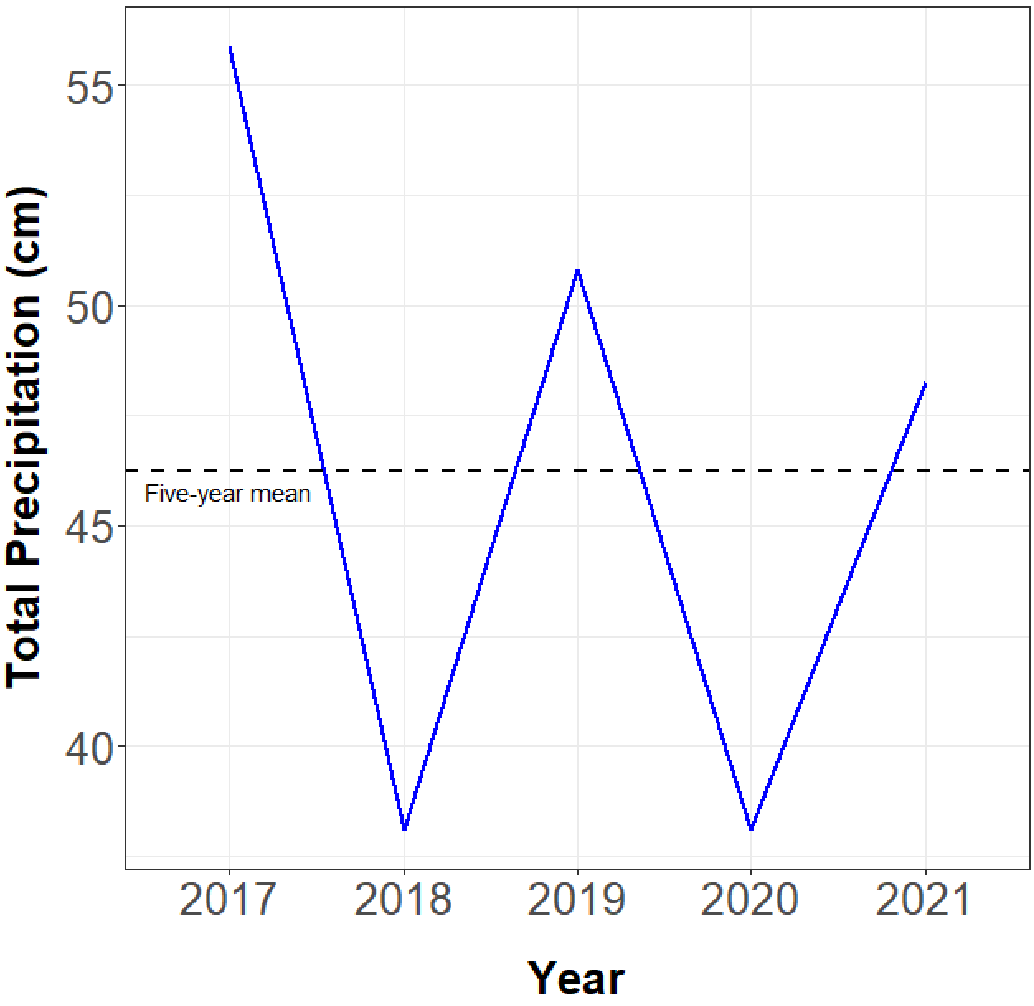


Figure 1.3 Total annual precipitation (cm) averaged across the D-16 and D-34 mule deer study area in Colorado.

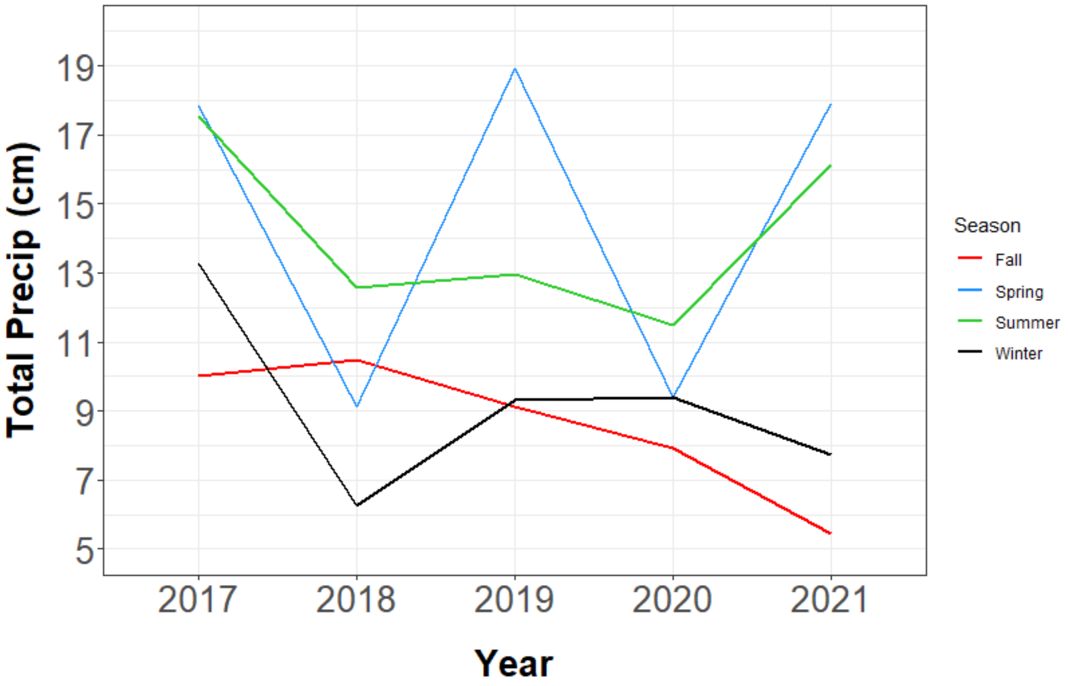


Figure 1.4 Total precipitation (cm) within seasons averaged across the D-16 and D-34 mule deer study area in Colorado.

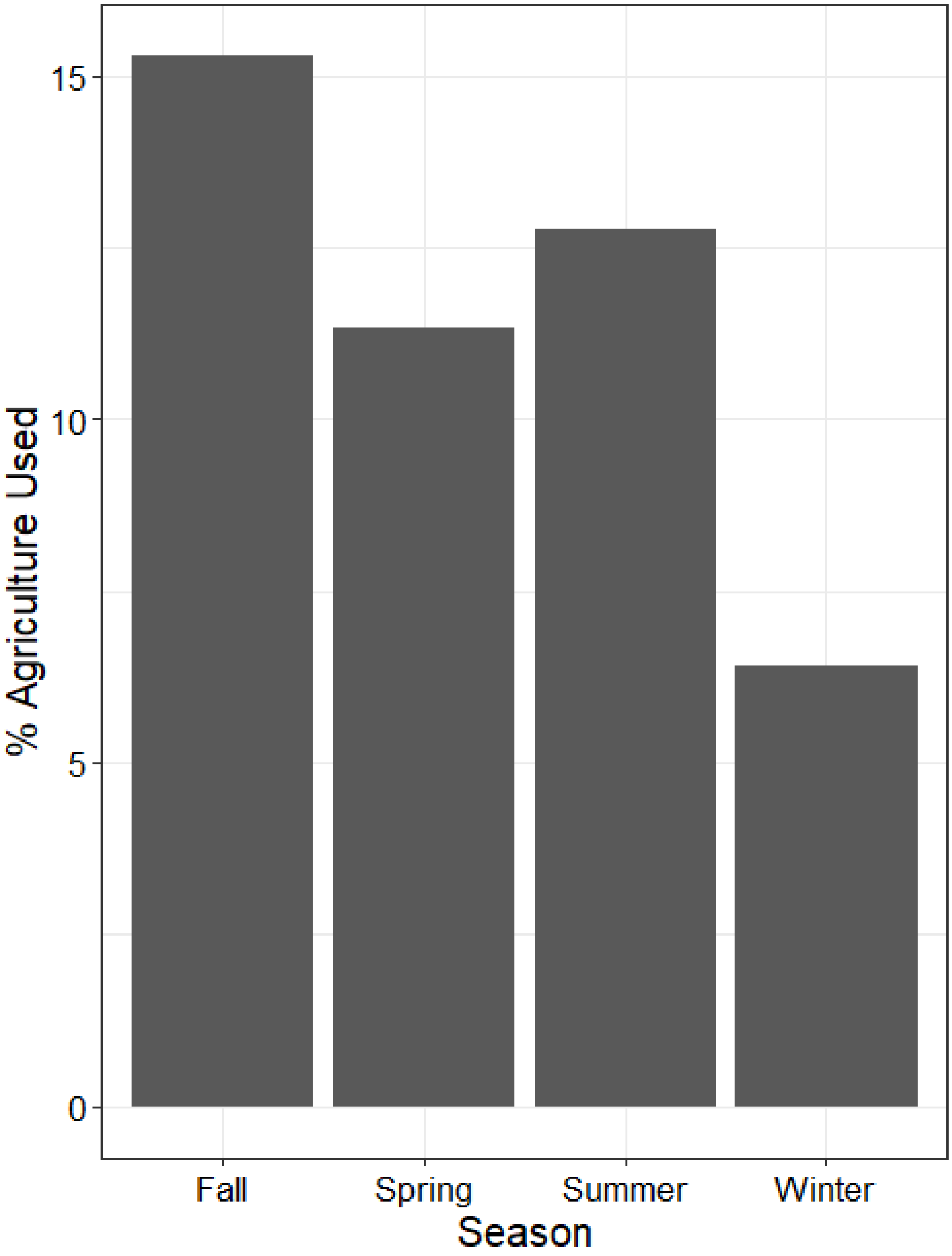


Figure 1.5 Average percentages of agriculture used by mule deer in the D-16 and D-34 herds in Colorado by season.

Total Population Predicted Selection

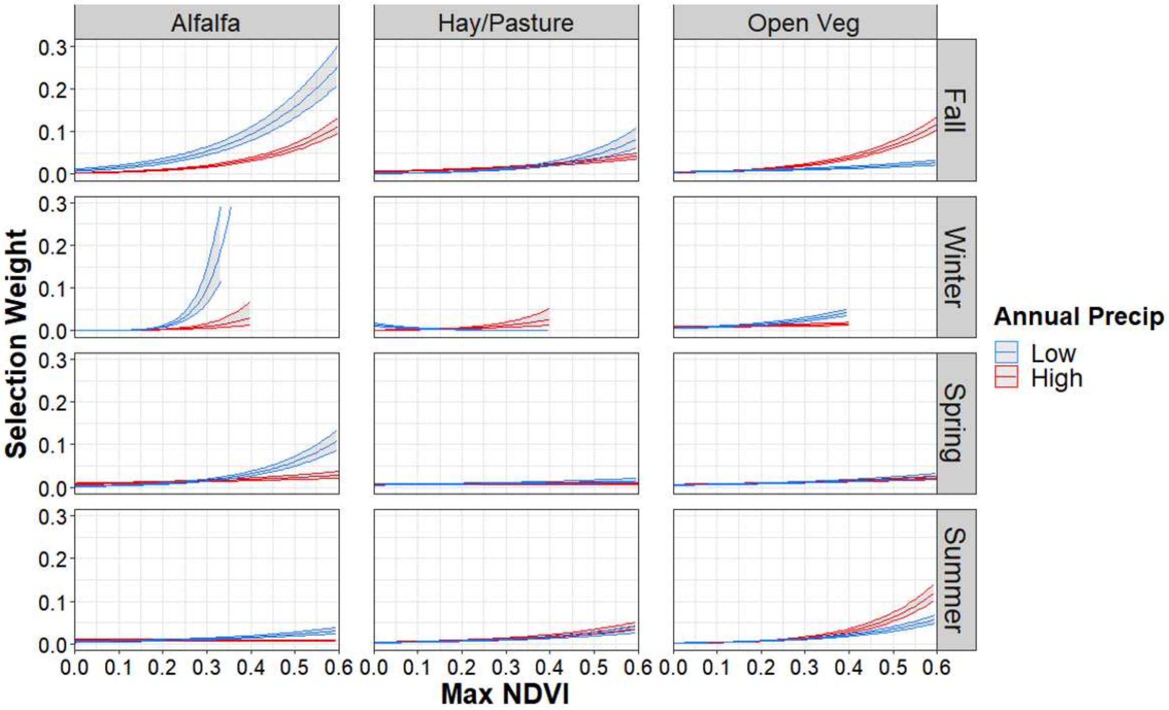


Figure 1.6 Predicted effects of seasonal maximum NDVI on mule deer selection (total population) for alfalfa, hay, and open natural vegetation for model: Selection ~ Resource Type*max NDVI + (1|Individual) across seasons and in high and low precipitation years. This graph depicts the combined effect that resource type and NDVI have on mule deer selection in the D-16 and D-34 mule deer herds south-central Colorado.

Total Population: Coefficients for Main Effects

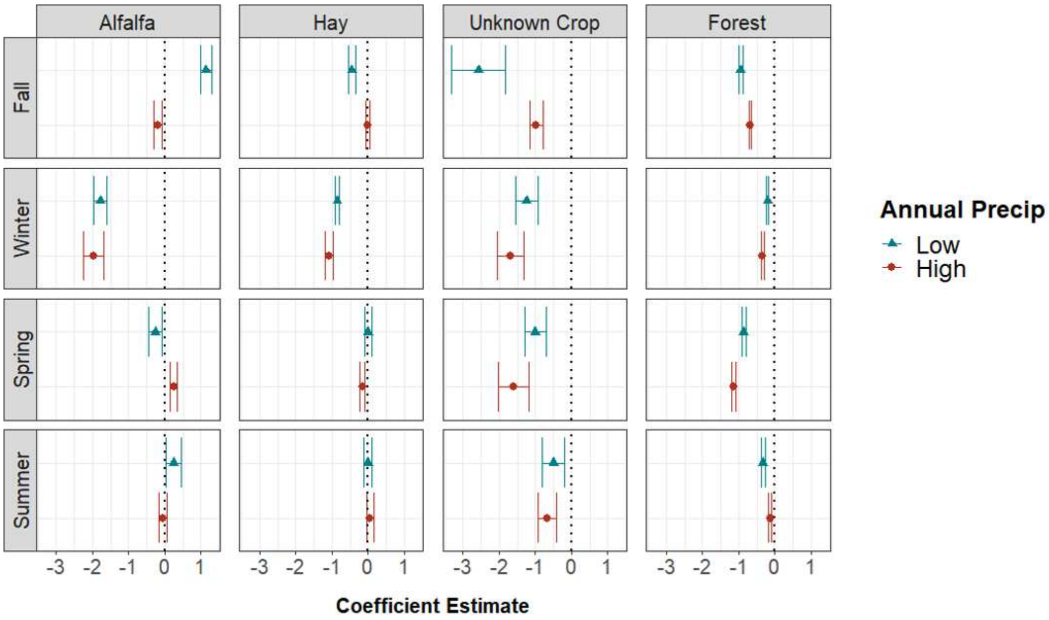


Figure 1.7 Beta coefficients for the main effects of resource type on mule deer selection and 95 percent confidence intervals for model: Selection ~ Resource Type*max NDVI + (1|Individual). Models were run separately for each season and for high/low annual precipitation years. The reference class for coefficients is open natural vegetation. These coefficients represent the log-odds of selection for resources when NDVI of all resources is zero. See Appendix Table A1.1 for full output of RSF coefficients. Data for this analysis were collected in the D-16 and D-34 mule deer herds in south-central Colorado.

Total Population: Coefficients for Interactive Effects

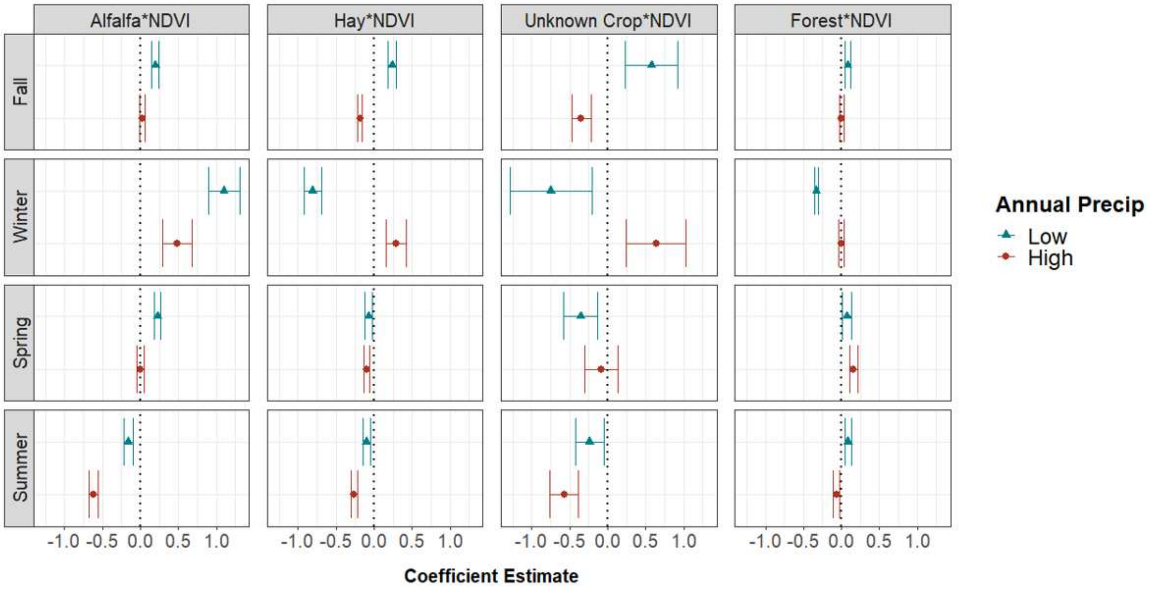


Figure 1.8 Beta coefficients for interactive effects of resource type*max NDVI on mule deer selection and 95 percent confidence intervals for model: Selection ~ Resource Type*max NDVI + (1|Individual). Models were run separately for each season and for high/low annual precipitation years. The reference class for coefficients is open natural vegetation*NDVI. These coefficients represent the effect that productivity of resources has on mule deer selection. See Appendix Table A1.1 for full output of RSF coefficients. Data for this analysis were collected in the D-16 and D-34 mule deer herds in south-central Colorado.

Resident Predicted Selection

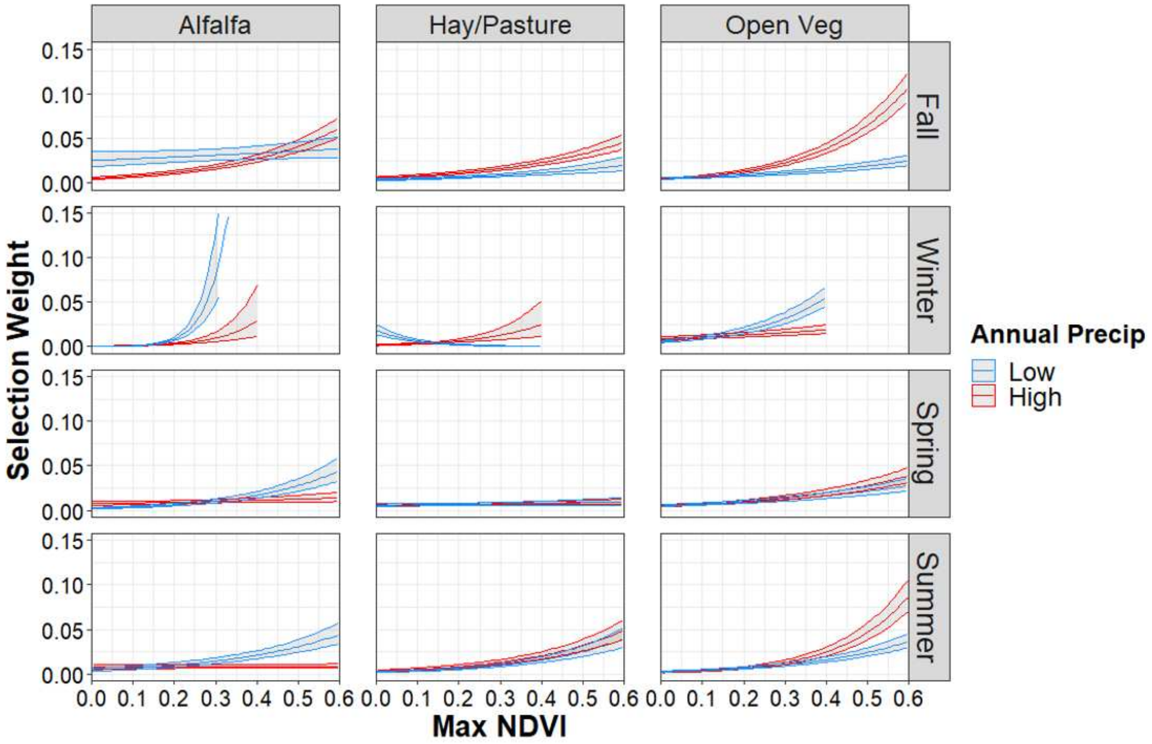


Figure 1.9 Predicted effects of seasonal maximum NDVI on resident mule deer selection for alfalfa, hay, and open natural vegetation for model: Selection ~ Resource Type*max NDVI + (1|Individual) across seasons and in high and low precipitation years. This graph depicts the combined effect that resource type and NDVI have on mule deer selection in the D-16 and D-34 mule deer herds in south-central Colorado.

