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MULE DEER POPULATION DYNAMICS IN SPACE AND TIME: ECOLOGICAL MODELING TOOLS FOR MANAGING UNGULATES

by

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Mule Deer Population Dynamics in Space And Time: Ecological Modeling Tools For Managing Ungulates

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ABSTRACT

Ecologists aim to understand and predict the effect of management actions on population dynamics of animals, a difficult task in highly variable environments. Mule deer (*Odocoileus hemionus*) occupy such variable environments and display volatile population dynamics, providing a challenging management scenario. I first investigate the ecological drivers of overwinter juvenile survival, the most variable life stage in this ungulate. I tested for both direct and indirect effects of spring and fall phenology on winter survival of 2,315 mule deer fawns from 1998 – 2011 across a wide range of environmental conditions in Idaho, USA. I showed that early winter precipitation and direct and indirect effects of spring and especially fall plant productivity (NDVI) accounted for 45% of observed variation in overwinter survival. I next develop predictive models of overwinter survival for 2,529 fawns within 11 Population Management Units in Idaho, 2003 – 2013. I used Bayesian hierarchical survival models to estimate survival from remotely-sensed measures of summer NDVI and winter snow conditions (MODIS snow and SNODAS). The multi-scale analysis produced well performing models, predicting out-of-sample data with a validation R^2 of 0.66. Next, I ask how predation risk and deer density influences neonatal fawn survival. I developed a spatial coyote predation risk model and tested the effect on fawn mortality. I then regressed both total fawn mortality and coyote-caused mortality on mule deer density to test the predation-risk hypothesis that coyote predation risk increased as deer density increased as low predation risk habitats were filled, forcing maternal females to use high predation risk habitats. Fawn mortality did not increase with density, but coyote predation increased with increasing deer density, confirming density-dependence in fawn mortality was driven by coyote behavior, not density per se. Finally, I use integrated population models (IPM) to collate the previous findings into a model that simultaneously estimates all mule deer vital rates to test ecological questions concerning population drivers. I test whether density-dependence or environmental stochasticity (weather) drives mule deer population dynamics. The vital rate most influenced by density was recruitment, yet across most populations, weather was the predominant force affecting mule deer dynamics. These IPM's will provide managers with a means to estimate population dynamics with precision and flexibility.

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CHAPTER 1. DISSERTATION OVERVIEW AND INTRODUCTION

A complex suite of biotic and abiotic processes drives ungulate population growth across varying environmental conditions. Our goal as ecologists is to understand and predict the effect of the environment in concert with management actions on population dynamics of animals, a particularly difficult task in highly variable environments. Across species, ungulate population growth is often driven by variation in recruitment (Gaillard et al. 2000) modified by the interplay of summer vs. winter nutrition, weather, and predation (Nilsen et al. 2009). The population growth of my study species, mule deer (*Odocoileus hemionus*), is sensitive to adult female survival (Unsworth et al. 1999, Hurley et al. 2011), but juvenile survival shows the widest variation, often in response to weather (Bishop et al. 2005), similar to juvenile survival across many ungulate species (Portier et al. 1998, Gaillard et al. 2000, Coulson et al. 2001). This variation in juvenile survival often drives mule deer population dynamics (Unsworth et al. 1999) and many other temperate ungulates (Festa-Bianchet and Smith 1994, Raithel et al. 2007). Recruitment may also vary spatially, depending on the effect of weather on nutritional quality (Pettorelli et al. 2005), winter energy expenditure (Bartmann et al. 1992, Parker et al. 2009), and spatial variation in predation (Mackie et al. 1998, Bishop et al. 2009). This spatial variation suggests that site-specific ecotype productivity was modified by weather and local predation conditions (Lukacs et al. 2009). Given this complexity, a clear understanding of the interaction between forage quality, winter weather, and predation risk is necessary to accurately predict population performance with environmental change.