Migrant Predicted Selection

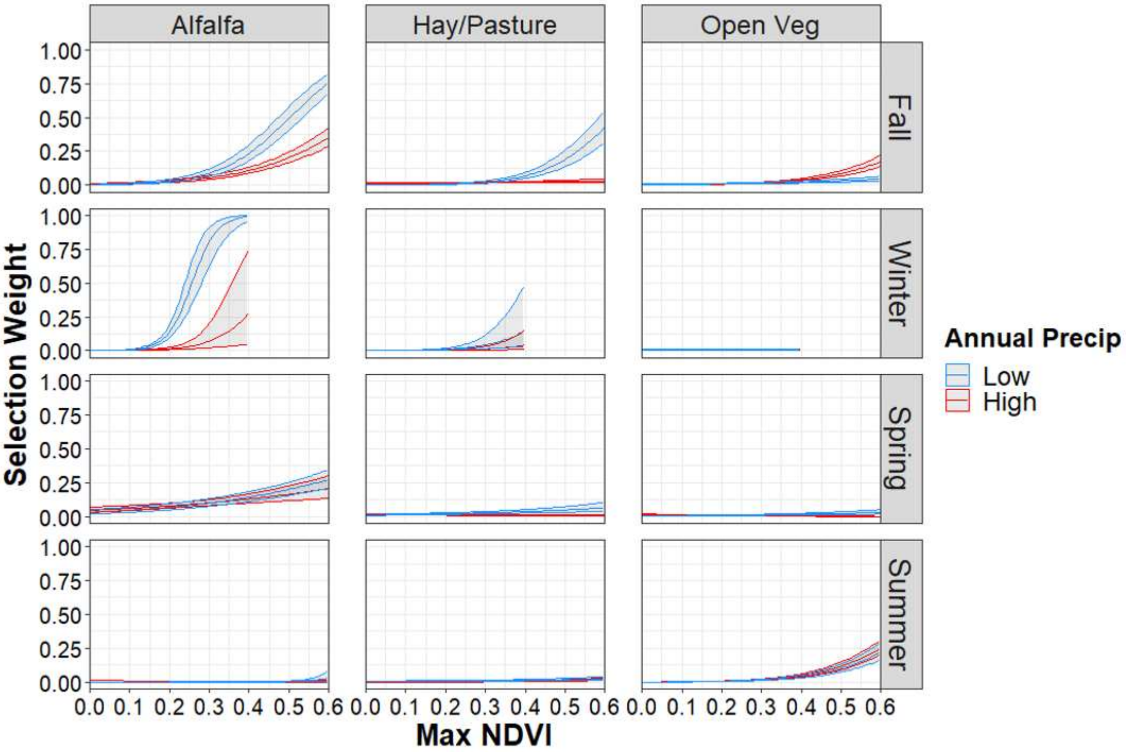


Figure 1.10 Predicted effects of seasonal maximum NDVI on migrant deer selection (total population) for alfalfa, hay, and open natural vegetation for model: Selection ~ Resource Type*max NDVI + (1|Individual) across seasons and in high and low precipitation years. This graph depicts the combined effect that resource type and NDVI have on mule deer selection in the D-16 and D-34 mule deer herds in south-central Colorado.

Migrant vs. Resident: Coefficients for Interactive Effects

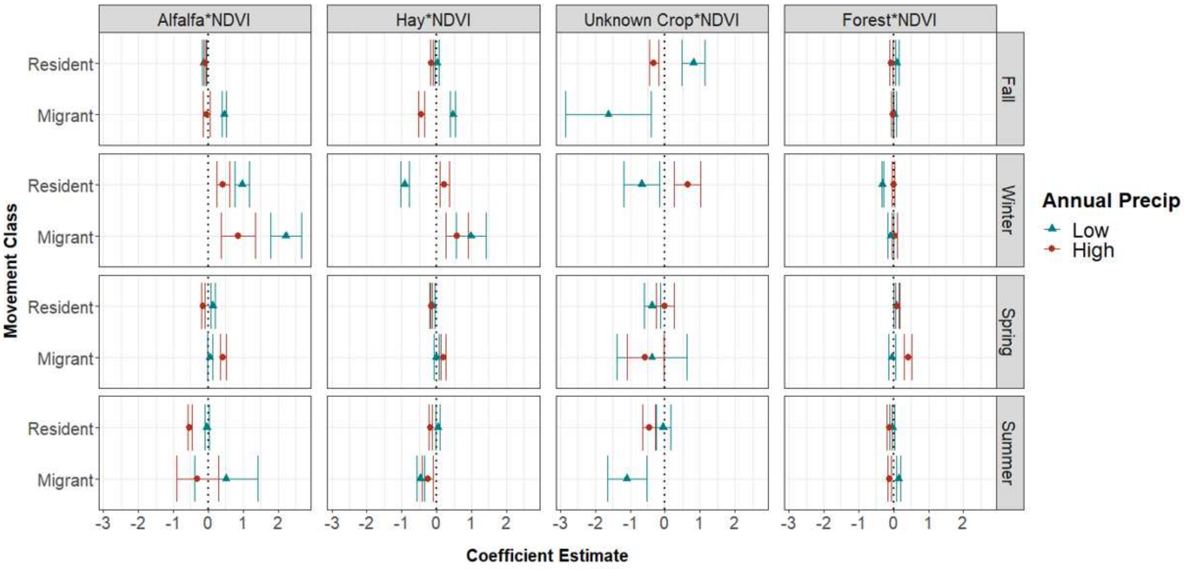


Figure 1.11 Beta coefficients for interactive effects of resource type*max NDVI and 95 percent confidence intervals for model: Selection ~ Resource Type*max NDVI + (1|Individual). Models were run separately by migratory strategy, for each season, and for high/low annual precipitation years. The reference class for coefficients is open natural vegetation*NDVI. These coefficients represent the effect that productivity of resources has on mule deer selection in the D-16 and D-34 mule deer herds in south-central Colorado. See Appendix Table A1.1 for full output of RSF coefficients.

Migrant vs Resident: Coefficients for Main Effects

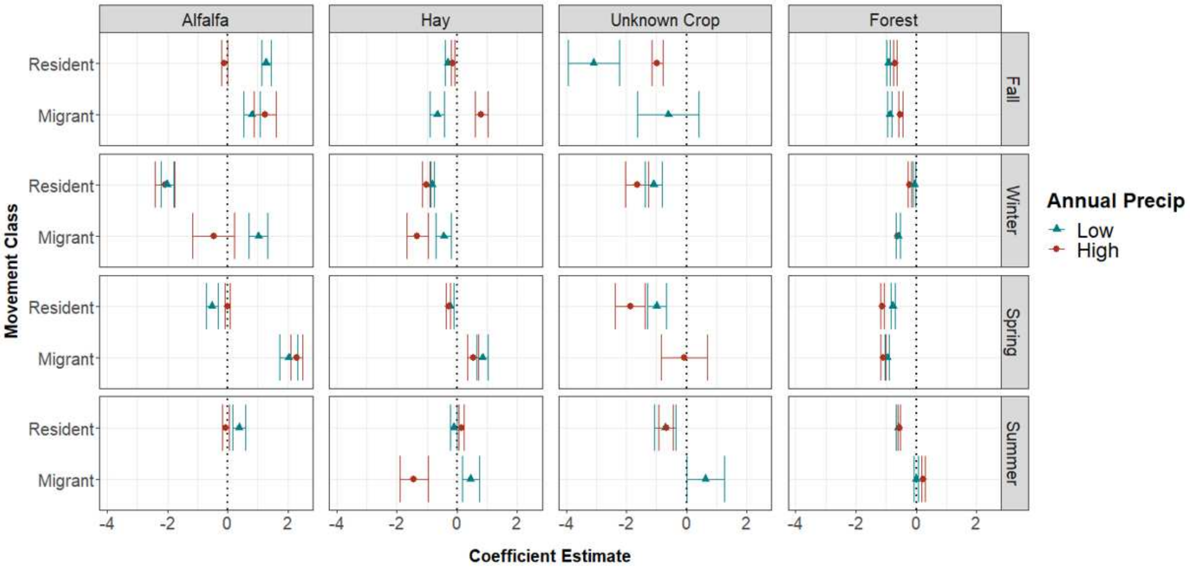


Figure 1.12 Beta coefficients for main effects of resource type and 95 percent confidence intervals for model: Selection ~ Resource Type*max NDVI + (1|Individual). Models were run separately by migratory strategy, for each season, and for high/low annual precipitation years. The reference class for coefficients is open natural vegetation. These coefficients represent the log-odds of selection for agricultural resources when NDVI of all resources is zero. We removed selection coefficients for migrants for several resources/seasons (alfalfa/summer & unknown crop/fall high, spring low, summer high and winter) because the intervals around these estimates were too wide to display on the plot. See Appendix Table A1.1 for full output of RSF coefficients. Data for this analysis were collected in the D-16 and D-34 mule deer herds in south-central Colorado.

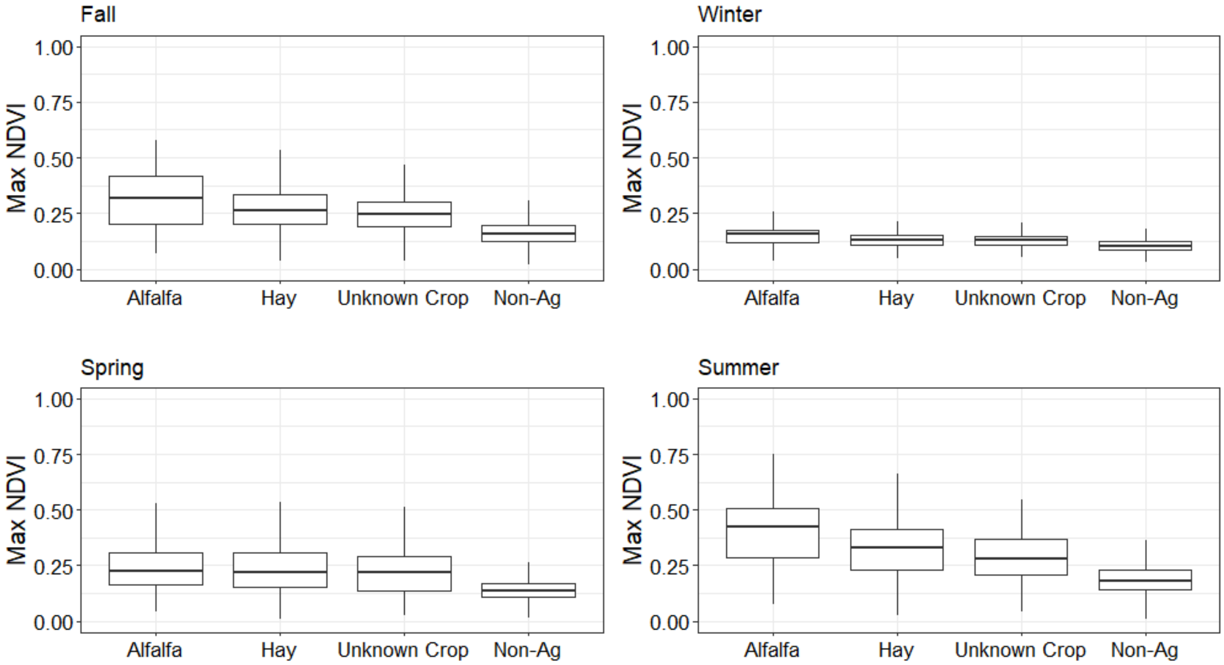


Figure 1.13 Distribution of maximum NDVI values by resource type and season from our sample of locations available to mule deer in their annual home ranges in the D-16 and D-34 mule deer herds in south-central Colorado.

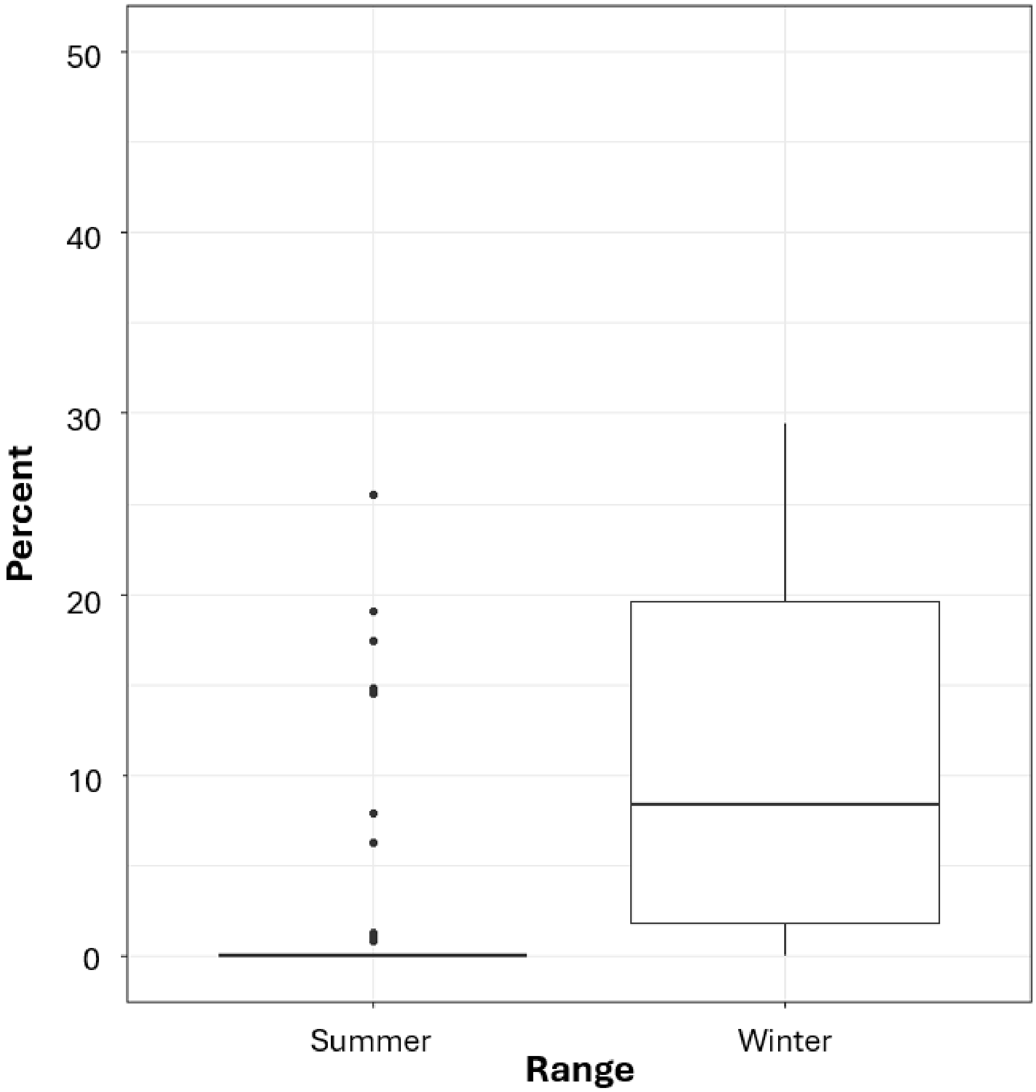


Figure 1.14 Percentage of agriculture available within summer versus winter ranges of migratory deer in the D-16 and D-34 mule deer herds in south-central Colorado.

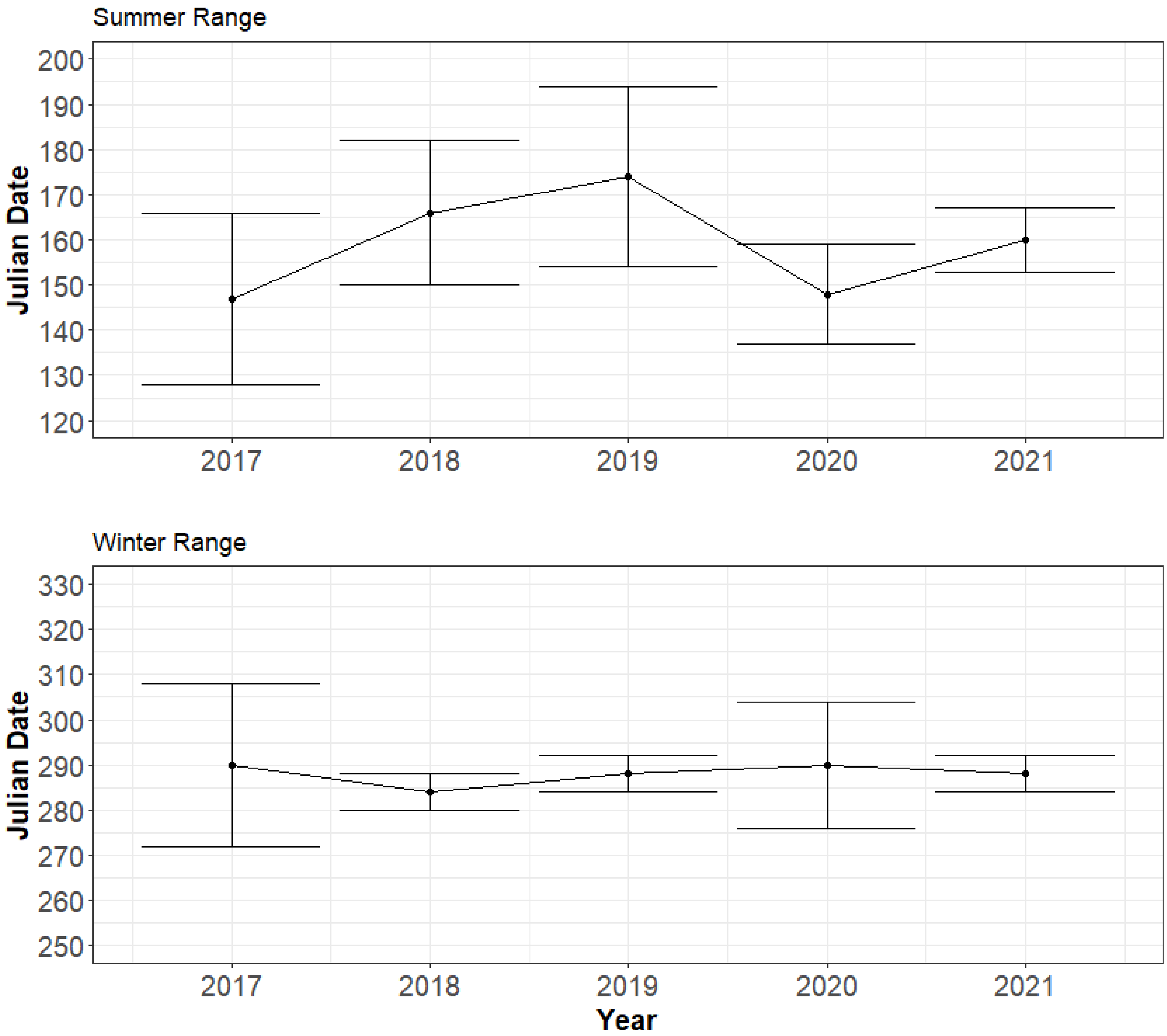


Figure 1.15 Mean annual timing of arrival and 95% confidence intervals for migratory mule deer that had agriculture available in their home ranges with the D-16 and D-34 study area in south-central Colorado.

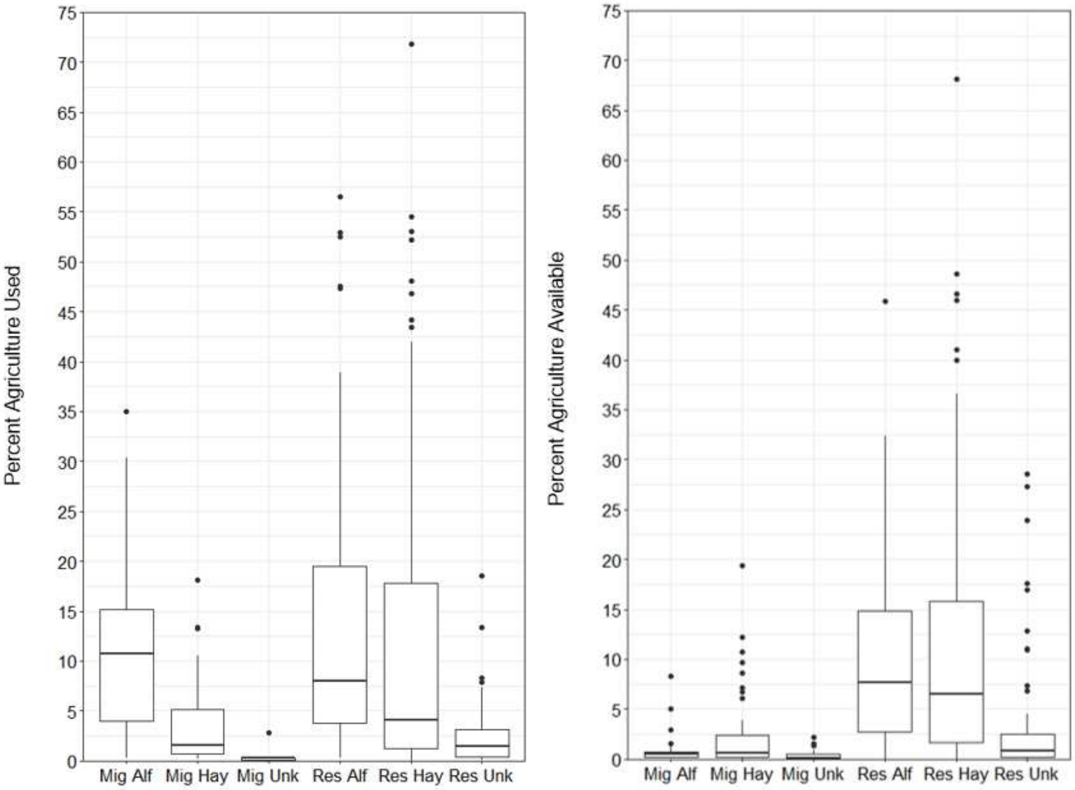


Figure 1.16 Percentages of agriculture used versus available in the annual home ranges of migratory and resident mule deer that have agriculture available to them in the D-16 and D-34 mule deer herds in south-central Colorado. Alf=Alfalfa, Hay=Hay/Pasture, Unk=Unknown crop.

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CHAPTER TWO

Mule Deer (*Odocoileus hemionus*) Survival in Partially Migratory Herds

SUMMARY

Migration can be an optimal tactic for herbivores to maximize their foraging opportunities in most seasonal systems. Though migrations often benefit ungulate nutrition, long-distance movement may be risky for wildlife. Migratory strategies are declining across many ungulate populations, which suggests that these movements may negatively affect ungulate fitness in some systems. We assessed how migratory strategies influenced one component of mule deer (O*docoileus hemionus*) fitness in two partially migratory herds in south-central Colorado. We examined how factors of habitat, climate, and migration strategy mediated survival of both fawns and adult female deer. We found that survival of migrant adult females was slightly higher over a five-year period, but that resident survival was higher in some years. Additionally, migration routes and conditions of seasonal ranges appeared to influence whether migration benefited deer survival. We found that migratory fawns had higher survival in the first six months of their lives but that residents had higher over-winter survival, although there was considerable uncertainty in the differences between migrant and resident fawn survival estimates in all occasions. We also found that summer plant productivity positively influenced survival of migrant fawns and adult females. Our results support the theory that partial migration persists in populations because multiple migration strategies yield some selective advantage under variable conditions.

INTRODUCTION

Migration is an adaptation that allows herbivores to track nutritious forage as the quantity and quality of vegetation changes seasonally across landscapes (Monteith et al. 2011, Robb et al. 2019). Migrations permit ungulates to spread out across the landscape during summer rather than concentrate at high densities, as is common on winter range (Garrott et al. 1987, Monteith et al. 2011). Despite the benefits of migration, non-migratory behavior is still ubiquitous in many ungulate populations. Migratory strategies in ungulates are also decreasing globally (Harris et al. 2009), which suggests the costs of this behavior outweigh the benefits at large scales (Middleton et al. 2013). Decreases in migratory tactics have been linked to changes in habitat quality due to expanding development of natural landscapes and climate change (Robb et al. 2019). Decreasing fitness associated with migration would be especially concerning for migratory mule deer (*Odocoileus hemionus*) populations because, unlike elk and pronghorn, mule deer rarely switch strategies (Sawyer et al. 2019b). Mule deer exhibit strong fidelity to their seasonal movements regardless of fluctuations in habitat quality due to climatic factors (Garrott et al. 1987, Sawyer et al. 2019b, Morrison et al. 2021), which brings into question whether migratory populations can adjust their behaviors outside of selective processes.

Evaluating factors that impact mule deer fitness has been a research priority across the western United States since widespread population declines first became a concern in the 1960s and 1970s (Wallmo 1981, Unsworth et al. 1999, Ballard et al. 2001). Declines of some mule deer populations have slowed, reversed, and halted in recent years, but most populations continue to be below historic levels and current management objectives (Mule Deer Working Group 2021). The mechanisms that contributed to mule deer population declines have varied across systems; however, loss and degradation of habitat, disease, high rates of competition and predation, and changing weather patterns can all potentially limit mule deer populations (Ballard et al. 2001, Forrester and Wittmer 2013, Bergman et al. 2015). The relative contributions these factors have had on widespread mule deer declines are disputed (Forrester and Wittmer 2013); however, there is general agreement that periods of decline have tended to coincide with low fawn recruitment (Carpenter 1998), thus fawn survival is often an important indicator of population trends. Survival of adult female mule deer tends to be high in comparison (Gaillard et al. 1998); however, because ungulate population growth is most sensitive to changes in adult female survival (Gaillard et al. 1998), this parameter is also important to monitor to predict long-term population health.

The effect that migratory strategy has on mule deer survival in partially migratory herds has been considered surprisingly infrequently given how extensively mule deer have been researched (but see Nicholson et al. 1997, Gogan et al. 2019, Schuyler et al. 2019, Schuyler et al. 2023). However, the recent advent of GPS technology has greatly enhanced our ability to identify migratory strategies with ease and to link the effects of migration and associated habitat use to fitness components (Ortega 2023). Migratory behavior, or lack thereof, mediates how deer are exposed to environmental variables that affect their survival. For example, precipitation generally has a positive effect on fawn recruitment (Bishop et al. 2005, Lomas and Bender 2007, Monteith et al. 2014) and high-elevation ranges, which are often used by migratory ungulates in summer (Russell 1932, Bischof et al. 2012, Middleton et al. 2013), tend to receive more precipitation than low-elevation areas. However, agriculture, where present, may augment the benefit of resident behavior because irrigated forage may be comparable, or better, than forage on high elevation ranges (Middleton et al. 2013). Migration may also help ungulates avoid predation (Fryxell et al. 1988, Hebblewhite and Merrill 2007), although some studies have documented that migrants are more vulnerable to predation during the migratory period and in dry years (Nicholson et al. 1997, Peterson et al. 2022).

Most mule deer research has focused on populations where deer are predominantly migratory. This may be because migratory tactics are still favored in most mule deer populations across the western US (Garrott et al. 1987, Brown 1992, Nicholson et al. 1997, Schuyler et al. 2019), even though resident behavior in ungulates is becoming more common. Some studies that have examined mule deer survival in partially migratory populations where migrant strategies are dominant have identified consistently higher survival of migrants (Schuyler et al. 2019). Other studies have identified alternating patterns in annual survival, whereby the strategy that most benefits mule deer in a given year changes depending on climatic conditions (Nicholson et al. 1997). If the dominance of a strategy within a region is indicative of its benefits, it would also be useful to compare survival of migrants and residents in resident-dominant herds. Additionally, few survival studies have examined the effects of migratory strategy on fawn survival. Examining this would be pertinent, given that mule deer populations appear to be primarily limited by fawn recruitment.

Quantifying how migratory strategy affects fawn survival may be challenging in some systems. Deer fawns generally have low survival (Forrester and Wittmer 2013), which means individuals often die before their migration strategies can be identified. Fawn migration strategies can be definitively classified when 1) migrants and residents are spatially segregated on the range where they are captured 2) the migratory strategy of their maternal doe is known, or 3) the fawn survives long enough to exhibit migratory behavior (or lack thereof). In some systems, many individuals will not meet these criteria. Migrant and resident ungulates often co-occur on the same winter ranges (Hebblewhite and Merrill 2009, Robinson et al. 2010), which makes identifying strategies of winter-captured fawns difficult if they die before spring migration. Migrant deer may also choose to summer in areas occupied by resident deer (McClure et al. 2005), although this behavior is less common. Studies that are unable to classify the migratory strategies of all individuals typically use a third category for individuals that could not be classified (Schyler et al. 2019). Using a dummy category may be acceptable when there are only a handful of unclassified individuals. However, in cases where many individuals are unclassified, ignoring uncertainty in state classification will bias results if that variable strongly influences survival (Kendall et al. 2012).

To address these gaps in our understanding of migration and its effect on mule deer fitness, we modeled survival of adult female mule deer and fawns using data collected by Colorado Parks and Wildlife (CPW) in two partially migratory mule deer herds in south-central Colorado. Deer in this region are primarily resident, but migratory strategies are dominant in the northwest portion of our study area. We used known-fate models to estimate survival of adult female deer (Pollock et al. 1989, White and Garrott 1990). We modeled survival of fawns using a state uncertainty approach (Nichols et al. 2004, Kendall et al. 2012) to account for individuals whose migratory strategy we could not identify. This approach partitions the survival probability of unclassified individuals into the estimates of migrant and resident survival, which mitigates potential bias. The objectives of our study for both adult females and fawns were: 1) to test for differences in survival of migratory and resident deer 2) to model the effects of habitat and weather on deer survival overall and 3) to test for interactive effects of environment and migration strategy on survival.

For our first objective, we hypothesized that survival of resident deer would be higher overall, given that this strategy was dominant in our study region. We also predicted that the location of summer and winter ranges (i.e. Game Management Units, GMUs, Fig. 2.1) may influence survival and that deer who utilized the dominant tactic on mixed-strategy ranges would generally have higher survival. We also predicted that patterns in migrant and resident survival may fluctuate among years and that these fluctuations would be tied to climatic factors. For our second objective, we hypothesized that environmental variables such as temperature, precipitation, and forage quality would affect mule deer survival and that these variables would more strongly influence survival of fawns compared to adult females. We expected precipitation and forage quality would positively affect deer survival. We predicted that temperature would positively affect survival in winter but negatively influence summer survival. For our third objective, we suspected that migrants and residents would be differentially exposed to environmental variables, which could result in differing strengths of environmental effects relative to these categories. We also hypothesized that differential exposure to habitat and weather variables would partially explain any differences in survival that we detected between migrant and resident deer (see Tables 2.1 & 2.2 for a comprehensive list of survival covariates and predicted effects).

METHODS

Study Area

All deer data used for this project were collected in adjacent deer Data Analysis Units (DAUs) D-16 and D-34 in south-central Colorado (Fig. 2.1). DAUs are intensive CPW big game monitoring areas that encompass the total annual range of specific herds. The D-16 boundary extends as far north as Leadville, follows the Arkansas River south to Salida, bends east with the river to Cañon City, then follows highways 24, 285, and 9 north to the continental divide. This

6138 square kilometer area includes parts of Teller, Park, Lake, Fremont, and Chaffee counties. D-16 encompasses 4 GMUs: 49, 57, 58, and 581 (Fig. 2.1). Fifty-seven percent of D-16 is public land, with most private land falling within GMUs 58 and 581 on the eastern side of the study area. GMU 49 contains the Mosquito Range, which includes the highest elevations of the study area with areas >4300 meters. The lowest parts of the study area are in GMU 581, where elevation reaches a minimum of 1615 meters. Annual precipitation ranges from highs > 64cm at high elevation to lows <23cm in the valleys (Grigg 2020). The area contains some agriculture, mainly native grass hay and alfalfa crops (Grigg 2020). DAU D-34 is located south of D-16 and is bound to the north by the Arkansas River between Salida and Cañon City. D-34 contains 5 GMUs: 86, 861, 691, 69, and 84 (Fig. 2.1). The western DAU boundary follows the divide of the Sangre de Cristo mountains from Salida down to Colorado Hwy 69 then heads east until reaching I-25 where it extends north to the Arkansas River. In contrast to D-16, the 6537 square kilometer area of D-34 is 62% private land. The highest point in D-34 spans above 4300 meters and lowest point below 1525 meters. Annual precipitation is only slightly lower than D-16 with >50 cm of precipitation falling at the upper ranges in wet years and < 15 cm in lower valleys in dry years. Agriculture is a common land use in the DAU, with irrigated hay and alfalfa fields also being the dominant crops and more use of land by livestock than in D-16 (Vitt 2020).

Migratory behavior is more common in D-16 than in D-34, and the distance and direction of migrations vary widely across the study area. Some sub-populations within the region are entirely resident or migrant, while others are mixed. Migratory strategies are dominant in the northwestern corner of the study region (GMUs 49 & 57). Most migratory deer summer at high elevation in the Mosquito or Sangre de Cristo Mountain ranges, while others move to comparatively low-elevation areas inhabited year-round by resident deer. Low-elevation summer ranges are, therefore, not always distinct to migrants or residents, making it difficult to classify the movement behavior of deer captured on these summer ranges when mortalities occur before completion of the fall migration period. Predators such as mountain lions (*Puma concolor*), bobcats (*Lynx rufus*), coyotes (*Canis latrans*), and black bears (*Ursus americanus*) also inhabit these ranges. The region also supports populations of other ungulates, including elk (*Cervus canadensis*) and pronghorn (*Antilocapra americana*). Plant communities are variable across the study region. Alpine willows and subalpine spruce, fir, and aspen forests are common at high elevation. Mid-elevation montane forests include ponderosa pine (*Pinus ponderosa*), lodgepole pine (*Pinus contorta*), and Douglas fir (*Pseudotsuga menziesii*). Pinyon-juniper systems are common at mid-low elevation ranges. Low-elevation communities include semi-desert shrubland and shortgrass prairie. Cottonwoods, willow, and currant are common within riparian areas.

Deer Capture and Mortality Monitoring

Adult Females

We applied GPS collars to 50-60 adult female mule deer annually within the D-16 and D-34 study areas between 2017-2021. We conducted captures over several days between late February through early March each year. Deer were captured via helicopter, assessed for pregnancy, weighed, scored for body condition, and fit with GPS collars. We collected maximum rump fat measurements via ultrasound (Stephenson et al. 2002, Cook et al. 2010). We assessed age at capture by examining tooth wear (Erickson et al. 1970). During 2020 captures and in the seasons following, we fit pregnant deer with Vectronic vaginal implant transmitters (VITs) that communicate with the GPS collars and send a birth notification email when the VIT sensor detects a drop in temperature and lack of motion. We typically captured adults at one location per sub-unit (GMU) of each herd to obtain a representative sample of deer across our study area. The location and the number of deer we captured in each area varied from year to year.

We collared most adult deer with Vectronic Vertex Plus Iridium collars, allowing two-way satellite communication. The GPS receiver of these collars has a mean accuracy of 8-15 meters. We typically programmed collars to take a location every 13 hours and remain on the same animal for at least two years unless the individual died during that period. In some summers, we increased fix rates to 4 hours for deer without VITs between June-July to spot clustered points indicating parturition. Collars deployed during 2017 and 2018 remained on the same animal until their death or until the collar battery died. Collars we deployed in 2019-2021 were equipped with timed drop-off mechanisms that deploy after two years of monitoring.

Fawns

Between 2017-2021, we collared approximately 120 neonate fawns annually. Until the 2020 fawn season, these captures were mostly opportunistic. In 2020, we began capturing fawns of collared adult deer, using VITs and identifying GPS birth clusters. We suspect that opportunistic captures may have been biased towards resident fawns because deer tended to occur at higher densities on resident summer ranges, thus making resident fawns easier to capture. We weighed captured fawns, measured their hind foot length, and fit them with expandable Vectronic Vertex Mini Globalstar GPS collars. When we captured twins or triplets, only the first individual located was collared. Fawn locations were stored onboard collars at a continuous 2-hour rate. Collars transmitted 1 location per day. The additional 11 locations onboard could only be downloaded upon retrieval of the collar. These collars were built to last approximately one year, after which the band degrades and falls off. Given their expandable design, some collars dropped off on fences before reaching this one-year mark. To augment fawn samples to monitor overwinter survival, we conducted additional fawn captures between October-January by ground darting and via helicopter. We aimed to redeploy all functional Vertex Mini collars retrieved from neonate fawn mortalities or premature drops during the preceding season.

Predictor Variables for Survival

Adult females

We estimated monthly survival of adult females between June 1 – May 31. This timeline approximates the biological year of mule deer. Our survival model began in June 2017 and continued through May 2022. We resampled individuals in our model that were monitored over multiple years. We tested other temporal effects including year, season, and linear and quadratic trend structures. Since we expected that survival might not be constant across time, we chose to fit these trend structures in case there were patterns in adult female survival that could be described with fewer parameters than the full time-varying structure. We selected a set of additional model covariates a priori based on factors we suspected might result in differential survival of migrant and resident deer or overall survival. Predictor variables (Table 2.1) include environmental, population, or individual-based covariates. All environmental covariates were derived seasonally and at two scales: the game management unit (GMU) and seasonal home ranges of individuals (Schuyler et al. 2019). Environmental covariates included NDVI, temperature, and precipitation. Population-level covariates included GMU (sub-populations), and Data Analysis Unit (DAU, annual range population D-16 or D-34). Individual-level covariates included age at June 1, movement strategy, migration distance, and percent ingesta free body fat at capture (IFBF). When we did not have a covariate value for each individual, we replaced missing values with the mean value of continuous covariates.

To categorize the migratory strategies of deer, we used Migration Mapper (Merkle et al. 2022, v.3), which allows for migration classification via net squared displacement (NSD, Bunnefeld et al. 2011) and visual examination of location data. We considered an animal migratory if they resided on two distinct ranges for an extended period (Dingle and Drake 2007, Peterson et al. 2022), net-squared displacement graphs displayed a sigmoid or double sigmoid curve (Bunnefeld et al. 2011), and movements between seasonal ranges ≥ 5 miles in distance. We classified deer as resident if they did not migrate by July 1. We observed a few migrations past July 1, but we only documented this behavior in the northwestern region where nearly all deer are migratory (GMU 49). We also assigned deer as migrants or residents if they died before the migratory period, but their ranges occurred in regions where deer were exclusively migratory or resident. We assigned animal movement strategy as 'unknown' if they died before their movement class could be classified and resided on mixed-strategy winter ranges (n=5).

To assign time-specific environmental covariates at the proper spatial scale, we assigned migratory animals to a seasonal GMU. We used winter and summer GMU as covariates in our model but only used fall and spring GMU IDs to assign GMU-scale environmental variables to individuals. We assumed resident deer reside within the same GMU across all seasons. We filtered GPS locations of migratory individuals by 3-month seasonal intervals and extracted GMU from a shapefile against these locations in R. When individuals were found in multiple GMUs within a season, we chose whichever GMU a deer had taken more points in. We next created seasonal home ranges (SHRs) for individuals. We created 100% minimum convex polygon (MCP, Mohr 1947) annual home ranges for resident individuals. For migratory individuals, we used migration start and end dates to partition points collected on summer versus winter range, then created summer and winter range MCPs from those points. Finally, we generated 1000 random locations within each seasonal home range and 10,000 random locations within each GMU and extracted each environmental variable. We then assigned the mean value of environmental variables for each SHR and GMU.

We used the Normalized Difference Vegetation Index (NDVI) as a proxy for forage quality. We derived NDVI using Landsat 8 satellite imagery, which collects images every 16 days at a 30 x 30-meter resolution. We calculated mean NDVI values across years and seasons. We then derived mean seasonal NDVI at GMU and SHR scales by extracting NDVI values from our random locations. We filtered these random locations to only include grass and shrub land covers. NDVI values of forested land covers index the canopy cover rather than the understory, so they are not appropriate to use as an index of forage quality (Hurley et al. 2014). We repeated this process for precipitation and temperature variables. We extracted total precipitation at GMU and SHR scales for spring and winter using DayMet weather data (Thornton et al. 2020) derived at a 1km x 1km scale. We also used DayMet to calculate maximum summer temperature and minimum winter temperature at these two scales. We estimated seasonal temperatures as the mean of monthly maximums or minimums across 3-month seasons.

To estimate migration distance for all individuals, we measured the straight-line distance between the mean center of seasonal ranges. We measured this distance for both migrant and resident individuals. Although resident deer remain in the same general area year-round, many individuals exhibit range shifts across seasons. We established mean range centers for migrants by averaging UTMs of summer and winter range locations, respectively. We repeated this process for residents using points collected during summer (June-Aug) and winter (Dec-Feb). Next, we calculated the distance to the closest water source from each range center (Nicholson et al. 1997) and classified whether either range fell within the boundaries of a mule deer concentration area. These concentration areas are high-density mule deer ranges, identified by a GIS layer created by Colorado Parks and Wildlife (2011). We also extracted elevation at the mean centers of each season range using the R package 'elevatr' (Hollister et al. 2023), which utilizes the US Geological Survey's Elevation Point Query Service. We then calculated the percentage of developed land within each seasonal range. We extracted development, shrub, grass, and water classifications from the National Land Cover Database's 2019 land cover layer (NLCD, Dewitz and US Geological Survey 2021). We also calculated the percentage of agriculture on each seasonal range using a data layer derived by the Colorado Division of Natural Resources in 2020 (CDWR 2015 and 2020).

To estimate percent ingesta-free body fat (IFBF) for captured deer, we used regression equations developed by Cook et al. (2010) for mule deer where measurements of maximum subcutaneous rump fat are first scaled by weight ($\text{Scaled Max Fat} = \text{Rump fat}/(\text{Weight}^{0.63})*0.142$), then estimated %IFBF as: $5.63+11.35*\text{Scaled Max Fat}$. We included %IFBF for individual females the first year they entered the model but assumed this value would not carry over across years. We replaced individual IFBF with the mean population value when an individual was resampled over multiple years. We resampled hind foot length at capture across years, assuming this body measurement would stay constant once deer reach adulthood. We estimated age at June 1 by adding 0.5 years to age at February/March capture, then adding one year for each additional year an individual was included in the model.

Fawns

We estimated monthly fawn survival by age over 12 monthly intervals. Fawns in this region are typically born mid-June through early July, with a mean birth date of June 20. Therefore, age corresponds roughly to a time structure beginning June 20 to June 19 of the following year. Individuals entered the model either as neonates (first occasion) or as winter-captured fawns. We assumed winter-captured fawns were born on the mean birth date for fawns in their GMU. Winter-captured fawns entered the model at their estimated age – i.e. months elapsed between their estimated date of birth and their capture date. We tested for other age grouping structures, including 3-month intervals approximating seasons, monthly trends (linear, quadratic, logarithmic), and year effects. Fawn survival tends to be lowest soon after birth (Pojar and Bowden 2004). Therefore, we expected a possibly increasing logit-linear, potentially plateauing, pattern in survival. We also considered that survival might decrease again in winter (quadratic) when environmental conditions tend to be most limiting for mule deer. We used a similar set of covariates to our adult model. We used weight at capture in place of IFBF and did not estimate migration distance because many fawns were only monitored on one range. We also considered effects of sex and age at capture for neonates.

To estimate neonate age at capture, we used a regression equation developed by C.R Anderson (CPW, unpublished data). Anderson used AIC model selection to identify the best predictors of fawn age, using data from VIT fawns where true age was known. Weight at capture was identified as the best predictor of fawn age. We assumed their regression equation, created using data from fawns captured in the Piceance Basin of Colorado, would apply to our study area. The fawns we captured at a known age of zero days had similar mean birth weights to Piceance deer (3.45kg Piceance, 3.57 kg south-central CO). We therefore estimated age at capture as weight (kg)-3.42)/0.3. We assumed a minimum age at capture of zero and a maximum age of 7 days. Next, we back-calculated hind foot at birth for fawns by regressing foot length at capture as a function of age: HF(cm) = 24.76 + 0.42*age; r^2 =0.58, p <0.001 (Bishop 2008, Bishop 2009). Hind foot at birth was therefore estimated as age at capture multiplied by the slope of our regression equation subtracted from hind foot at capture.

Our process for extracting GMU-level environmental covariates was identical to our adult model, but we used a different approach to estimate seasonal home ranges. Since early fawn survival is typically low, fawns often die before enough location data is collected to establish their seasonal home ranges. For this reason, we used buffered circles around the mean center of seasonal ranges as a proxy for home ranges to examine the influence of environmental covariates at the home range scale. We created buffers with an area of 130 hectares for each fawn (Riley and Dood 1984; Geduldig 1981). We used locations collected during summer (June-August) and winter (December-February) to establish the mean center of seasonal ranges. To find the mean values of environmental covariates at the home range scale, we again sampled 1000 random locations within each circle, then calculated the mean or proportional values of all points depending on the covariate.

We used 3 methods to classify movement behavior for fawns: 1) by identifying migrations, or lack thereof, over a specified period (see below), 2) by capture location, and 3) via identifying the migration strategy of their maternal doe. Individuals remained unclassified if we could not identify their migration strategy using the above criteria. For method 1, individuals began as unclassified at capture and became migratory or resident when they revealed that behavior. We used the same general methods described for adults using Migration Mapper software to identify migrations. Fawns captured as neonates were classified as migratory if they exhibited migratory behavior as defined for adults. We only classified neonate-captured fawns as residents if they survived to January 1 and did not migrate before that point. We classified winter-captured fawns in a similar manner, except that they became residents in their final capture occasion only if they survived and did not migrate by that point. To classify fawn migration strategies based on their capture location, we used methods as described for adults. In instances where the migration strategy of the maternal doe was known, we assigned fawns to the same strategy. All other individuals that did not meet the above criteria were left unclassified.