Prediction, however, is complicated by many factors as ungulates exist over a wide range of environmental conditions, with their densities driven by a combination of these large-scale processes, life-history trade-offs and resource selection (Senft et al. 1987, Bowyer and Kie 2006). Densities of ungulates are positively correlated with both primary productivity (Crete and Daigle 1999, Melis et al. 2009) and the spatial variation in forage because this increases access to high quality forage (Fryxell 1988, Wang et al. 2006). Forage quality alone, however, does not determine ungulate density on landscapes with predation. Ungulates may adopt behavioral strategies to avoid predation, reducing the actual nutrition given the constraints of predation risk, resulting in a lower realized nutrition and thus lower growth rates (Hopcraft et al. 2010). Effects of predation are also strongest in lower productivity (Melis et al. 2009), and the degree to which predation is compensatory or additive depends on the interaction of forage quality and density (Bartmann et al. 1992, Ballard et al. 2001). Such trade-offs may also be influenced by both density-independent forces (i.e., weather) or density-dependence (Hopcraft et al. 2010).

It has long been known that increasing density reduces the strength of selection for high-quality patches because of density-dependent competition for forage (Fretwell and Calver 1969, McLoughlin et al. 2010). It is through such density-dependent changes in habitat selection that changes in population dynamics ultimately occur, although the effects of density-dependent resource selection on populations are unclear for many ungulate species (McLoughlin et al. 2010). Despite the uncertainty about how density-dependence in resource selection translates to population growth, density dependence is perhaps the most important paradigm in ungulate population ecology (Eberhardt 2002, Bonenfant et al. 2009). As ungulate density increases under this paradigm, we expect declines in juvenile survival first, followed by fecundity, and finally, adult survival (Gaillard et al. 2000). Density-dependent changes in resource selection likely drive these widespread patterns in ungulate demography, but it has been challenging to link resource selection to fitness consequences (McLoughlin et al. 2010). Regardless, understanding the underlying mechanism of density effects on vital rates is difficult to measure because each rate is dependent on other vital rates. After decades of research on mule deer, scientists have been similarly unable to link habitat to population growth because of uncertainty in the relative role of summer versus winter forage quality, and the interacting effects of predation (Ballard et al. 2001).

The wide annual variation of mule deer populations also poses a challenge for their conservation and management. Mule deer are an economically important harvested species in western North America necessitating intensive monitoring of population status. Because juvenile survival and recruitment are the most variable, these key vital rates have become the monitoring priority of wildlife managers attempting to predict changes in ungulate populations (e.g., Montana Adaptive Harvest Management 2001, Idaho Mule Deer Management Plan 2008, Lukacs et al. 2009). Neonate survival (birth to 6 months of age) may be adequately measured via age ratio surveys (December fawn ratios) when coupled with estimates of adult female age structure and age-specific fecundity (Harris et al. 2008). But wildlife managers must still rely on expensive radiotelemetry-based estimates of overwinter survival combined with population models to make ungulate harvest decisions (White and Bartmann 1998, Montana Adaptive Harvest Plan 2001, Idaho Mule Deer Management Plan 2008). Another challenge is that wildlife managers must often submit harvest recommendations for the upcoming year by early January, limiting the information available on overwinter survival estimate at the time of season setting. Ideally, managers would benefit from some reliable way of predicting overwinter survival based on weather and an ecologically-based definition of ungulate habitat quality. Ultimately, population models that link summer forage quality and winter weather to populations are critically needed for understanding the ecology and management of ungulates. An applied goal of my Dissertation is to provide statistical tools to meet that need. The following chapters progressively identify the underlying mechanisms of mule deer population dynamics and then use these relationships to predict population growth, with the ultimate goal of improving harvest management.

My Dissertation focuses on mule deer populations in Idaho, but my goal was to elucidate relationships applicable throughout western North America to improve management of this species. I also hope that my approach to develop large-scale predictive models of ungulate population dynamics can be expanded across species. I incorporated intrinsic (behavior, density) and extrinsic processes (weather, forage quality, and predation risk) into stochastic survival and population models to predict growth rates across a diverse range of habitat quality, predation, and weather conditions. In most chapters, I develop statistical models using large sample sizes (>2,000 individuals) of different age-classes of mule deer (juveniles, adult females) across large spatial scales usually from 6 to 13 populations over long temporal scales from 1995–2014. These large spatiotemporal datasets provide a unique opportunity to test fundamental and applied questions about mule deer ecology and management.