Since the migratory status of a fawn is tied to the behavior of its maternal doe, unclassified neonate fawns may still be considered migrants, even if they do not survive to complete a migration. Movements made outside of the first year of life were not considered when classifying the fawns as migrants or residents. Deer typically follow the same migration patterns as their doe for their first year of life but will sometimes switch strategies as yearlings or adults (Nelson 1998). We identified some individuals monitored as both fawns and yearlings that switched movement behaviors as they changed age class. Therefore, movements made by yearlings may not indicate their behavior as fawns. We assumed that migrations occurring before age 1 were completed before they had been driven off by their doe, a process that typically occurs shortly before summer parturition (Monteith et al. 2007, Jakopak et al. 2019). Females are constrained to migrate before parturition, but yearlings are not limited to that timeline. We assumed that most late summer migrations made by new yearlings were likely resident fawns exhibiting exploratory behavior.

Survival Analyses

Adult Model

We estimated monthly survival of adult female deer using known-fate survival models (Pollock et al. 1989, White and Garrott 1990) in program MARK (White and Burnham 1999). We evaluated models using the small-sample Akaike Information Criterion (AICc; Hurvich and Tsai 1989) to identify the top model that described variation in survival. We also used AIC to identify the top model that included a migration covariate if that variable was not in our overall top model. To avoid an overly large set of candidate models, we modeled survival in stages; we initially built single-factor models with all covariates, then combined competing variables in multi-factor models (Schuyler et al. 2019). We first identified the best structure on time, then we modeled all environmental covariates in single-factor models, and additively with the best time structure identified in the previous stage. We tested the effect of all seasonal environmental covariates on survival within both current and future seasons. We tested single slope and time-varying environmental covariate structures. Next, we modeled all other individual and population covariates as single factors, including both constant and competitive time structures. We next tested interactions between migration strategy and all covariates. If a model with an interaction between migration strategy and another variable performed better than the single factor or additive models, we also tested for an interaction between DAU and that same variable. DAU D-34 has considerably more resident deer than D-16, so we tested for these interactions to assess whether migration strategy or some other unmodeled feature of the DAU was producing the effect. For all interactive models, we tested the equivalent structure as an additive model. We ran Pearson's correlation tests between top-ranking covariates and removed models from this initial candidate set if another correlated variable ($r > 0.5$) we modeled had a lower AIC. We also removed redundant variables (lower ranked alternate time-varying covariate structures and variables derived at different scales) and covariates we identified as 'pretending' with time or migratory strategy (Burnham and Anderson 2002). We retained all covariates that ranked higher than our null model and improved fit when combined with the best structure on time. In the final modeling stage, we ran all possible (biologically tenable) combinations of multi-factor models (Doherty et al. 2012) using variables retained from the previous stage. To avoid overparameterizing our models, we assumed we needed a minimum sample size of 30 for each covariate we added to a parameter and did not allow the number of covariates per parameter to exceed this minimum.

Fawn Model

We used a multistate state-uncertainty (Nichols et al. 2004) modeling approach within program MARK (Kendall et al. 2012) to estimate known-fate survival of migrant and resident fawns, where migratory status was unknown at the time of collaring. Because we monitored dead and live individuals, we modeled death as a state and used the state transition parameter ψ to estimate survival probability (Devineau et al. 2014). The probability of survival is therefore equivalent to the probability of remaining in the same state – i.e. ψ (migrant to migrant) or ψ (resident to resident). We assumed individuals could not transition between migratory and resident states because mule deer typically establish their movement strategy as adults and stick to the same behavior for life (Sawyer et al. 2019b). From here on out, we use \`S\` instead of ψ to describe fawn survival for consistency with our adult model. The survival probability of unclassified individuals is then partitioned by fitting two additional parameters, π and δ. The mixture parameter π is used to estimate the probability of being a migrant or resident given an individual was unclassified at first capture. All individuals in our model began as unclassified at their first capture, unless their migration strategy was known in the first occasion (known strategy of maternal doe or captured on a distinctly migrant/resident range). We tested whether including effects of age class at capture, year, or GMU at capture on π improved model fit. Some GMUs in the study area are almost entirely resident or migrant, so we expected this covariate would help partition our data.

The δ parameter estimates the probability of being unclassified upon redetection, given an individual is a true migrant or resident. δ is initially informed by the proportions of migrant, resident, and unknown classifications in each occasion. All individuals known at first capture returned to an unclassified state in the second occasion and remained unclassified until the occasion they migrated, passed the threshold to become a resident, or transitioned into a dead state. We set up our initial models using age class at capture (neonate or winter captures) as a group structure to fit δ. Individuals captured as neonates become migrants in the occasion that they begin their fall migration. Therefore, we fixed $\delta^{u|M}$ (unclassified | migrant) to 1.0 prior to the occasion of the first migration for all individuals captured as neonates. Individuals captured as neonates became residents if they did not migrate before the occasion of the last detected fall migration (month 7, around January 1). We fixed $\delta^{u|R}$ (unclassified | resident) and $\delta^{u|M}$ to 0 for the neonate group at this occasion because all surviving individuals became classified after that point. Prior to this occasion, all $\delta^{u|R}$ parameters were fixed to 1. For fawns captured in winter, unclassified individuals became migrants in the occasion they began their spring migration. Again, we fixed $\delta^{u|M}$ to 1 for all winter-captured fawns prior to the occasion of the first spring migration. Winter-captured fawns became residents in their last occasion if they did not migrate before that period. We fixed $\delta^{u|R}$ and $\delta^{u|M}$ to 0 for the winter-capture group in the last occasion because all surviving individuals became classified after that point. Prior to this occasion, all $\delta^{u|R}$ parameters were fixed to 1. We also tested whether using a linear trend on the remaining δ parameters for $\delta^{u|M}$ improved model fit.

After fitting δ and π, we examined structures on survival, which was our primary interest. We tested for effects on survival using the same approach described in our adult model. We first evaluated the best age structure, then proceeded to fit single-factor covariates using both the best age structure identified and a null age structure. Since examining differences in survival between migrants and residents was our primary interest, we included models with and without survival separated by movement strategy at each stage. We again tested interactions between movement strategy and all covariates. We then tested all possible combinations of covariates after advancing variables using the same criteria as our adult model.

RESULTS

Adult Female Survival Models

We found that migratory adult female deer in our system had higher survival overall compared to resident deer, but this pattern was not consistent across the entire study region or in all years. All variables that we advanced into the ‘all possible combinations’ phase of survival modeling appeared in models within <2 ΔAIC of our top model, which only obtained 3.36% of the model weight (Table 2.3). Models that ranked within <2 ΔAIC accounted for 33% of the total model weight. When we examined competitive single factor and interactive variables in isolation, interactive effects of migration strategy accounted for almost all the model weight (Table 2.4). Our assessment of cumulative model weights similarly inferred that models that included a migration covariate carried 99.9% of the total model weight. The low weights of our top models were likely due in part to having a large set of similarly competitive candidate models; however, it could also suggest that there may have been considerable variation in survival that was not explained by our model covariates.

Our top model suggested that adult female survival was best explained by 1) a constant time structure 2) an effect of age in June, and 3) an interaction between migration strategy and distance to water on winter range. Under this model, age in June negatively affected survival ($\hat{\beta}_{age}$ = -0.14, LCI = -0.26, UCL = -0.03). Distance to water affected migrants and residents differently (Fig. 2.2); wintering further from water negatively affected migrants ($\hat{\beta}_{wat\_mig}$ = -0.0011, LCL = -0.0018, UCL= -0.0004) but minimally affected residents ($\hat{\beta}_{wat\_res}$ = 0.0002, LCL= -0.0002, UCL = 0.0007). Effects of age and migration strategy ($\hat{\beta}_{mig}$ =1.25, LCL = 0.36, UCL = 2.15) were both considered significant as defined by non-zero overlap of beta coefficients (Table 2.5). The effect of distance to water was significant for migrants but not residents. Estimated annual survival for migrants was slightly higher than residents ($\hat{S}_{migrant}$ = 0.84, LCL = 0.78, UCL = 0.89; $\hat{S}_{resident}$ = 0.82, LCL = 0.77, UCL = 0.86, Fig. 2.3) but there was considerable overlap in the 95% confidence intervals for these estimates. Average survival for the total population was high ($\hat{S}_{total\_population}$ = 0.81, LCL = 0.77, UCL = 0.84).

The second-ranked model also explained some important variation in regional survival of migrant and resident adults and was extremely competitive (ΔAIC=0.08). This model suggested that survival varied by 1) a constant time structure 2) an interaction between migration strategy and residence in GMU 581 during summer 3) an interaction between migration strategy and summer range NDVI at the GMU scale, and 4) age in June. Effects in this model were all significant except for the main effect of GMU 581 and the effects for individuals with unclassified migration strategies (Table 2.6). Summer NDVI positively affected survival of migrant adults ($\hat{\beta}_{mig*su\_ndvi}$ = 33.29, LCL = 8.95, UCL = 57.63, Fig. 2.4), but negatively affected resident survival ($\hat{\beta}_{res*su\_ndvi}$ = -13.45, LCL = -26.64, UCL = -0.24). GMU 581 is located on the northeastern side of our study area (Fig 2.1) and is unique in that migrants from the western and central side of the study area (GMUs 57 & 58) move east to summer on this range among resident deer. We found that 27% of deer in our sample that summered in GMU 581 were migrants from other GMUs. Resident deer in GMU 581 had notably higher survival than deer that migrated to GMU 581 in the summertime ($\hat{S}_{resident\_581}$ = 0.88, LCL = 0.78, UCL = 0.93; $\hat{S}_{migrant\_581}$ = 0.67, LCL = 0.46, UCL = 0.82, Fig. 2.5). Sixty percent of the mortalities of migratory deer that summered in GMU 581 occurred during the migratory period. Survival of resident deer in GMU 581 was similar to overall survival of migrant deer in the rest of the study area ($\hat{S}_{migrant}$ = 0.87, LCL=0.80, UCL=0.92). Outside of GMU 581, migrants had higher survival compared to residents ($\hat{S}_{resident}$ = 0.80, LCL = 0.74, UCL= 0.85).

Our model for migration strategy*year (ΔAIC = 13.3) did not outcompete a constant effect of migration strategy; however, the results of this model suggest considerable differences across years that are worth noting given our objectives. Additionally, this model outcompeted our null model and had a similar -2log(L) compared with our top two models of adult female survival, suggesting that it explained a similar amount of variation but was heavily penalized for a high number of parameters. This model suggested that migrants had considerably higher survival than residents in 2018 and 2019, similar survival in 2017, and lower survival than residents in 2020 and 2021 (Fig. 2.6). Other variables that were included in competitive models (<2 ΔAIC) were fall NDVI on winter range (- effect), winter range NDVI in the spring preceding the start of the model (- effect), GMU 37 summer range (+ effect), and GMU 58 summer range (- effect); however, none of these effects were significant.

Fawn Survival Models

A covariate for migration strategy did not make it into our top model for fawn survival, but the top model that included a migration covariate was competitive (ΔAIC = 1.25, Table 2.7) and suggested that migratory fawns had higher survival than residents through 6 months of age, but resident fawns had higher survival between 7 months to 1 year. As with our models for adults, weight was broadly distributed across all competitive fawn models (Table 2.7). Our top model of fawn survival only accounted for 2.2% of the total model weight, while all models with <2 ΔAIC accounted for 40%. When we modeled the effects of single factor and interactive variables in isolation, age accounted for nearly all the model weight and our examination of cumulative model weights revealed that models that contained age as a covariate accounted for 99.9% of the total model weight. However, adding other variables to the age effect revealed these variables did contribute some weight (Table 2.8). Age and an additive effect of winter range elevation accounted for considerably more weight than all other variables (age + elevation (WR) AICc Weight = 0.64) and models that included elevation accounted for 94% of cumulative model weight. The weights of other variables were relatively low in comparison, but environmental variables had slightly higher weights than those in our adult model (Table 2.8).

Under the top-ranked model, fawn survival was best explained by 1) age in months 2) elevation of winter range 3) summer NDVI at the GMU scale 4) fall NDVI on winter range 5) percentage of development on summer range 6) hind foot length at birth and 7) sex. Fawn survival was lowest in the first month of life ($\hat{S}_{m1}$=0.78, LCL=0.74, UCL=0.81) then increased through age 4 months, fluctuated in ages 5-8 months (Fig. 2.7), then became high and stable after fawns reached 9 months of age ($\hat{S}_{m9\text{-}12}$ = 0.97, LCL=0.95, UCL=0.98). Our best single-factor model for age included variable survival between ages 1-8 months with a constant effect across ages 9-12. Annual survival of all fawns in our study region was 0.38, (LCL=0.33, UCL=0.42, 95% CI estimated using the delta method, Cooch and White 2015). We suspect these estimates may be biased high, given that we captured fawns within the first week of their life, and therefore may have underestimated mortalities that occurred soon after birth.

Winter range elevation negatively affected fawn survival in winter and spring (effect on ages 4 - 12 months, $\hat{\beta}_{elevation}$ = -0.0008, LCL = -0.0014, UCL = -0.0003, Fig. 2.8). Elevation of winter range was correlated with winter temperature (r = -0.61). We chose to use the former variable because it had a lower AIC in our preliminary model set. Summer NDVI ($\hat{\beta}_{su\_ndvi}$ = 8.4, LCL= 1.78, UCL= 15.12) and hind foot length ($\hat{\beta}_{hind}$ = 0.15, LCL= 0.008, UCL= 0.30) positively influenced fawn survival in the first 3 months of life. Fall NDVI on winter range and percentage of development on summer range both positively affected fawn survival in those respective seasons, but these effects were not significant (Table 2.9). Sex had a slight effect on fawn survival in the first 3 months of life; female neonates had higher survival than males during this period (Table 2.9), but the differences were not significant.

Our top model that included a migration covariate suggested that a difference in survival was best explained by 1) age in months 2) elevation of winter range 3) fall NDVI on winter range 4) precipitation in spring preceding the start of our model, and 5) an interaction between migration strategy and distance to water on winter range. This model estimated that survival of migrant fawns was higher in all occasions until fawns reached 6 months of age, at which point survival to age 1 of residents was estimated to be slightly higher (Fig. 2.9). The difference in monthly survival estimates of migrant and resident fawns was greatest in their first month of life ($\hat{S}_{m1\_mig}$= 0.81, LCL= 0.73, UCL= 0.86; $\hat{S}_{m1\_res}$= 0.76, LCL= 0.72, UCL=0.80). Annual survival of migrant and resident fawns was similar ($\hat{S}_{annual\_mig}$ = 0.38 LCL= 0.27, UCL= 0.49; $\hat{S}_{annual\_res}$ = 0.38, LCL= 0.33, UCL= 0.43) because high winter survival of residents compensated for their low summer survival. However, there was considerable overlap in the 95% confidence intervals for estimates of migrant and resident survival in all occasions. The effects of age, winter elevation, and fall NDVI were similar to our top model (Table 2.10). Precipitation in spring prior to model start positively affected fawn survival and the effect was significant ($\hat{\beta}_{prev\_spring\_precip}$ = 0.017, LCL= 0.004, UCL= 0.029). Similarly to our adult model, distance to water on winter range had opposite effects on migrant and resident fawn survival (Fig. 2.10); resident fawns that resided further from water on their winter range had a higher chance of survival ($\hat{\beta}_{wat\_res}$ = 0.0005, LCL= 3.6E-06, UCL= 0.0009), while the inverse was true for migrants ($\hat{\beta}_{wat\_mig}$ = -0.0008, LCL= -0.0015, UCL= -0.0002). This effect was significant for both migrants and residents. Herd was also included in our top model variables; fawn survival was lower in the northern population (D-16), although this difference was not significant.

We found that the probability an unknown fawn was a resident or migrant at first capture (π), was best explained by capture GMU. Our top model classified that 86% of individuals that were unknown at first capture were residents (Table 2.11). The estimate for π was similar for our top model including a migration covariate. This model classified 87% of unknown fawns as residents at first capture (Table 2.12). We found that the probability a migrant or resident fawn was unknown in a given occasion (δ) was best explained by capture age class (neonate or winter-captured fawn) and a linear trend on age (a proxy for time in this model). The probability that a migratory fawn was unclassified decreased over time as more individuals completed their migrations.

Migration Strategies & Environmental Variables

Our adult sample consisted of 262 females that we resampled across years for a total sample of 672 unique deer-years. We classified 63% of adult female deer as resident, 35% as migrants, and 2% as unknown. In D-16, we classified the percent of migrant adult female deer per winter range GMU as 100% in GMU 49, 92% in GMU 57, 21% in GMU 58, and 0% in GMU 581 (Fig. 2.11). In D-34, we classified the percent of migrant adult female deer per winter range GMU as 52% in GMU 86, 15% in GMU 691, and 8% in GMU 84 (Fig. 2.11). Due to small sample sizes of deer in GMUs 861 and 69, we included deer from 861 in the above classifications for GMU 86 and merged GMU 69 deer into our classifications for 691. The mean distance of migrations in our study area was 45 km, and range shifts of resident adults between summer and winter averaged 1 km. Our sample of fawns consisted of 820 unique individuals. We initially classified 39% of fawns as residents, 15% as migrants, and 46% as unknown. Our top model suggested that 86% of unknown individuals were residents, which means approximately 21% of fawns we captured were migrants. This suggests our sample of fawns was skewed towards residents as we had suspected.

Migrant and resident deer were differentially exposed to the environmental variables that affected their survival. Migrant deer tended to reside in GMUs that were slightly more productive in summer (mean NDVI: 0.174 migrants (± 0.023 SD), 0.155 residents (± 0.022)), which we found positively influenced survival of both adult and fawn migrants. Variables that were related to conditions on winter range that influenced fawn survival tended to favor residents; resident winter ranges typically received more precipitation in spring (mean precipitation (mm): migrants = 31 (±16.8 SD), residents = 40 (±25.1 SD)), and tended to be at lower elevations (mean elevation (meters): migrants = 2411 (±247 SD), residents = 2291 (± 340

SD)), which we found positively influenced fawn survival. On average, migrants and residents utilized optimal strategies relative to locating themselves near water on their winter range, given this variable had opposite effects on migrant and resident deer. Migrants tended to be located closer to water on their winter range compared to residents (mean distance to water (meters), migrants = 845 (±648 SD), residents = 1179 (±734 SD)).

DISCUSSION

We detected apparent tradeoffs in survival of mule deer relative to their migratory strategy. Migratory adult female deer in south-central Colorado tended to have higher survival than residents overall, but this pattern differed among years and depended on summer range location. Migratory adults had higher survival than residents in 2018 and 2019, lower survival in 2020 and 2021, and similar survival in 2017, although there was considerable overlap in the 95% confidence intervals of these annual estimates. Migratory adults that summered in GMU 581 had lower survival than residents of GMU 581 or migrants that summered elsewhere. Migratory fawns had higher survival than residents in the first six months of their life, but lower overwinter survival. There again was considerable uncertainty surrounding these differences in each occasion. Annual survival of migrant and resident fawns was similar, suggesting that higher overwinter survival of residents compensated for their lower summer survival.

To our knowledge, this study is the first to use a state uncertainty approach (Nichols et al. 2004, Kendall et al. 2012) to model how migratory strategies influence survival when the migratory status of individuals is not always known. As with all modeling, this approach is not without limitation, and we acknowledge some potential for misclassification. For example, we made some assumptions about fawn movements within their first year of life that may have been violated in some instances – e.g. all fawn movements made within age 1 were representative of the behavior of the maternal doe, no individual migrated after our threshold periods, etc. Still, we believe this approach offered the most accurate method to estimate strategy-dependent survival in the face of uncertainty. This approach could be useful for estimating survival in other partially migratory populations where animals use multiple migration tactics within an overlapping geographic area and could include possible extensions for individuals that switch migratory tactics.

The persistence of partial migration within a population often indicates that multiple migratory strategies yield some selective advantage under variable conditions (Lack 1968, Chapman et al. 2011, Ortega 2023). Our results support this theory, but only partly elucidate the benefits of each strategy. Although we found annual differences in the benefits of migration on adult female survival, the environmental variables in our top models don't fully explain this variation. Nicholson et al. (1997) found that migratory mule deer in southern California had higher survival than residents in years of normal precipitation, but lower survival in dry years. Although we did not test for effects of annual precipitation in our model, yearly fluctuations in summer NDVI mirrored patterns in annual precipitation in our system and positively influenced survival of migrant deer. However, this variable does not fully explain annual variation because migrant adults sometimes had lower survival than residents in years of higher summer NDVI.

Habitat variables, such as summer NDVI, fluctuate annually but also vary geographically within years; thus, it can be difficult to disentangle how spatial versus temporal components of environment drive these effects on survival. For example, in mountainous regions, precipitation generally increases with elevation (Inouye and Wielgolaski 2013), thus, higher-elevation summer ranges will typically be more productive in summer, even in years of below-average precipitation. Summer NDVI will therefore generally be higher on migrant ranges but will also vary annually depending on weather patterns. Contrary to our hypothesis, resident adults were negatively influenced by summer NDVI at the GMU scale. We detected the same pattern at the scale of summer home ranges, although the effect was stronger at the GMU scale. This could suggest some spatial association between GMUs used by resident deer that have generally high NDVI and other variables we did not include in our models.

We found that survival of both migrant and resident fawns was positively associated with summer NDVI. A positive association between ungulate recruitment and summer productivity has been documented in multiple systems (Griffin et al. 2011, Hurley et al. 2017, Van De Kerk et al. 2020) and was consistent with our expectations; however, the positive effect on resident fawns is puzzling given that the same variable negatively influenced survival of resident adults. High adult female mortality typically corresponds with lower fawn survival (Giuliano et al. 1999), especially when doe mortalities occur in summer when fawns are dependent on nursing to survive (Gaillard et al. 2000). We found other differences in patterns of adult and fawn survival that were difficult to explain in light of this presumed dependence of fawns on their mothers. For example, we did not detect the same annual fluctuations in survival of migrant and resident fawns that we found in adults (fawn models for year and migration*year did not outcompete our null model).

One variable that consistently affected survival of both adults and fawns was distance to water on winter range. Interestingly, distance to water had opposite effects on survival of migrants and residents. Resident deer that wintered closer to water tended to have lower survival while the inverse was true for migrants. We also found that residents on average resided further from water on winter range than did migrants, suggesting deer were utilizing the strategy that most benefited them in a given area. We hypothesized that there may be tradeoffs associated with residing near water sources (Nicholson et al. 1997, Long et al. 2009); free-standing water enhances nutrition (Barboza et al. 2009, Mckee et al. 2015), but the risk of predation may increase near water (Smereka et al. 2020). Therefore, the opposite effects of distance to water that we detected relative to migratory strategy may indicate that tradeoffs of forage vs predation risk are different on predominantly migrant versus resident winter ranges. Lower survival of resident deer near water may be indicative of an increased risk of predation or higher predator densities; however, without having directly included variables related to predator densities, this is largely speculative. Winter ranges used primarily by migrant deer are often lower quality than resident ranges (Henderson et al. 2017). It may therefore benefit migrants to reside closer to riparian areas where moisture likely increases forage quality.

Winter range quality may be limiting over-winter survival of fawns that use migrant-dominant ranges in our system. We found that migratory fawns tended to have lower over-winter survival rates than resident fawns. Additionally, most conditions that enhanced fawn survival, such as increased spring precipitation on winter range and lower winter range elevation, tended to be more favorable on resident ranges. Area managers have noted that winter range is heavily browsed in the northwest region of the study area (GMU 49), where most deer utilize migratory tactics. Henderson et al. (2017) found that quality of winter range strongly influenced whether white-tailed deer chose to migrate or remain resident. Other studies have documented that density dependence predicted migratory propensity in ungulates (Mysterud et al. 2011, White et al. 2014), which further suggests that migration may be essential in areas of low-forage availability. Migrating to high-quality summer ranges may therefore be necessary for mule deer that winter in the northwestern part of our study region.

Migrations did not benefit mule deer across our entire study region, however. Adult females that migrated east to GMU 581 in summer had notably lower annual survival rates compared to migrants in other regions and compared to GMU 581 residents. In turn, GMU 581 residents had considerably higher survival than residents elsewhere. We found that most mortalities of migrants that summered in GMU 581 tended to occur during the migratory period, suggesting that deer may be exposed to hazards along this migration route. This is consistent with the findings of other studies that migratory deer are often vulnerable to predation during their migrations (Nicholson et al. 1997) and that risks of migration may depend more on the route taken than factors such as migration distance or duration (Sawyer et al. 2019a).

Disentangling effects of environment versus predation on mule deer survival is a challenging task and remains a major source of debate (Ballard et al. 2001, Forrester and Wittmer 2013). We found evidence that summer NDVI, a variable that presumably enhances the nutrition of both fawns and adults, positively influenced survival of migrant deer. However, we found minimal support for effects of covariates related to nutrition on deer survival, such as %IFBF. This brings into question the extent to which the positive association between NDVI and migrant survival is related to nutrition versus predation in this system. We may be detecting positive effects of summer NDVI on migrant survival because migration sometimes helps ungulates to escape predation (Fryxell et al. 1988, Hebblewhite and Merrill 2007). Alternatively, ‘no effect’ results may indicate that the variable used was insufficient to detect an effect. For example, we may have detected effects of IFBF if we had collected body metrics of deer in fall rather than late winter. We only collected body measurements of adults once in late winter; deer in the poorest condition may not have survived winter by this point (Bergman et al. 2018). Additionally, we did not test for effects of maternal condition on fawn survival, which has been shown to be important in other systems (Lomas and Bender 2007, Monteith et al. 2014), because we only had a small sample of individuals where this metric was known. Environmental variables appeared to have a slightly stronger effect on fawn survival compared to adults, thus even if adult females are not nutritionally limited, forage quality may still be a factor limiting recruitment of fawns.

Even if we are not fully able to disentangle how ultimate causes of mortality influence migrant and resident survival, the persistence of partial migration does appear to be contributing to presently high and stable survival of mule deer in south-central Colorado. Many have theorized that partial migration results in an Evolutionary Stable Strategy (Maynard Smith 1982) when each tactic provides benefits under variable conditions, but few studies have documented this effect (Chapman et al. 2011). Quantifying the long-term effects of migratory strategies on ungulate fitness would require long-term monitoring of multiple fitness components, which is often difficult to accomplish. However, our results do suggest that regional deer populations would likely decline if deer were unable to migrate, particularly in the northwest region of our study area where migratory strategies are dominant, and deer may be limited by their winter range habitat. Additionally, resident strategies in the eastern portion of our study area appear to be sustained by high-quality annual ranges, although it is unclear how changing weather patterns or increasing development of natural landscapes might affect resident deer in the long term. Our results contribute to a larger body of research that suggests protecting migration corridors and winter range habitat is crucial for the long-term health of ungulate populations (Sawyer et al. 2009, Webb et al. 2013, Malpeli 2022), and therefore should remain a management priority.

TABLES AND FIGURES

Table 2.1 Description of survival predictor variables for adult female mule deer and fawns in the D-16 and D-34 herds in Colorado

Category	Covariate	Scale	Model	Description
Environmental	Precipitation	GMU, SHR	F, A	Winter total and spring total
	Temperature	GMU, SHR	F, A	Summer max, winter min
	NDVI	GMU, SHR	F, A	Seasonal mean for shrub and grassland landcovers only
Population	GMU		F, A	Summer and Winter
	DAU		F, A	Annual herds (D-16, D-34)
	Year		F, A	Bio Year (June start)
	Month		A	June-May
	Season		A	Jun-Aug, Sept-Nov, Dec-Feb, Mar-Apr
Individual	Age	Monthly F, annual A	F, A	Fawn age: age by month. Adult age: at June 1
	Sex		F	Male, female, unknown
	Mig. Strategy		F, A	Migrant, resident, unknown
	Migration Dist.		A	Dist. between mean center of seasonal ranges
	Hind Foot		F, A	Adult HF= at capture, Fawn HF=at birth
	% IFBF		A	
	Weight/neonate capture age		F	Weight at capture/estimated age at capture (estimated for neonates only)
	Dist. to Water	Mean Center SHR	F, A	Measured from mean centers of seasonal ranges
	% Development	SHR	F, A	Impervious surfaces – e.g. houses or roads
	Elevation	Mean Center SHR		Elevation at mean center of seasonal ranges
	% Agriculture	SHR	F, A	Combined % hay and alfalfa
	Concentration	Mean Center (SHR)	F, A	Binary, summer or winter range center overlaps with a mule deer concentration area

Abbreviated terms key

F: Fawn
A: Adult
GMU: Game Management Unit
DAU: Data Analysis Unit (Herd)
SHR: Seasonal Home Range (i.e. summer and winter)
IFBF: Ingesta Free Body Fat
Wi: Winter
Su: Summer

Table 2.2 Description of predicted effects of covariates used for survival analyses of fawns and adult female mule deer in the D-16 and D-34 herds in south-central Colorado.

Covariate	Effect	Description of Predicted Effect
Precipitation	+ ++Mig	Precipitation enhances forage quality and hiding cover for mule deer, and a positive effect of precipitation on mule deer survival has been documented in numerous systems (+, Lomas and Bender 2007, Monteith et al. 2014, Schuyler et al. 2019). Nicholson et al. (1997) found that migrant deer had higher survival than residents in higher precipitation years (++Mig) but found the reverse pattern in low precipitation years. Winter precipitation can physically tax animals (Gilbert et al. 1970, Bartmann and Bowden 1984), but these effects are likely minor in areas such as south-central Colorado that only receive a moderate amount of winter precipitation.
Temperature	-Su +Wi	Extreme summer heat or winter cold can physically stress wildlife (Boone 2019). Animals may spend less time foraging in high heat, which will affect nutrition and milk production (-Su). Likewise, deer may increase their movements in colder temperatures (Gates and Hudson 1979), which burns energy and could weaken deer already in poor condition (+Wi).
NDVI	+	Summer nutrition plays a critical role in fawn survival (Tollefson et al. 2011). Summer plant productivity should therefore positively affect fawn recruitment. Forage quality in spring and fall may influence survival because deer are more resilient to winter energy deficits if they can access high-quality forage on either end of this season (Hurley et al. 2014). Winter plant productivity is generally low, but small increases in quality could have a strongly positive effect on survival.
GMU		Survival may be site specific. Factors that we did not include in our analysis that likely influence location-specific survival include predator densities, harvest pressure, or inter/intra-specific competition for resources. Additionally, predominance of migratory strategies differs across GMUs, which may be indicative that a certain strategy benefits deer in some locations more than others.
DAU		See GMU description.
Age	+Fa -Ad	Early mortality of fawns is typically high (Pojar and Bowden 2004) then gradually decreases as fawns becomes more capable (+Fa). It is generally accepted that large mammals experience a 'senescence effect' in survival (Jean-Michel et al. 1993), thus survival of adults likely declines with age (-Ad).
Sex	-Male	Survival of male fawns is typically lower (Bishop et al. 2005) or equal (White et al. 1987) than that of female fawns.
Mig. Strategy	+/0/-	Migrations generally allow deer to access high-quality forage (+Mig). Some studies suggest migrations help ungulates avoid predation (Fryxell 1998, Hebblewhite and Merrill 2009), but this is not the case in all systems (Sawyer et al. 2019, Nicholson et al. 1997). Resident strategies may be more favorable in areas where ranges offer high-quality forage year-round (+ Res, Middleton et al. 2013). The dominance of a strategy within a region may indicate its benefit at a large scale (+ Res). Tradeoffs could exist in utilizing a migratory vs resident strategy (Nicholson et al. 1997), which result in a net neutral effect of migration on survival (0).
Migration Dist.	+/-	Some studies have found that long-distance migrants receive a better nutritional payoff than short distance (+, Ortega et al. 2023). However, movement is inherently risky for wildlife (Fletcher et al. 2019) and thus some longer migrations could lower survival (-).
Hind Foot	+	Longer hind foot length may give deer an advantage in escaping predators. This metric is frequently included in mule deer survival analyses, and positively affects deer survival in some systems (White et al. 1987, Bishop 2007)
% IFBF	+/0	Monteith et al. (2014) documented a positive effect of march body fat on adult female survival. Higher percentages of body fat in spring may buffer female deer against the energy losses accrued during summer when lactation demands a large amount of their energy (+). Some studies have suggested that body fat also influences predation risk, whereby certain predators select for deer in weaker condition (+, Krumm et al. 2010). However, body fat may only influence survival in systems where many deer are in

		poor condition; deer in south-central CO generally have a high percentage of body fat, so a difference may not be detectable (0).
Weight/Age at cap	+	We used fawn weights to approximate neonate age at capture, thus both variables represent the effect of capturing neonates on day 1-7 of their life. Early morality of fawns is typically high (Pojar and Bowden 2004), so fawns with higher weights (assumed to be older) will typically have higher survival.
Dist. to Water	+Su -Wi	Access to freestanding water allows for greater intake of food (+, Barboza et al. 2009, Mckee et al. 2015). Mule deer select for water source around summer parturition (Long et al. 2009), when their mobility is limited and need for water may be higher due to demands of lactation (+Su, Cain et al. 2006, Long et al. 2009). Some studies have documented relative avoidance of water sources in non-summer seasons (Nicholson et al. 1997, Long et al. 2009), possibly due to tradeoffs of exposure to greater predation risk near riparian areas (-, Smereka et al. 2020). Nicholson et al. (1997) documented migrants resided closer to water in summer compared to residents, suggesting possible trade offs in survival relative to choice of summer ranges.
% Development	+/-	Studies have found varying effects of human development on ungulate survival. Development may shelter ungulates from predation (+, Hebblewhite and Merrill 2009), but potentially degrades habitat and exposes wildlife to threats, such as car collisions (-, Webb et al. 2011).
Elevation	+ Su -Wi	Deer that use high elevation ranges in the summertime (i.e. migrants) typically have prolonged access to high-quality forage (+ Su, Monteith et al. 2011). Predator densities may also be lower at high elevation if predators can seek resident prey and do not need to follow migratory ungulates to high elevation. In winter, deer that utilize higher elevation ranges are likely exposed to harsher winter weather, while deer at lower elevation likely experience milder conditions and may access better winter forage.
% Agriculture	+/- ++Res	Hay and alfalfa fields provide high-quality forage for mule deer (+). Agriculture has been hypothesized to negate the benefits of ungulate migration because agricultural forage may be equally (or more) high-quality than forage on high-elevation summer ranges (++Res, Middleton et al. 2013). Agricultural fields can also be hazardous to deer fawns; we have documented deaths due to mowing, being run over by pivot sprinklers, and acidosis (-); however, these sources of mortality appear to be rare.
Concentration	+/-	High densities of deer may degrade habitat quality. Density may therefore negatively influence survival (-, White and Bartmann 1998). Density may also mediate the probability of predation. Predators are often attracted to high densities of prey (Murray et al. 1994), but the chance of predation may be lower due to a ‘safety-in-numbers' effect (+, White and Warner 2007).

Table 2.3 Adult female mule deer survival models within <2 delta AIC of top model. Data used for analyses were collected in the D-16 and D-34 mule deer herds in south-central Colorado.

Model	Δ AICc	Weight	K	-2log(L)
mig*dist water (WR)+age	0.00	0.0336	7	890.32
age+mig*summer ndvi (GMU)+mig*GMU 581 (SR)	0.09	0.0322	10	884.39
mig*dist water (WR)+age+fall ndvi (WR)	0.32	0.0287	8	888.63
mig*dist water (WR)+age+prev. spring ndvi (WR)	0.42	0.0273	8	888.73
mig*dist water (WR)+age+GMU 37 (SR)	1.22	0.0183	8	889.53
age+fall ndvi (WR)+mig*summer ndvi (GMU)+mig*GMU 581 (SR)	1.25	0.0180	11	883.54
mig*dist water (WR) +age+mig*GMU 581 (SR)	1.29	0.0177	10	885.58
mig*dist water (WR)+age+GMU 58 (SR)	1.57	0.0153	8	889.89
age+mig*summer ndvi (GMU)+GMU 58 (SR) +mig*GMU 581 (SR)	1.74	0.0141	11	884.03
age+fall ndvi (WR)+mig*GMU 581 (SR)	1.76	0.0140	8	890.07
mig*dist water (WR)+age+fall ndvi (WR)+prev. spring ndvi (WR)	1.78	0.0138	9	888.09
mig*dist water (WR)+age+prev. spring ndvi (WR)+GMU 58 (SR)	1.85	0.0133	9	888.15
mig*dist water (WR)+age+fall ndvi (WR)+GMU 37 (SR)	1.86	0.0133	9	888.16
mig*dist water (WR)+age+mig*summer ndvi (GMU)	1.89	0.0131	10	886.18
mig*dist water (WR)+age+prev. spring ndvi (WR) +GMU 37 (SR)	1.91	0.0129	9	888.21
age+mig*summer ndvi (GMU)+prev. spring ndvi (WR) +mig*GMU 581 (SR)	1.92	0.0129	11	884.21
age+mig*GMU 581 (SR)	1.96	0.0126	7	892.28

Abbreviated terms key

mig: migratory strategy
GMU: game management unit
dist water: distance to water
age: age in June
prev. spring: spring prior to model start
(SR): summer range scale
(WR): winter range scale
(GMU): GMU scale

Table 2.4 Model weights of single factor variables (including interactions) for competitive variables from our adult female mule deer survival model set. Data used for analyses were collected in the D-16 and D-34 mule deer herds in south-central Colorado.

Model	**Δ AICc**	**Weight**	**K**	**-2log(L)**
mig*dist water (WR)	0.00	0.5187	6	896.14
mig*summer ndvi (GMU)	1.74	0.2176	6	897.87
mig*GMU 581 (SR)	2.25	0.1680	6	898.39
mig	3.42	0.0940	3	905.56
fall ndvi (WR)	13.97	0.0005	2	918.12
age	14.82	0.0003	2	918.97
GMU 37 (SR)	15.14	0.0003	2	919.29
prev. spring ndvi (WR)	15.30	0.0003	2	919.45
GMU 58 (SR)	16.06	0.0002	2	920.21
null	16.35	0.0002	1	922.51

Abbreviated terms key

mig: migratory strategy
GMU: game management unit
dist water: distance to water
age: age in June
prev. spring: spring prior to model start
(SR): summer range scale
(WR): winter range scale
(GMU): GMU scale

Table 2.5 Beta estimates for the top adult female mule deer survival model: migrant*dist. Water (WR) + age. Data used for analyses were collected in the D-16 and D-34 mule deer herds in south-central Colorado.

Variable	**Estimate**	**SE**	**LCI**	**UCI**
intercept	1.9394	0.4457	1.0658	2.8130
mig	1.2531	0.4580	0.3554	2.1508
unknown	-6.2097	4.8487	-15.7132	3.2938
dist. water (WR)	0.0002	0.0002	-0.0002	0.0007
mig*dist. water (WR)	-0.0011	0.0004	-0.0018	-0.0004
unknown* dist. water (WR)	0.0000	0.0028	-0.0055	0.0055
age	-0.1421	0.0585	-0.2567	-0.0275

Abbreviated terms key
mig: migrant
unknown: unknown migratory strategy
dist water: distance to water
age: age in June
(WR): winter range scale

Table 2.6 Beta estimates for adult female mule deer survival model: migrant*GMU 581 (SR) + migrant*Summer NDVI (GMU) + age. Data used for analyses were collected in the D-16 and D-34 mule deer herds in south-central Colorado.

Variable	Estimate	SE	LCI	UCI
intercept	4.2344	1.1483	1.9838	6.4850
mig	-5.0489	2.0895	-9.1443	-0.9534
unknown	-5.7475	153.4837	-306.5757	295.0806
age	-0.1442	0.0579	-0.2577	-0.0307
summer NDVI (GMU)	-13.4456	6.7326	-26.6415	-0.2497
mig*summer NDVI (GMU)	33.2915	12.4186	8.9510	57.6319
unknown*summer NDVI (GMU)	-1.0261	935.7751	-1835.1454	1833.0931
GMU 581 (SR)	0.7307	0.3973	-0.0479	1.5093
mig*GMU 581 (SR)	-1.7959	0.6397	-3.0498	-0.5421
unknown*GMU 581 (SR)	-0.1000	872.5057	-1710.2112	1710.0112

Abbreviated terms key
mig: migratory strategy
unknown: unknown migratory strategy
GMU: game management unit
age: age in June
(SR): summer range scale
(GMU): GMU scale

Table 2.7 Mule deer fawn survival models within <2 delta AIC of top model. Data used for analyses were collected in the D-16 and D-34 mule deer herds in south-central Colorado.

Model	Δ AICc	Weight	K	-2log(L)
age+elevation (WR)+develop (SR)+summer ndvi (GMU)+hind foot+fall ndvi (WR)+sex	0.00	0.0224	29	5292.62
age+elevation (WR)+develop (SR)+prev. spring precip (WR)+summer ndvi (GMU)+hind foot+fall ndvi (WR)	0.02	0.0222	28	5294.66
age+elevation (WR)+prev. spring precip (WR)+summer ndvi (GMU)+hind foot+fall ndvi (WR)+sex	0.15	0.0209	29	5292.76
age+elevation (WR)+prev. spring precip (WR)+summer ndvi (GMU)+hind foot+fall ndvi (WR)	0.18	0.0205	27	5296.85
age+elevation (WR)+develop (SR)+summer ndvi (GMU)+hind foot+fall ndvi (WR)	0.18	0.0205	27	5296.85
age+elevation (WR)+develop (SR)+prev. spring precip (WR)+summer ndvi (GMU)+hind foot+sex	0.35	0.0189	29	5292.96
age+elevation (WR)+develop (SR)+summer ndvi (GMU)+hind foot+sex	0.70	0.0158	28	5295.34
age+elevation (WR)+develop (SR)+prev. spring precip (WR)+summer ndvi (GMU)+hind foot	0.72	0.0156	27	5297.39
age+elevation (WR)+prev. spring precip (WR)+summer ndvi (GMU)+hind foot+sex	0.85	0.0147	28	5295.49
age+elevation (WR)+summer ndvi (GMU)+hind foot+fall ndvi (WR)	0.88	0.0144	26	5299.57
age+elevation (WR)+prev. spring precip (WR)+summer ndvi (GMU)+hind foot	0.88	0.0144	26	5299.58
age+elevation (WR)+develop (SR)+summer ndvi (GMU)+hind foot	0.89	0.0144	26	5299.58
age+elevation (WR)+develop (SR)+prev. spring precip (WR)+hind foot+fall ndvi (WR)+sex	0.92	0.0142	29	5293.53
age+elevation (WR)+prev. spring precip (WR)+hind foot+fall ndvi (WR)+sex	1.04	0.0133	28	5295.68
age+elevation (WR)+summer ndvi (GMU)+hind foot+fall ndvi (WR)r+sex	1.08	0.0131	28	5295.72
Mig*dist water (WR)+age+elevation (WR)+prev. spring precip (WR)+fall ndvi (WR)	1.25	0.0120	28	5295.89
age+elevation (WR)+develop (SR)+prev. spring precip (WR)+summer ndvi (GMU)+fall ndvi (WR)+sex	1.27	0.0119	29	5293.88
age+elevation (WR)+prev. spring precip (WR)+summer ndvi (GMU)+fall ndvi (WR)+sex	1.42	0.0110	28	5296.06
age+elevation (WR)+prev. spring precip (WR)+hind foot+fall ndvi (WR)	1.42	0.0110	26	5300.11
age+elevation (WR)+summer ndvi (GMU)+hind foot	1.59	0.0102	25	5302.30
age+elevation (WR)+develop (SR)+prev. spring precip (WR)+hind foot+sex	1.62	0.0100	28	5296.26
age+elevation (WR)+develop (SR)+prev. spring precip (WR)+hind foot+fall ndvi (WR)	1.67	0.0098	27	5298.33
age+elevation (WR)+prev. spring precip (WR)+summer ndvi (GMU)i+hind foot+fall ndvi (WR)+D-16	1.68	0.0097	28	5296.32
age+elevation (WR)+develop (SR)+summer ndvi (GMU)+hind foot+fall ndvi (WR)+D-16	1.73	0.0095	28	5296.37
age+elevation (WR)+prev. spring precip (WR)+hind foot+sex	1.74	0.0094	27	5298.41
age+elevation (WR)+prev. spring precip (WR)+fall ndvi (WR)+sex	1.75	0.0094	27	5298.42
age+elevation (WR)+summer ndvi (GMU)+hind foot+sex	1.78	0.0092	27	5298.45
age+elevation (WR)+develop (SR)+prev. spring precip (WR)+fall ndvi (WR)+sex	1.87	0.0088	28	5296.51

age+elevation (WR)+develop (SR)+prev. spring precip (WR)+summer ndvi (GMU)+sex	1.97	0.0084	28	5296.61

Abbreviated terms key
mig: migratory strategy
GMU: game management unit
dist water: distance to water
develop: % development
age: age in months
prev. spring: spring prior to model start
(SR): summer range scale
(WR): winter range scale
(GMU): GMU scale

Table 2.8 Table of single factor variables weights of most competitive variables from our mule deer fawn survival model set with an additive effect of age. Data used for analyses were collected in the D-16 and D-34 mule deer herds in south-central Colorado.

Model	Δ AICc	Weight	K	-2log(L)
age + elevation (WR)	0.00	0.643	23	5312.28
age + prev. spring precip (WR)	3.48	0.113	23	5315.76
age + summer ndvi (GMU)	4.11	0.082	23	5316.39
age + fall ndvi (WR)	5.68	0.038	23	5317.95
age + hind foot	5.91	0.033	23	5318.19
age + D-16	6.49	0.025	23	5318.77
age + sex	6.95	0.020	24	5317.21
age + % development (SR)	7.58	0.015	23	5319.86
age	7.63	0.014	22	5321.93
age + mig*dist water (WR)	8.09	0.011	25	5316.33
age + mig	9.28	0.006	23	5321.56
null	178.73	0.000	14	5509.16

Abbreviated terms key
mig: migratory strategy
GMU: game management unit
dist water: distance to water
age: age in months
prev. spring: spring prior to model start
(SR): summer range scale
(WR): winter range scale
(GMU): GMU scale

Table 2.9 Beta estimates for the top mule deer fawn survival model (age+elevation (WR)+develop(SR)+summer ndvi (GMU)+hind foot+fall ndvi (WR)+sex). Reference class for sex = unknown sex. Data used for analyses were collected in the D-16 and D-34 mule deer herds in south-central Colorado.

Variable	Estimate	SE	LCI	UCI
intercept	5.3607	0.7392	3.9120	6.8095
age1	-8.1068	2.3768	-12.7654	-3.4482
age2	-7.5304	2.3784	-12.1921	-2.8688
age3	-7.2774	2.3794	-11.9411	-2.6137
age4	-2.4940	1.2214	-4.8880	-0.1000
age5	-2.8681	1.2021	-5.2243	-0.5120
age6	-1.4648	1.1894	-3.7959	0.8664
age7	-0.9417	0.2543	-1.4400	-0.4434
age8	-0.6646	0.2813	-1.2159	-0.1132
elevation (WR)	-0.0008	0.0003	-0.0014	-0.0003
develop (SR)	0.0172	0.0102	-0.0027	0.0372
summer ndvi (GMU)	8.4529	3.4028	1.7835	15.1223
hind foot	0.1544	0.0749	0.0077	0.3012
fall ndvi (WR)	13.0778	8.1061	-2.8101	28.9657
female	-1.2027	1.0393	-3.2397	0.8343
male	-1.4161	1.0381	-3.4507	0.6186

Abbreviated terms key
develop: % development
ageX: age in months
(SR): summer range scale
(WR): winter range scale
(GMU): GMU scale

Table 2.10 Beta estimates for the top mule deer fawn survival model that included a migration covariate: (Mig*dist water (WR)+age+elevation (WR)+prev. spring precip (WR)+fall ndvi (WR)). Data used for analyses were collected in the D-16 and D-34 mule deer herds in south-central Colorado.

Variable	Estimate	SE	LCI	UCI
intercept	5.0465	0.7554	3.5660	6.5270
mig	0.4118	0.2261	-0.0312	0.8549
age1	-4.5483	0.7998	-6.1159	-2.9807
age2	-3.9739	0.8069	-5.5555	-2.3923
age3	-3.7283	0.8153	-5.3264	-2.1303
age4	-2.7749	1.2710	-5.2661	-0.2837
age5	-3.1636	1.2537	-5.6210	-0.7063
age6	-1.7582	1.2364	-4.1816	0.6653
age7	-0.9196	0.2549	-1.4191	-0.4201
age8	-0.6413	0.2820	-1.1940	-0.0887
elevation (WR)	-0.0008	0.0003	-0.0014	-0.0003
prev. spring precip (WR)	0.0165	0.0063	0.0042	0.0288
fall ndvi (WR)	16.5463	8.4688	-0.0526	33.1453
dist water (WR)	0.0005	0.0002	3E-06	0.0009
mig*dist water (WR)	-0.0008	0.0003	-0.0015	-0.0002

Abbreviated terms key

mig: migratory strategy
ageX: age in months
dist water: distance to water
prev. spring: spring prior to model start
(SR): summer range scale
(WR): winter range scale
(GMU): GMU scale

Table 2.11 Top mule deer fawn survival model (age+elevation (WR)+develop(SR)+summer ndvi (GMU)+hind foot+fall ndvi (WR)+sex) results for pi and delta. 'Neo' refers to deltas for fawns captured as neonates and 'Wint' refers to winter-captured fawns. Data used for analyses were collected in the D-16 and D-34 mule deer herds in south-central Colorado.

Parameter	Estimate	SE	LCL	UCL
Pi R|u	0.862	0.026	0.804	0.905
Delta Neo u|M_2	0.968	0.014	0.924	0.987
Delta Neo u|M_3	0.864	0.034	0.782	0.918
Delta Neo u|M_4	0.573	0.050	0.472	0.668
Delta Neo u|M_5	0.221	0.049	0.140	0.332
Delta Neo u|M_6	0.057	0.024	0.024	0.126
Delta Wint u|M_{10}	0.966	0.023	0.875	0.992
Delta Wint u|M_{11}	0.508	0.070	0.373	0.641

Abbreviated terms key

R: resident
M_x: migrant occasion x
u: unknown migratory strategy
Neo: neonate-captured fawn
Wint: winter-captured fawn

Table 2.12 Results for pi and delta for the top mule deer fawn survival model that includes a migration covariate: (Mig*dist water (WR)+age+elevation (WR)+prev. spring precip (WR)+fall ndvi (WR). 'Neo' refers to deltas for fawns captured as neonates and 'Wint' refers to winter-captured fawns. Data used for analyses were collected in the D-16 and D-34 mule deer herds in south-central Colorado.

Parameter	Estimate	SE	LCL	UCL
Pi R|u	0.871	0.025	0.814	0.913
Delta Neo u|M_2	0.967	0.015	0.923	0.986
Delta Neo u|M_3	0.862	0.035	0.779	0.917
Delta Neo u|M_4	0.571	0.051	0.470	0.666
Delta Neo u|M_5	0.221	0.049	0.139	0.332
Delta Neo u|M_6	0.057	0.024	0.024	0.127
Delta Wint u|M_{10}	0.966	0.023	0.875	0.992
Delta Wint u|M_{11}	0.509	0.070	0.375	0.642

Abbreviated terms key
R: resident
M_x: migrant occasion x
u: unknown migratory strategy
Neo: neonate-captured fawn
Wint: winter-captured fawn

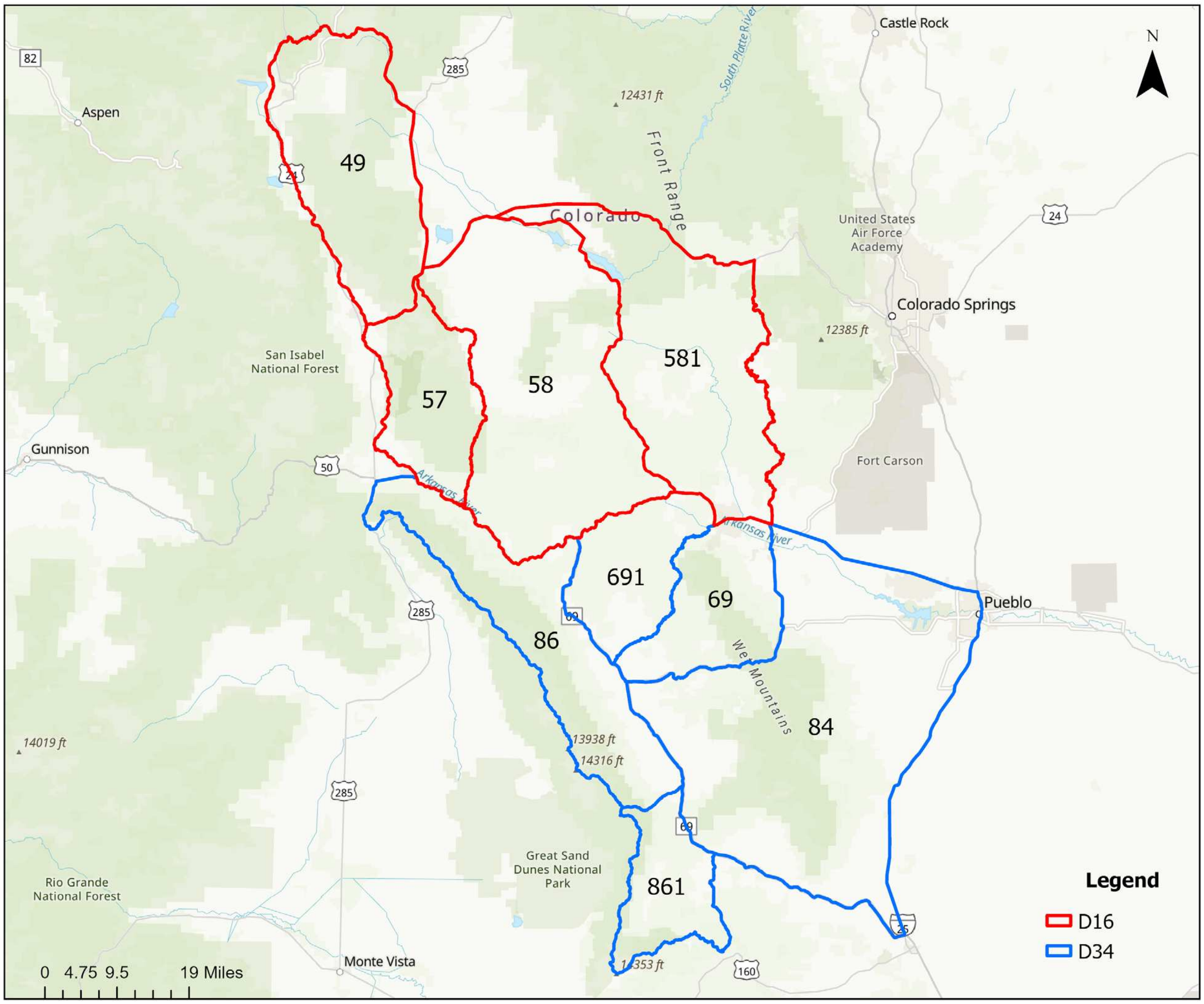

Figure 2.1 Mule deer data analysis units (DAU) D-16 and D-34 located in south-central Colorado. Smaller segments of each DAU are Colorado Parks and Wildlife Game Management Units. Some deer that winter in GMUs 57 and 49 migrate to GMUs outside of the study area in summer that are not pictured (37, 45, 48), but can be viewed at this link: <https://cpw.state.co.us/learn/Pages/Maps.aspx>

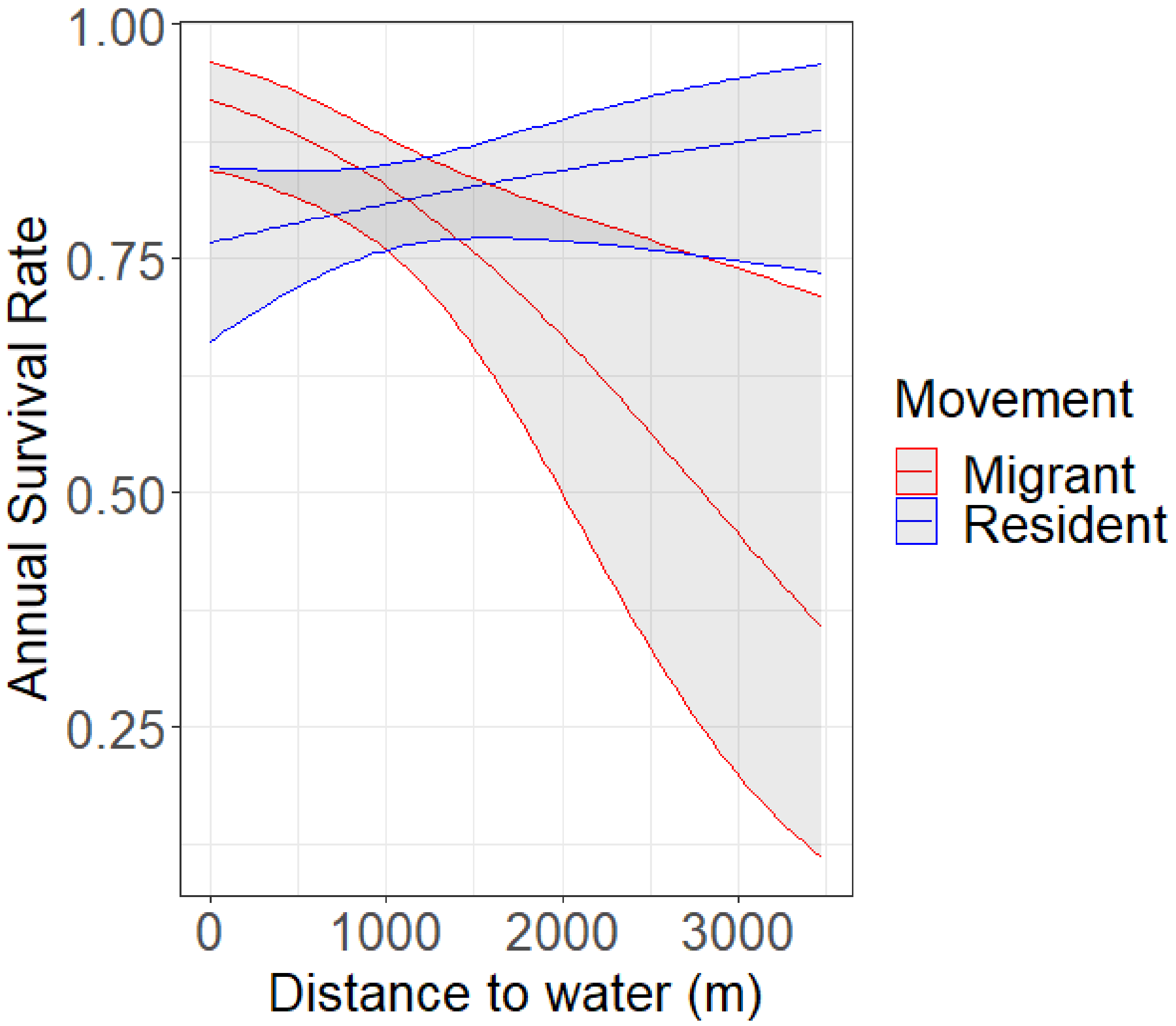

Figure 2.2 Effects of distance to water (m) on survival of migrant and resident adult female mule deer in the D-16 and D-34 herds in south-central Colorado from top model: migrant*dist. water (WR) + age.

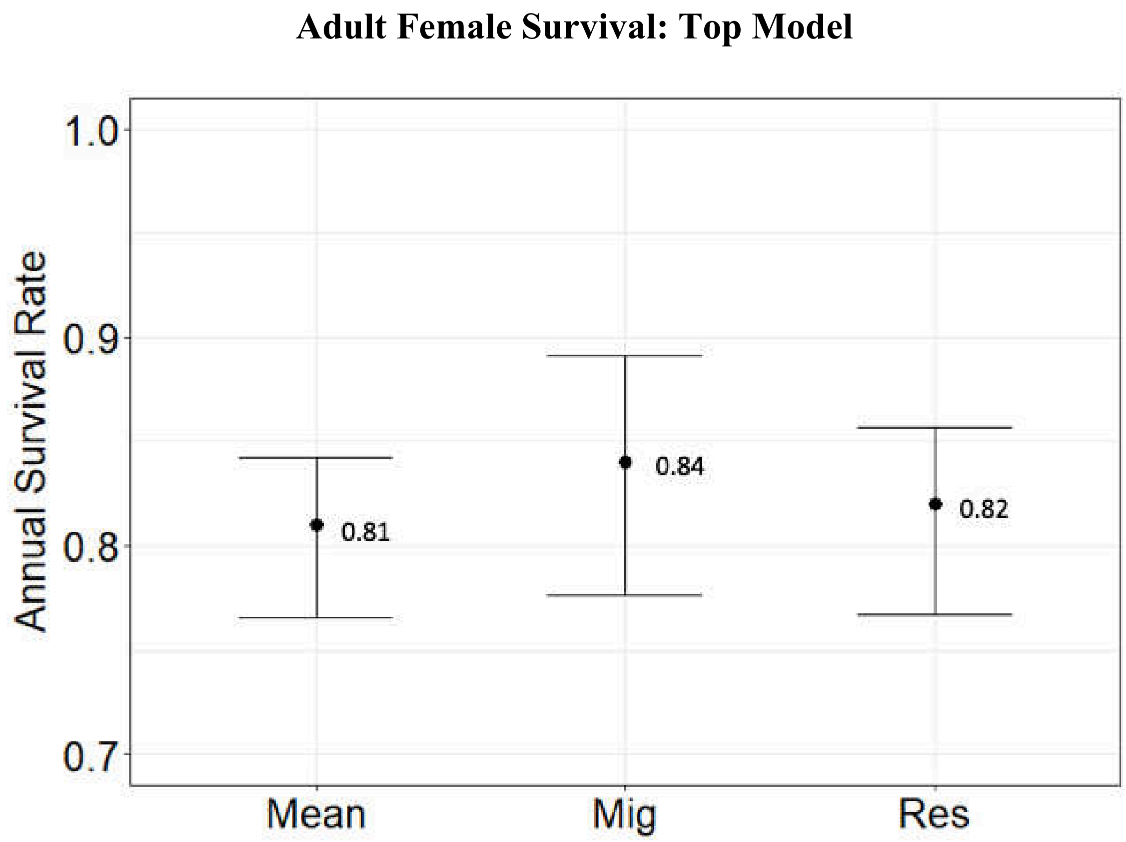

Figure 2.3 Annual survival rates of adult female mule deer for the top model (mig*dist. water (WR) + age) using separate mean values of individual covariates for migrants and residents. The estimate for the population mean includes individuals with an unknown migration strategy (n=5). Data used for analyses were collected in the D-16 and D-34 mule deer herds in south-central Colorado.

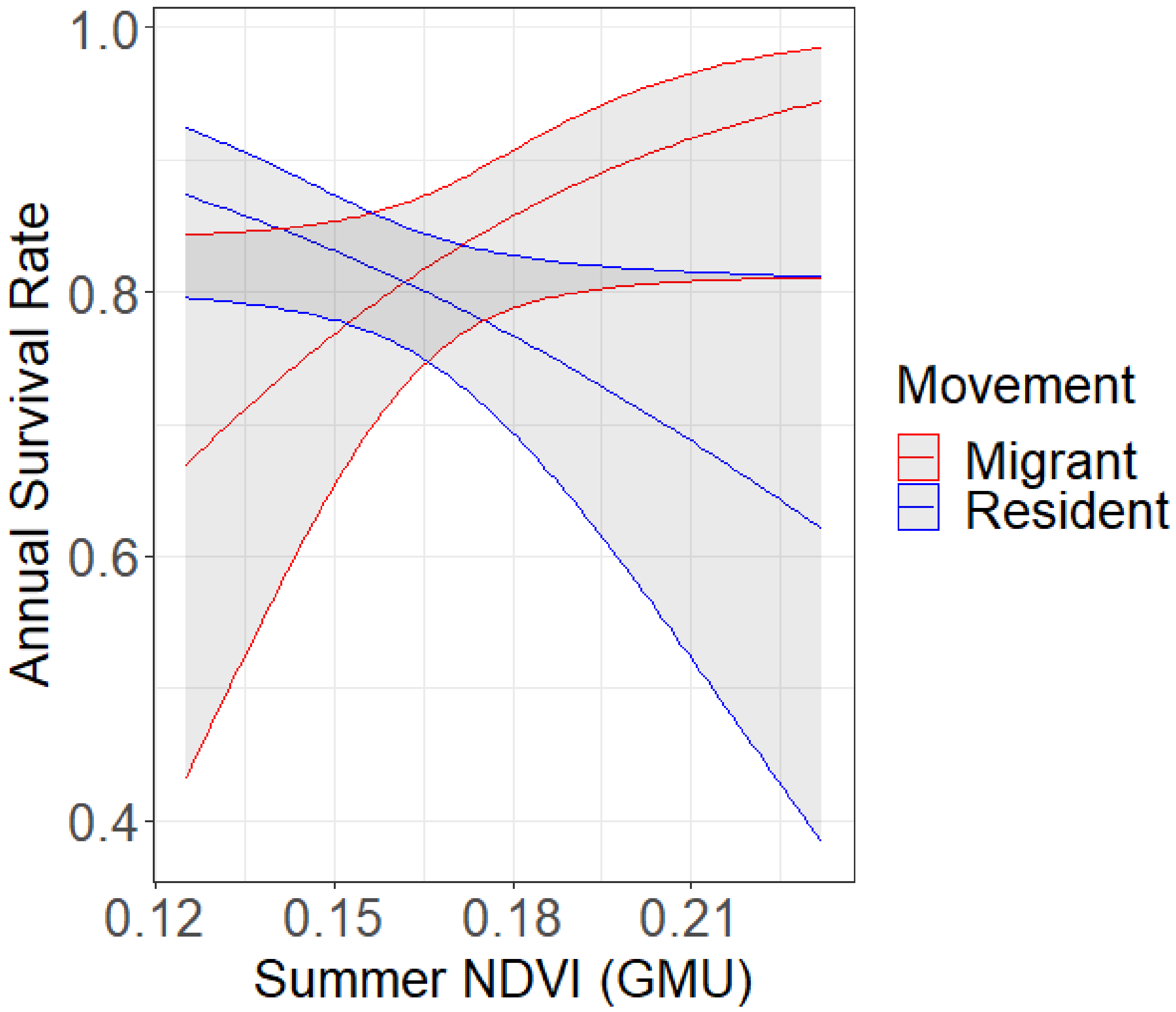

Figure 2.4 Effect of summer NDVI on survival of migrant and resident adult female mule deer in the D-16 and D-34 herds in south-central Colorado from the second ranked model: migrant*GMU 581 (SR) + migrant*Summer NDVI (GMU) + age.

Adult Female Survival: 2^{nd} Most Competitive Model

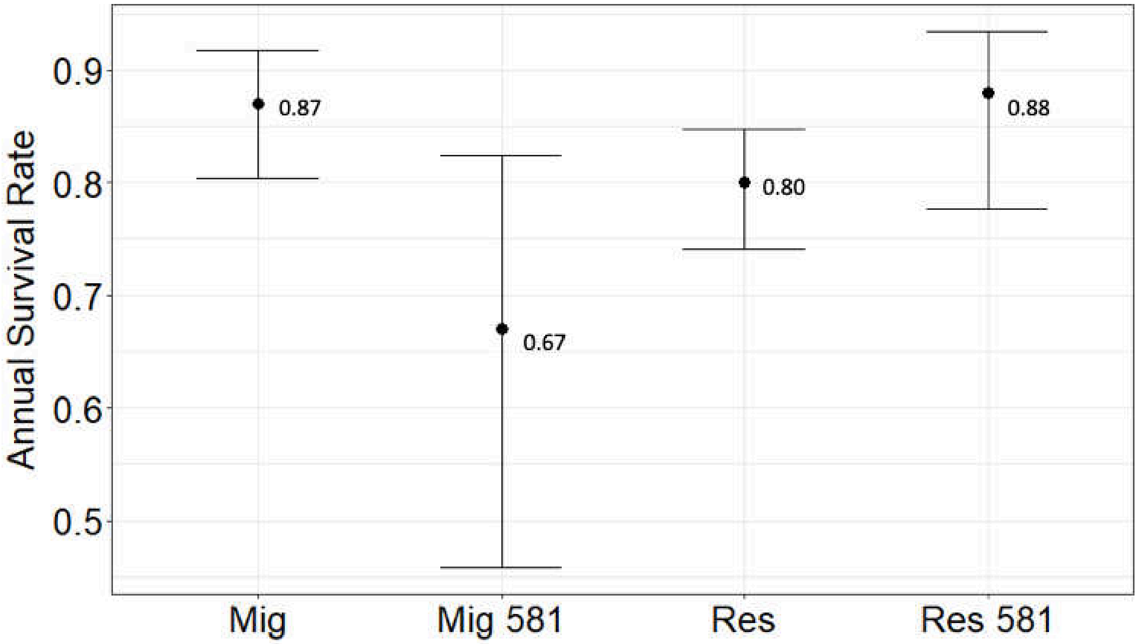

Figure 2.5 Annual survival rates of adult female mule deer from model: mig*summer ndvi (GMU) + mig*GMU 581 (SR) + age. Estimates were derived using separate mean values of individual covariates for migrants and residents. Data used for analyses were collected in the D-16 and D-34 mule deer herds in south-central Colorado.

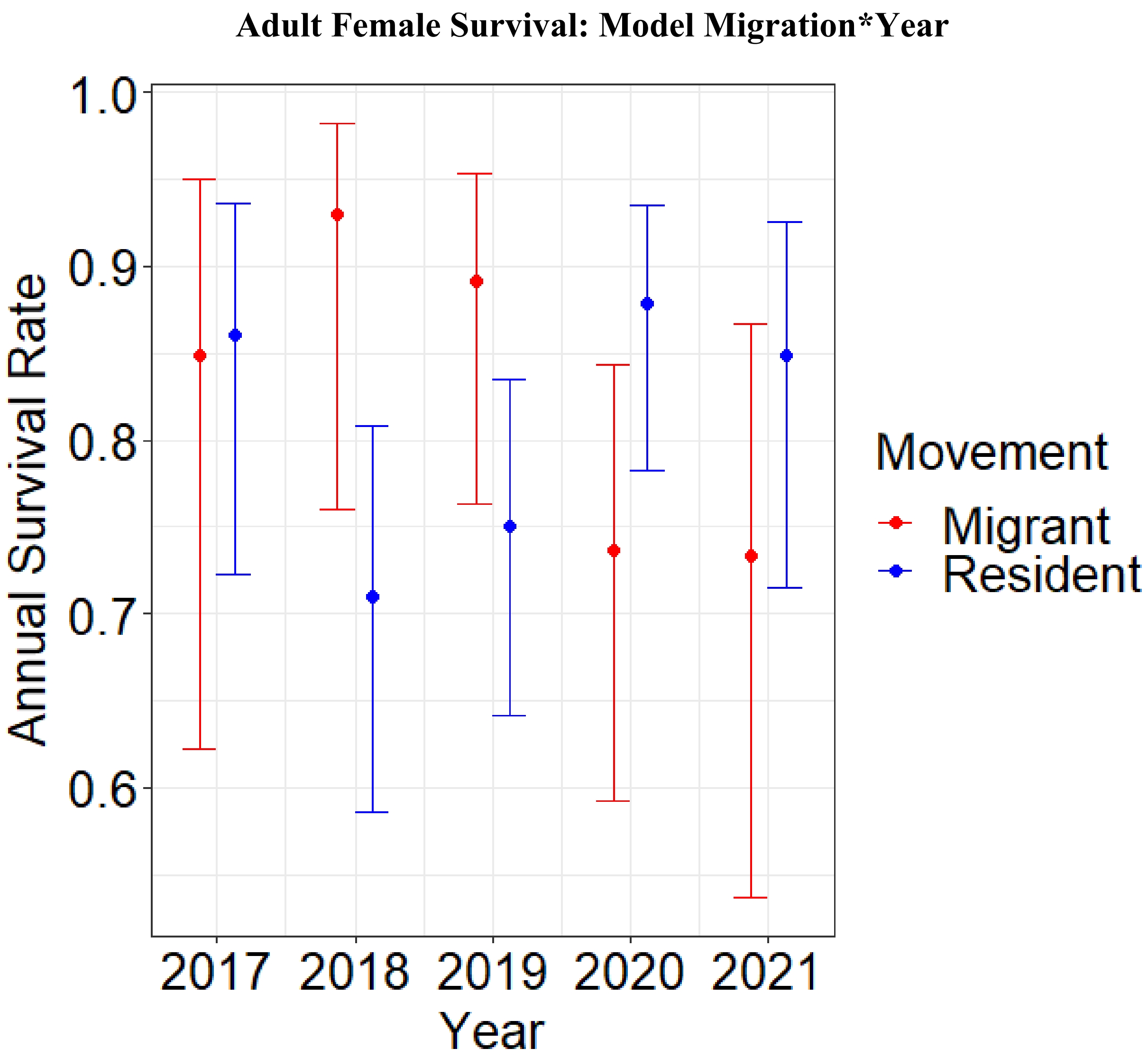

Figure 2.6 Annual survival by year for migrant and resident adult female mule deer from model: mig*year. Data used for analyses were collected in the D-16 and D-34 mule deer herds in south-central Colorado.

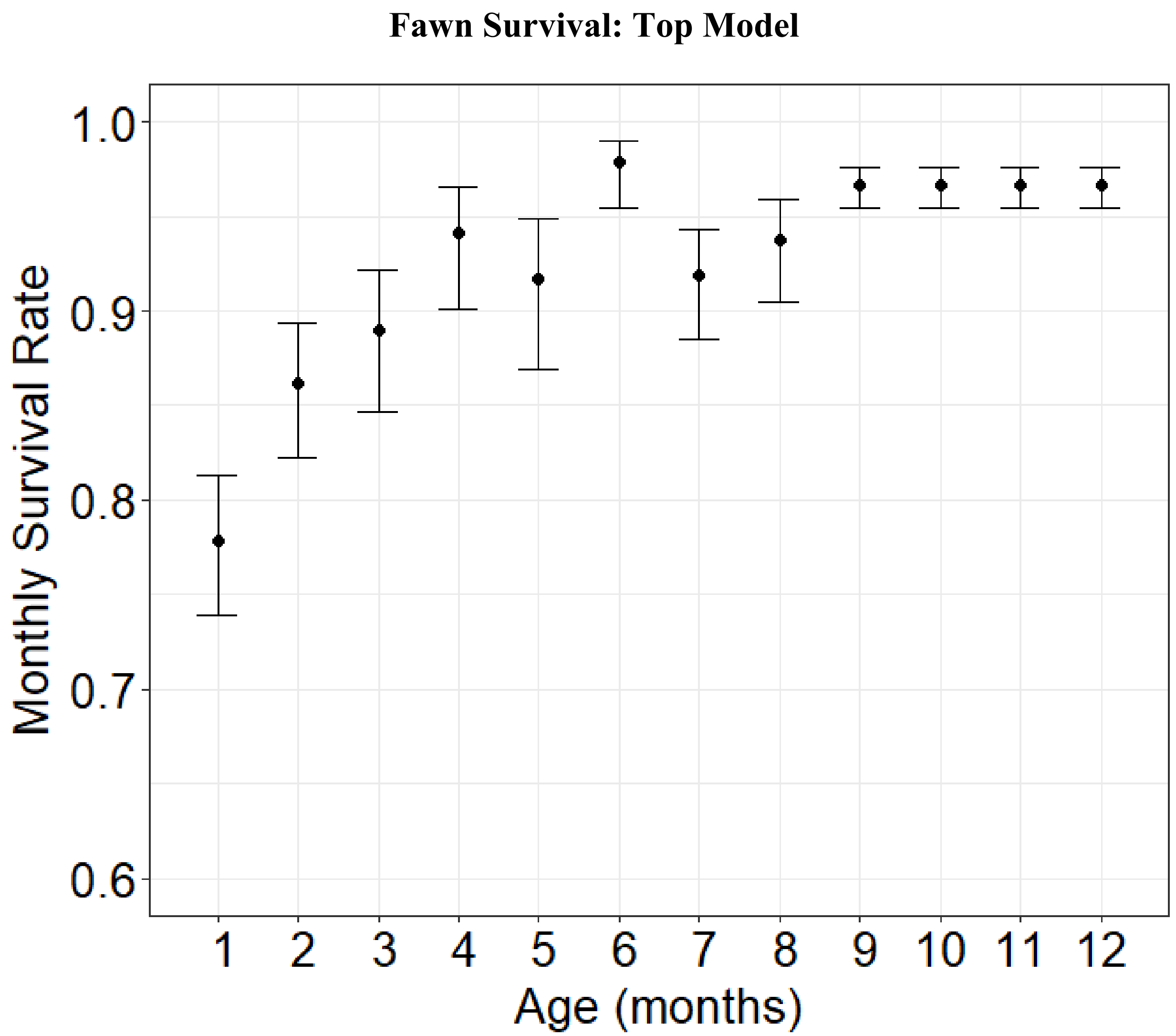

Figure 2.7 Monthly survival rate of mule deer fawns by age for the top model: (age+elevation (WR)+develop(SR)+summer ndvi (GMU)+hind foot+fall ndvi (WR)+sex) using the mean value of individual covariates. Data used for analyses were collected in the D-16 and D-34 mule deer herds in south-central Colorado.

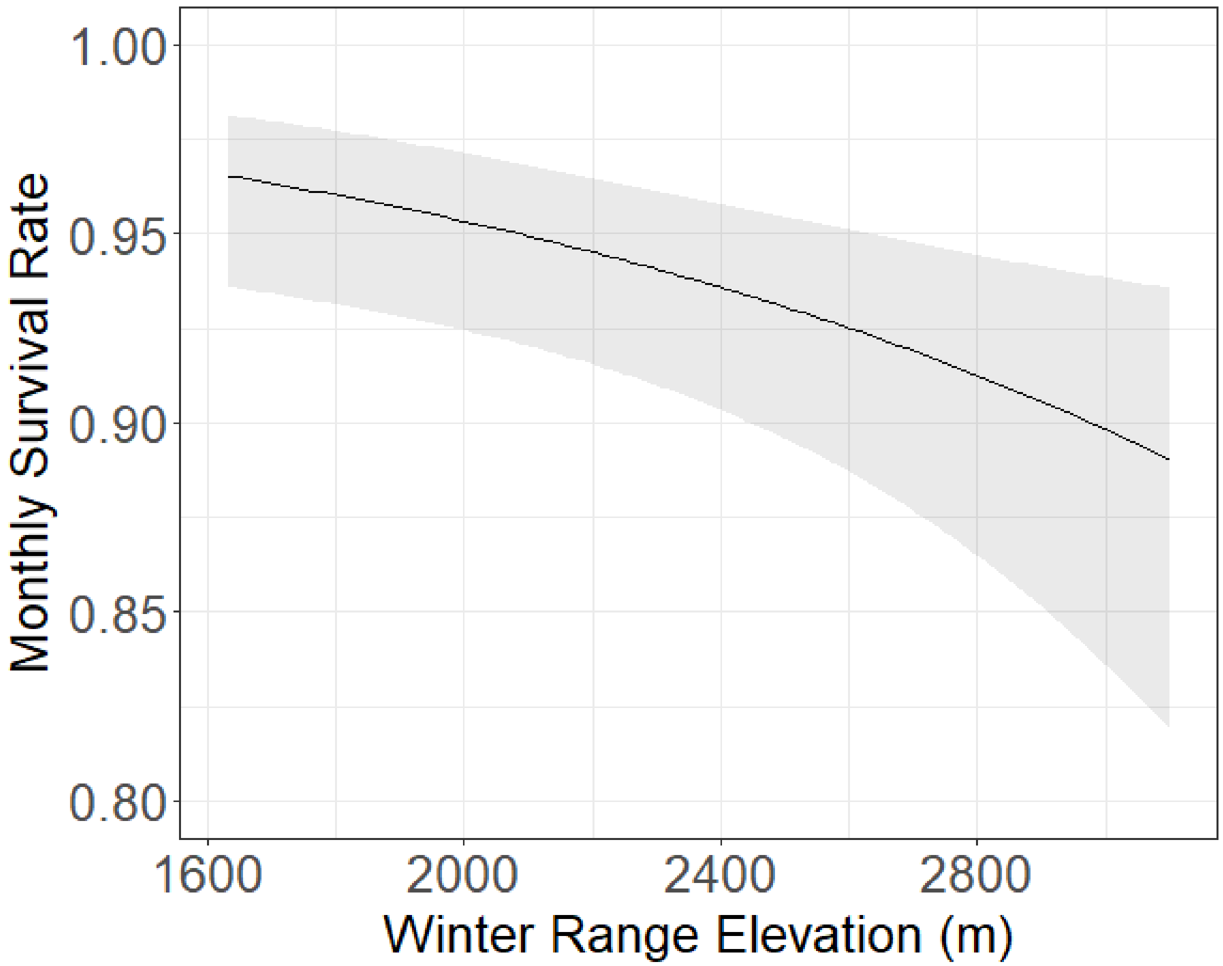

Figure 2.8 Effect of winter range elevation on survival of mule deer fawns at 8 months of age from our top model: (age+elevation (WR)+develop(SR)+summer ndvi (GMU)+hind foot+fall ndvi (WR)+sex). Data used for analyses were collected in the D-16 and D-34 mule deer herds in south-central Colorado.

Fawn Survival: Top Model for Migration

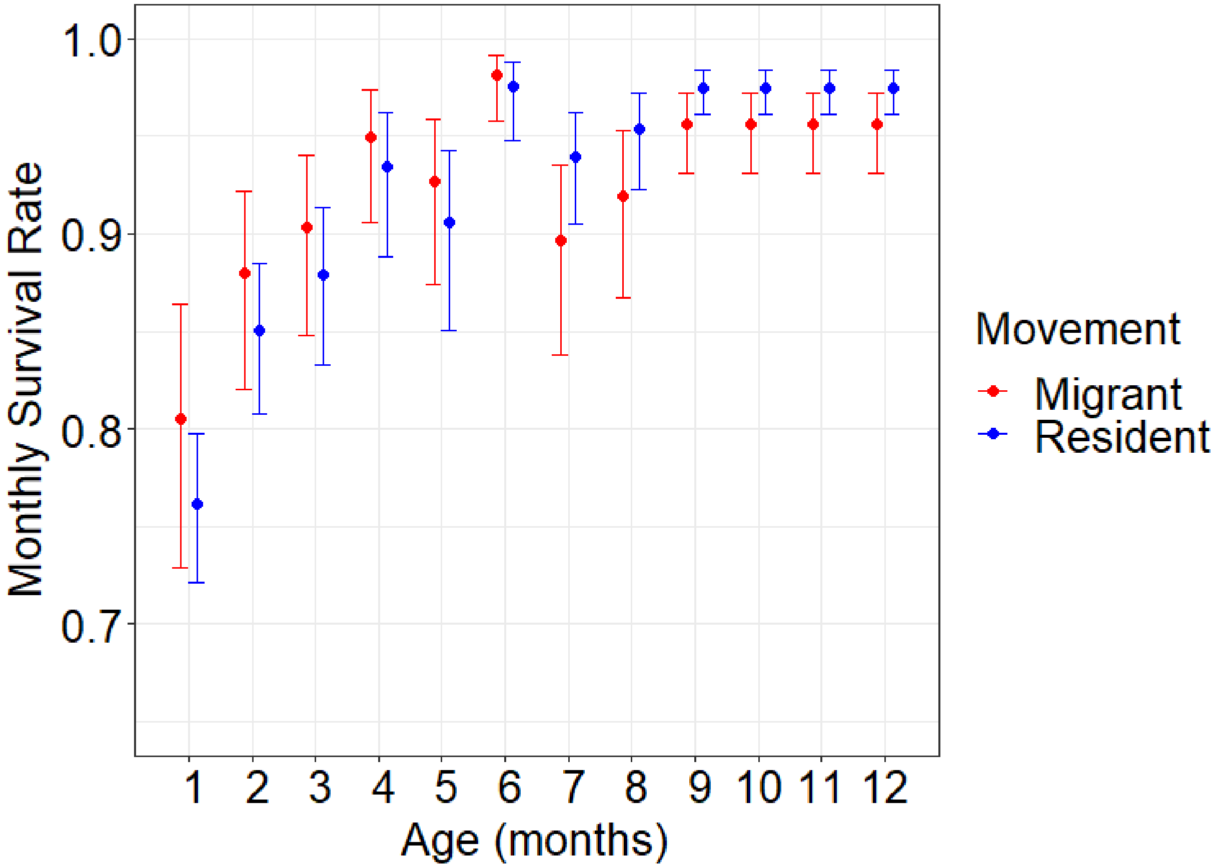

Figure 2.9 Monthly survival rate of mule deer fawns by age for the top model that included a migration covariate: (Mig* dist. water (WR)+age+elevation (WR)+prev. spring precip (WR)+fall ndvi (WR). Survival was estimated using separate mean values of model covariates for migrant and resident fawns. We used mean values of covariates from our adult deer data because we believed these values would be less biased than using the means of known migrant and resident fawns, given that we had so many unclassified fawns. Data used for analyses were collected in the D-16 and D-34 mule deer herds in south-central Colorado.

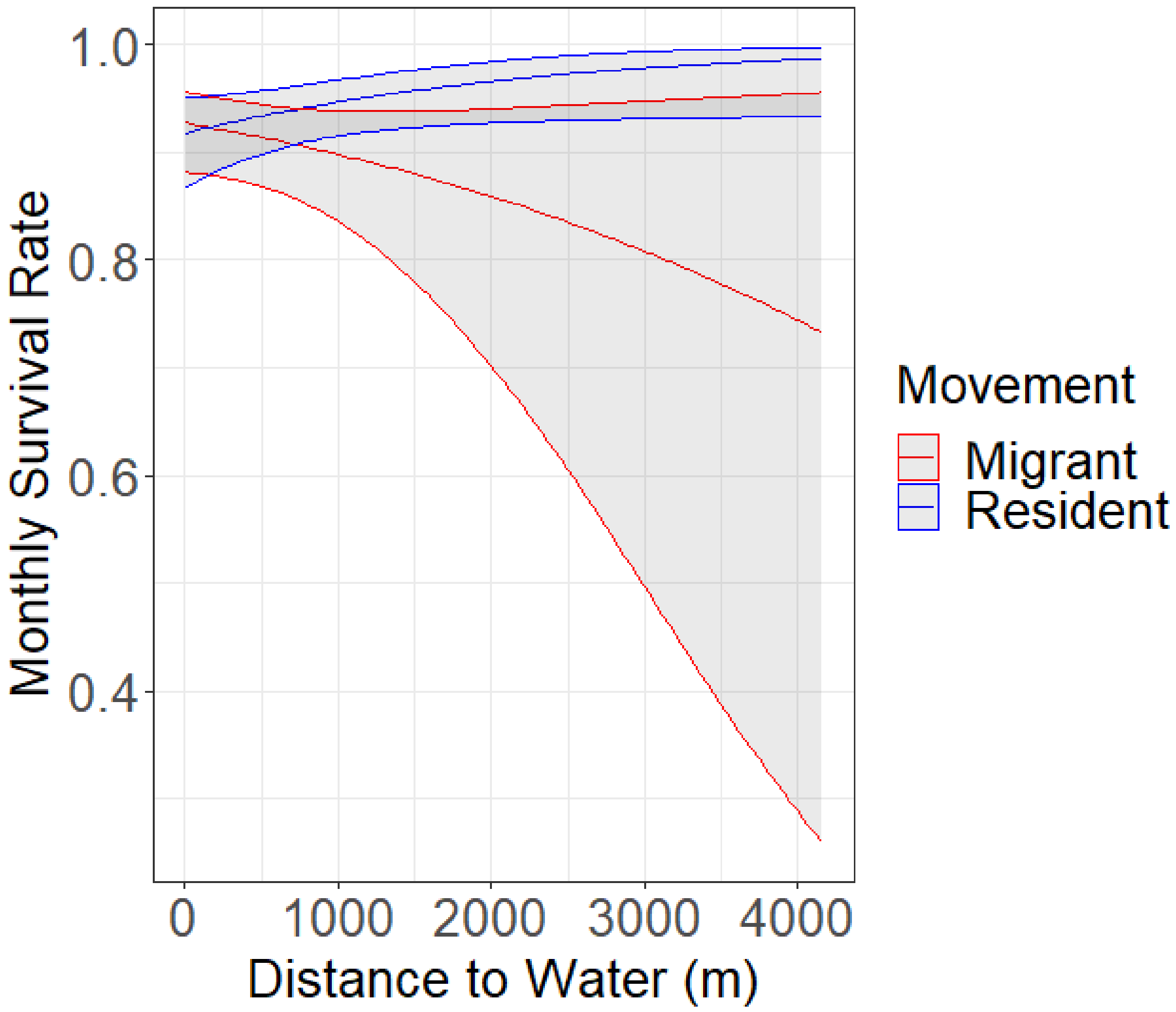

Figure 2.10 Effect plot for distance to water*migration on mule deer fawn survival at age 7 months from our top model that included a migration covariate: (Mig*dist. water(WR)+age+elevation (WR)+prev. spring precip (WR)+fall ndvi (WR). Data used for analyses were collected in the D-16 and D-34 mule deer herds in south-central Colorado.

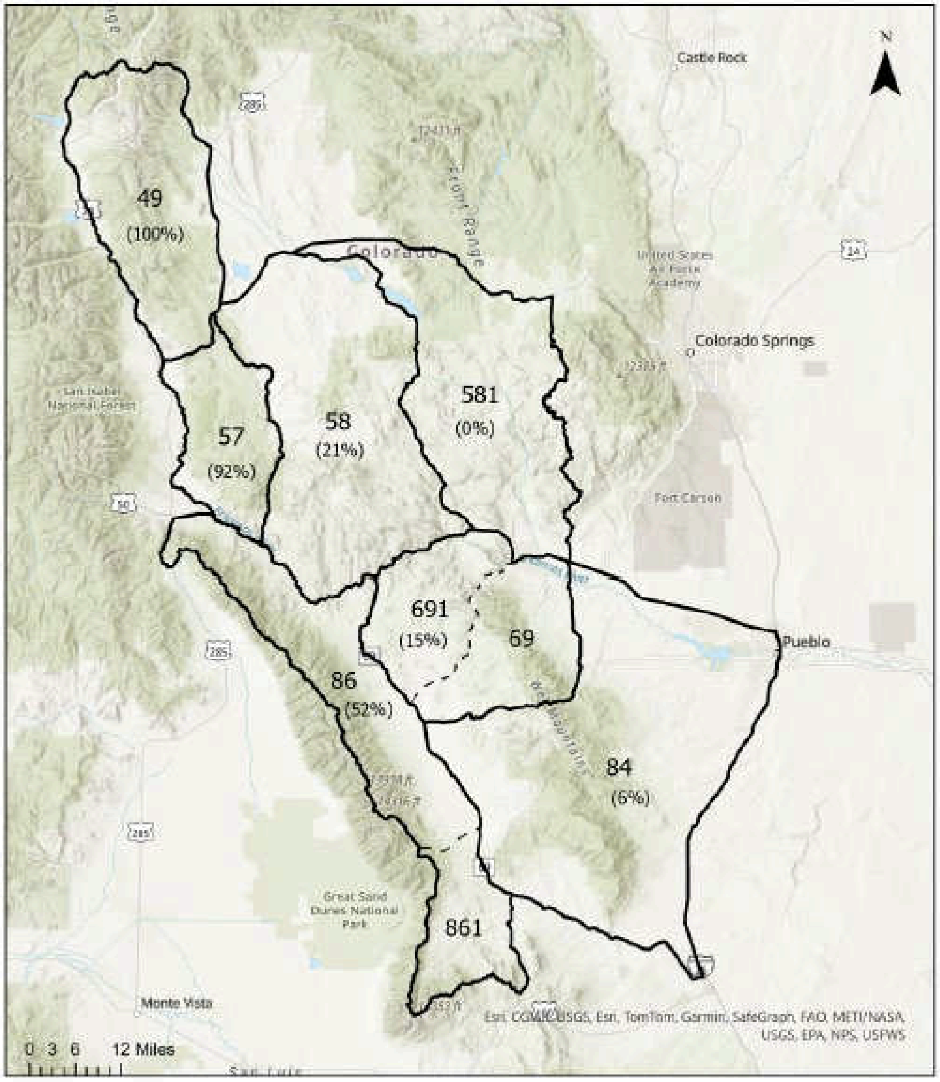

Figure 2.11 Map of GMUs in the D-16 and D-34 mule deer herds in south-central Colorado and the percentage of migratory adult female mule deer classified in each GMU during winter (in parentheses). Migrant classifications for GMU 86 are combined with GMU 861 because 861 had a small sample of deer. Likewise, migrant classifications for GMU 691 are combined with GMU 69 because 69 had a small sample of deer.

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APPENDIX

Table A1.1 Full output of chapter one beta coefficients, standard error, and 95% confidence intervals from all mule deer resource selection models. All models were run separately by season and for high/low annual precipitation years. Additional models were separated by migratory strategy. All models use structure: Selection ~ Resource Type*max NDVI + (1|Individual). The reference class for resource type coefficients is open natural vegetation. Data for these analyses were collected in the D-16 and D-34 mule deer herds in south-central Colorado.

Model	Term	Estimate	SE	LCI	UCI
All Fall High	Alfalfa * Max NDVI	0.023	0.020	-0.016	0.062
All Fall High	Forest * Max NDVI	0.003	0.015	-0.027	0.033
All Fall High	Hay * Max NDVI	-0.185	0.015	-0.215	-0.155
All Fall High	Unknown Crop * Max NDVI	-0.347	0.065	-0.474	-0.220
All Fall High	Alfalfa	-0.184	0.055	-0.292	-0.076
All Fall High	Forest	-0.689	0.019	-0.727	-0.651
All Fall High	Hay	-0.010	0.030	-0.068	0.048
All Fall High	Unknown Crop	-0.976	0.096	-1.164	-0.788
All Fall High	Max NDVI	0.417	0.007	0.403	0.431
All Fall Low	Alfalfa * Max NDVI	0.197	0.023	0.151	0.242
All Fall Low	Forest * Max NDVI	0.083	0.020	0.043	0.123
All Fall Low	Hay * Max NDVI	0.236	0.027	0.184	0.288
All Fall Low	Unknown Crop * Max NDVI	0.576	0.174	0.234	0.917
All Fall Low	Alfalfa	1.145	0.076	0.997	1.294
All Fall Low	Forest	-0.944	0.024	-0.991	-0.897
All Fall Low	Hay	-0.454	0.048	-0.548	-0.359
All Fall Low	Unknown Crop	-2.571	0.384	-3.324	-1.817
All Fall Low	Max NDVI	0.172	0.011	0.151	0.193
All Spring High	Alfalfa * Max NDVI	0.002	0.024	-0.045	0.048
All Spring High	Forest * Max NDVI	0.160	0.026	0.109	0.212
All Spring High	Hay * Max NDVI	-0.094	0.017	-0.128	-0.060
All Spring High	Unknown Crop * Max NDVI	-0.084	0.112	-0.303	0.135
All Spring High	Alfalfa	0.247	0.045	0.160	0.334
All Spring High	Forest	-1.138	0.022	-1.181	-1.094
All Spring High	Hay	-0.162	0.032	-0.225	-0.100
All Spring High	Unknown Crop	-1.592	0.215	-2.013	-1.171
All Spring High	Max NDVI	0.124	0.010	0.105	0.144
All Spring Low	Alfalfa * Max NDVI	0.227	0.022	0.184	0.271
All Spring Low	Forest * Max NDVI	0.072	0.029	0.015	0.130
All Spring Low	Hay * Max NDVI	-0.072	0.026	-0.123	-0.021
All Spring Low	Unknown Crop * Max NDVI	-0.356	0.114	-0.578	-0.133
All Spring Low	Alfalfa	-0.260	0.088	-0.432	-0.088
All Spring Low	Forest	-0.864	0.029	-0.920	-0.808
All Spring Low	Hay	-0.006	0.052	-0.108	0.096
All Spring Low	Unknown Crop	-0.997	0.156	-1.302	-0.692
All Spring Low	Max NDVI	0.156	0.011	0.134	0.178
All Summer High	Alfalfa * Max NDVI	-0.617	0.030	-0.676	-0.558
All Summer High	Forest * Max NDVI	-0.064	0.021	-0.105	-0.023
All Summer High	Hay * Max NDVI	-0.261	0.022	-0.305	-0.218
All Summer High	Unknown Crop * Max NDVI	-0.575	0.093	-0.758	-0.392
All Summer High	Alfalfa	-0.051	0.064	-0.177	0.074
All Summer High	Forest	-0.136	0.018	-0.171	-0.100
All Summer High	Hay	0.053	0.048	-0.041	0.147
All Summer High	Unknown Crop	-0.672	0.129	-0.924	-0.419
All Summer High	Max NDVI	0.604	0.009	0.587	0.622

All Summer Low	Alfalfa * Max NDVI	-0.160	0.031	-0.221	-0.099
All Summer Low	Forest * Max NDVI	0.089	0.024	0.041	0.136
All Summer Low	Hay * Max NDVI	-0.101	0.026	-0.152	-0.050
All Summer Low	Unknown Crop * Max NDVI	-0.240	0.096	-0.429	-0.052
All Summer Low	Alfalfa	0.253	0.107	0.044	0.462
All Summer Low	Forest	-0.331	0.026	-0.383	-0.279
All Summer Low	Hay	-0.002	0.056	-0.111	0.108
All Summer Low	Unknown Crop	-0.496	0.159	-0.808	-0.185
All Summer Low	Max NDVI	0.403	0.010	0.382	0.423
All Winter High	Alfalfa * Max NDVI	0.484	0.097	0.294	0.674
All Winter High	Forest * Max NDVI	0.002	0.017	-0.032	0.035
All Winter High	Hay * Max NDVI	0.294	0.067	0.162	0.426
All Winter High	Unknown Crop * Max NDVI	0.635	0.202	0.240	1.031
All Winter High	Alfalfa	-1.964	0.148	-2.253	-1.674
All Winter High	Forest	-0.346	0.021	-0.388	-0.305
All Winter High	Hay	-1.087	0.056	-1.197	-0.976
All Winter High	Unknown Crop	-1.691	0.184	-2.052	-1.330
All Winter High	Max NDVI	0.074	0.013	0.048	0.099
All Winter Low	Alfalfa * Max NDVI	1.101	0.104	0.897	1.305
All Winter Low	Forest * Max NDVI	-0.328	0.012	-0.352	-0.303
All Winter Low	Hay * Max NDVI	-0.807	0.059	-0.921	-0.692
All Winter Low	Unknown Crop * Max NDVI	-0.746	0.272	-1.280	-0.212
All Winter Low	Alfalfa	-1.778	0.093	-1.959	-1.596
All Winter Low	Forest	-0.207	0.018	-0.242	-0.172
All Winter Low	Hay	-0.856	0.033	-0.920	-0.792
All Winter Low	Unknown Crop	-1.242	0.157	-1.551	-0.934
All Winter Low	Max NDVI	0.305	0.007	0.293	0.318
Migrant Fall High	Alfalfa * Max NDVI	-0.051	0.047	-0.144	0.042
Migrant Fall High	Forest * Max NDVI	-0.029	0.024	-0.077	0.018
Migrant Fall High	Hay * Max NDVI	-0.435	0.048	-0.530	-0.340
Migrant Fall High	Unknown Crop * Max NDVI	1.990	654.303	-1280.444	1284.425
Migrant Fall High	Alfalfa	1.246	0.183	0.888	1.605
Migrant Fall High	Forest	-0.520	0.034	-0.587	-0.453
Migrant Fall High	Hay	0.806	0.105	0.599	1.012
Migrant Fall High	Unknown Crop	-22.559	2968.954	-5841.709	5796.591
Migrant Fall High	Max NDVI	0.542	0.018	0.507	0.577
Migrant Fall Low	Alfalfa * Max NDVI	0.457	0.036	0.386	0.528
Migrant Fall Low	Forest * Max NDVI	0.028	0.028	-0.027	0.082
Migrant Fall Low	Hay * Max NDVI	0.464	0.041	0.383	0.545
Migrant Fall Low	Unknown Crop * Max NDVI	-1.626	0.625	-2.851	-0.401
Migrant Fall Low	Alfalfa	0.815	0.138	0.544	1.085
Migrant Fall Low	Forest	-0.870	0.036	-0.941	-0.800
Migrant Fall Low	Hay	-0.658	0.123	-0.899	-0.416
Migrant Fall Low	Unknown Crop	-0.613	0.525	-1.642	0.416
Migrant Fall Low	Max NDVI	0.218	0.018	0.184	0.253
Migrant Spring High	Alfalfa * Max NDVI	0.425	0.042	0.342	0.508
Migrant Spring High	Forest * Max NDVI	0.411	0.052	0.309	0.514
Migrant Spring High	Hay * Max NDVI	0.193	0.038	0.118	0.269
Migrant Spring High	Unknown Crop * Max NDVI	-0.568	0.268	-1.093	-0.043
Migrant Spring High	Alfalfa	2.295	0.106	2.086	2.503
Migrant Spring High	Forest	-1.099	0.043	-1.183	-1.016
Migrant Spring High	Hay	0.534	0.093	0.352	0.716
Migrant Spring High	Unknown Crop	-0.081	0.391	-0.848	0.686

Migrant Spring High	Max NDVI	-0.283	0.024	-0.330	-0.236
Migrant Spring Low	Alfalfa * Max NDVI	0.048	0.035	-0.020	0.116
Migrant Spring Low	Forest * Max NDVI	-0.046	0.046	-0.136	0.043
Migrant Spring Low	Hay * Max NDVI	-0.007	0.039	-0.083	0.070
Migrant Spring Low	Unknown Crop * Max NDVI	-0.379	0.515	-1.388	0.630
Migrant Spring Low	Alfalfa	2.030	0.149	1.738	2.321
Migrant Spring Low	Forest	-0.960	0.04	-1.039	-0.882
Migrant Spring Low	Hay	0.842	0.093	0.660	1.025
Migrant Spring Low	Unknown Crop	-1.247	0.823	-2.859	0.366
Migrant Spring Low	Max NDVI	0.148	0.025	0.100	0.196
Migrant Summer High	Alfalfa * Max NDVI	-0.308	0.304	-0.904	0.287
Migrant Summer High	Forest * Max NDVI	-0.123	0.025	-0.172	-0.074
Migrant Summer High	Hay * Max NDVI	-0.253	0.083	-0.415	-0.091
Migrant Summer High	Unknown Crop * Max NDVI	-3.878	1.600	-7.015	-0.742
Migrant Summer High	Alfalfa	-2.561	1.237	-4.985	-0.136
Migrant Summer High	Forest	0.247	0.027	0.195	0.300
Migrant Summer High	Hay	-1.433	0.239	-1.901	-0.964
Migrant Summer High	Unknown Crop	-3.649	2.225	-8.011	0.713
Migrant Summer High	Max NDVI	0.695	0.015	0.665	0.725
Migrant Summer Low	Alfalfa * Max NDVI	0.519	0.462	-0.387	1.425
Migrant Summer Low	Forest * Max NDVI	0.149	0.032	0.086	0.212
Migrant Summer Low	Hay * Max NDVI	-0.466	0.056	-0.576	-0.355
Migrant Summer Low	Unknown Crop * Max NDVI	-1.096	0.286	-1.656	-0.536
Migrant Summer Low	Alfalfa	-5.494	2.337	-10.075	-0.913
Migrant Summer Low	Forest	0.003	0.038	-0.073	0.078
Migrant Summer Low	Hay	0.448	0.146	0.161	0.734
Migrant Summer Low	Unknown Crop	0.631	0.321	0.002	1.260
Migrant Summer Low	Max NDVI	0.648	0.021	0.607	0.689
Migrant Winter High	Alfalfa * Max NDVI	0.860	0.246	0.378	1.341
Migrant Winter High	Forest * Max NDVI	0.036	0.037	-0.036	0.108
Migrant Winter High	Hay * Max NDVI	0.584	0.157	0.277	0.891
Migrant Winter High	Unknown Crop * Max NDVI	0.030	1324.041	-2595.091	2595.151
Migrant Winter High	Alfalfa	-0.464	0.352	-1.154	0.225
Migrant Winter High	Forest	-0.597	0.036	-0.667	-0.527
Migrant Winter High	Hay	-1.324	0.183	-1.683	-0.965
Migrant Winter High	Unknown Crop	-16.091	931.746	-1842.314	1810.131
Migrant Winter High	Max NDVI	0.029	0.031	-0.032	0.090
Migrant Winter Low	Alfalfa * Max NDVI	2.229	0.226	1.785	2.672
Migrant Winter Low	Forest * Max NDVI	-0.08	0.048	-0.175	0.015
Migrant Winter Low	Hay * Max NDVI	0.981	0.218	0.553	1.409
Migrant Winter Low	Unknown Crop * Max NDVI	0.977	1119.975	-2194.174	2196.128
Migrant Winter Low	Alfalfa	1.021	0.16	0.708	1.335
Migrant Winter Low	Forest	-0.593	0.039	-0.669	-0.516
Migrant Winter Low	Hay	-0.449	0.127	-0.698	-0.200
Migrant Winter Low	Unknown Crop	-15.652	741.647	-1469.28	1437.975
Migrant Winter Low	Max NDVI	-0.099	0.036	-0.169	-0.029
Resident Fall High	Alfalfa * Max NDVI	-0.087	0.021	-0.129	-0.046
Resident Fall High	Forest * Max NDVI	-0.073	0.023	-0.118	-0.029
Resident Fall High	Hay * Max NDVI	-0.138	0.016	-0.17	-0.106
Resident Fall High	Unknown Crop * Max NDVI	-0.322	0.067	-0.452	-0.191
Resident Fall High	Alfalfa	-0.108	0.054	-0.213	-0.003
Resident Fall High	Forest	-0.695	0.024	-0.741	-0.648
Resident Fall High	Hay	-0.134	0.031	-0.194	-0.074

Resident Fall High	Unknown Crop	-0.973	0.095	-1.159	-0.788
Resident Fall High	Max NDVI	0.387	0.008	0.372	0.403
Resident Fall Low	Alfalfa * Max NDVI	-0.122	0.029	-0.179	-0.065
Resident Fall Low	Forest * Max NDVI	0.100	0.028	0.045	0.155
Resident Fall Low	Hay * Max NDVI	0.012	0.033	-0.053	0.078
Resident Fall Low	Unknown Crop * Max NDVI	0.815	0.172	0.478	1.152
Resident Fall Low	Alfalfa	1.284	0.083	1.122	1.446
Resident Fall Low	Forest	-0.917	0.031	-0.978	-0.856
Resident Fall Low	Hay	-0.299	0.050	-0.396	-0.202
Resident Fall Low	Unknown Crop	-3.082	0.434	-3.932	-2.232
Resident Fall Low	Max NDVI	0.165	0.012	0.141	0.190
Resident Spring High	Alfalfa * Max NDVI	-0.145	0.028	-0.200	-0.090
Resident Spring High	Forest * Max NDVI	0.114	0.031	0.053	0.176
Resident Spring High	Hay * Max NDVI	-0.159	0.019	-0.197	-0.121
Resident Spring High	Unknown Crop * Max NDVI	-0.003	0.127	-0.253	0.247
Resident Spring High	Alfalfa	-0.006	0.047	-0.099	0.086
Resident Spring High	Forest	-1.127	0.027	-1.179	-1.075
Resident Spring High	Hay	-0.290	0.034	-0.356	-0.223
Resident Spring High	Unknown Crop	-1.877	0.255	-2.378	-1.377
Resident Spring High	Max NDVI	0.209	0.011	0.188	0.230
Resident Spring Low	Alfalfa * Max NDVI	0.134	0.029	0.078	0.190
Resident Spring Low	Forest * Max NDVI	0.083	0.038	0.009	0.157
Resident Spring Low	Hay * Max NDVI	-0.117	0.033	-0.182	-0.052
Resident Spring Low	Unknown Crop * Max NDVI	-0.368	0.122	-0.608	-0.129
Resident Spring Low	Alfalfa	-0.516	0.099	-0.710	-0.321
Resident Spring Low	Forest	-0.769	0.037	-0.842	-0.696
Resident Spring Low	Hay	-0.238	0.061	-0.358	-0.119
Resident Spring Low	Unknown Crop	-0.995	0.159	-1.306	-0.683
Resident Spring Low	Max NDVI	0.167	0.012	0.142	0.191
Resident Summer High	Alfalfa * Max NDVI	-0.526	0.032	-0.588	-0.464
Resident Summer High	Forest * Max NDVI	-0.123	0.036	-0.193	-0.052
Resident Summer High	Hay * Max NDVI	-0.170	0.024	-0.217	-0.123
Resident Summer High	Unknown Crop * Max NDVI	-0.461	0.096	-0.649	-0.274
Resident Summer High	Alfalfa	-0.056	0.063	-0.179	0.067
Resident Summer High	Forest	-0.567	0.028	-0.622	-0.512
Resident Summer High	Hay	0.146	0.048	0.051	0.241
Resident Summer High	Unknown Crop	-0.686	0.127	-0.934	-0.437
Resident Summer High	Max NDVI	0.537	0.011	0.517	0.558
Resident Summer Low	Alfalfa * Max NDVI	-0.034	0.034	-0.100	0.032
Resident Summer Low	Forest * Max NDVI	-0.04	0.038	-0.113	0.034
Resident Summer Low	Hay * Max NDVI	0.035	0.030	-0.025	0.094
Resident Summer Low	Unknown Crop * Max NDVI	-0.051	0.106	-0.259	0.157
Resident Summer Low	Alfalfa	0.385	0.107	0.175	0.595
Resident Summer Low	Forest	-0.595	0.039	-0.672	-0.518
Resident Summer Low	Hay	-0.109	0.061	-0.228	0.011
Resident Summer Low	Unknown Crop	-0.715	0.181	-1.070	-0.360
Resident Summer Low	Max NDVI	0.321	0.012	0.297	0.346
Resident Winter High	Alfalfa * Max NDVI	0.432	0.099	0.238	0.626
Resident Winter High	Forest * Max NDVI	-0.001	0.021	-0.042	0.039
Resident Winter High	Hay * Max NDVI	0.225	0.070	0.088	0.361
Resident Winter High	Unknown Crop * Max NDVI	0.640	0.199	0.250	1.030
Resident Winter High	Alfalfa	-2.084	0.163	-2.403	-1.765
Resident Winter High	Forest	-0.215	0.027	-0.268	-0.162

Resident Winter High	Hay	-1.033	0.060	-1.151	-0.915
Resident Winter High	Unknown Crop	-1.649	0.191	-2.022	-1.275
Resident Winter High	Max NDVI	0.087	0.014	0.059	0.114
Resident Winter Low	Alfalfa * Max NDVI	0.974	0.110	0.757	1.190
Resident Winter Low	Forest * Max NDVI	-0.317	0.013	-0.342	-0.292
Resident Winter Low	Hay * Max NDVI	-0.912	0.058	-1.025	-0.798
Resident Winter Low	Unknown Crop * Max NDVI	-0.670	0.259	-1.178	-0.162
Resident Winter Low	Alfalfa	-2.012	0.108	-2.225	-1.800
Resident Winter Low	Forest	-0.049	0.020	-0.088	-0.009
Resident Winter Low	Hay	-0.819	0.033	-0.884	-0.754
Resident Winter Low	Unknown Crop	-1.095	0.148	-1.384	-0.806
Resident Winter Low	Max NDVI	0.329	0.007	0.317	0.342