In Chapter 2, I seek to understand the mechanisms driving fawn survival in winter, the most variable vital rate for mule deer across 13 populations of mule deer in Idaho. Despite the importance of nutrition, proximate causes of mule deer fawn mortality during winter is predation or malnutrition (Ballard et al. 2001, Hurley et al. 2011) in interaction with weather (Portier et al. 1998, Colman et al. 2001, Mech et al. 2001). Because of this interaction, the relative effects of predation and forage on ungulate survival are difficult to isolate (Kjellander et al. 2004, Pierce et al. 2004, Kauffman et al. 2007, Bishop 2009). Recent field studies on ungulates, however, emphasized the critical importance of late summer and fall nutritional ecology to the population performance of large herbivores. Important barriers to understanding the complex influence of growing season dynamics on ungulate survival are how to disentangle correlated plant phenology metrics and the time series nature of NDVI data in a quantitative approach that describes variation in plant quality across an entire growing season or discriminates between sites. To solve these issues, we jointly used functional analysis (Ramsay and Silverman 2005) to characterize seasonal variation in NDVI curves and path analyses (Shipley 2009) to assess the interplay of plant phenology and winter severity and disentangled relationships of nutrition and weather and their effects on population dynamics of ungulates.

In Chapter 3, I explore prediction in both a management and ecological context by developing fawn survival models that balance precision, bias and generality across space and time (Levins 1966). The ecological relationships I illuminated from Chapter 2 were used to create predictive models testing both the importance of remotely-sensed summer forage quality or winter snow conditions and the generality of models to predict winter fawn survival across a broad range of environments. One challenge in the development of predictive statistical models for survival is the complexity of dealing with integrating survival data across populations that are hierarchically structured in space and time (Lukacs et al. 2009). My solution was to use Bayesian hierarchical modeling, enabling the development of spatially structured, hierarchical and flexible statistical models (Royle and Dorazio 2006, Kery and Schaub 2012) which are inherently well-suited to prediction of animal movements and population ecology (Heisey et al. 2010, Geremia et al. 2014, Mouquet et al. 2015). I then developed general models appropriate for use by managers to estimate fawn survival in the absence of annual radiocollar data.

Chapter 4 combines predation risk with resource selection to describe potential reductions in carrying capacity of the landscape. Because of the challenge of estimating predation risk at large spatial scales, I focus on two populations in southern Idaho where I developed fine-scale measures of predation risk to mule deer fawns from their main predator, coyotes (*Canis latrans*). Assuming that predation risk can be spatially decomposed to depict the probability of death given a set of landscape features (Lima and Dill 1990, Hebblewhite 2005, Kauffman et al. 2007), maternal females should select lower risk habitats. However, if exclusive space use of adult females during fawn rearing created a despotic distribution with dominant females occupying both high forage quality and low predation risk habitats, fawn survival sink may be created as subordinate female mule deer are forced into lower quality forage and increased predation risk habitat at higher deer density. This density-dependent resource selection may reduce population productivity, negating the value of additional productive females on the landscape as total adult female numbers increase. To test this hypothesis, I first modeled occurrence of coyotes with a spatial model to estimate predation risk, and evaluate the relationship of coyote predation risk to neonate mule deer mortality. Next, I tested whether this relationship changed as mule deer populations increased and higher quality habitats were filled. I use two Game Management Units, one with active coyote removal (removal) and one without (reference; as described in detail in Hurley et al. 2011), predicting the effect of density would be increased in the reference (no coyote removals) area. In keeping with this prediction, survival of mule deer fawns did not change in the reference area and declined in the removal area with increasing mule deer density. Cause-specific mortality from coyotes, however, increased with deer density in the reference and to a lower degree in the removal area suggesting density-dependence driven by expansion of deer into lower quality habitat that was highly selected by coyotes. Thus overall changes in density-dependent mortality were compensatory. This enforces the idea that density dependence and compensatory mortality may operate on a despotic distribution caused by conspecific exclusion of maternal females from low predation risk habitats.

Through the use of integrated population models (IPM, Schaub et al. 2007) in Chapter 5, I then apply the results from the previous chapters to model population dynamics in six of my study areas with consistently high quality vital rate data. I use these models to understand the relative contribution of density-dependent and density-independent drivers of ungulate population dynamics, as well as their possible interaction. Many processes, such as predation or weather, can mimic density dependence by acting on vital rates in the same progression as expected by density often through density-climate interactions (Saether 1997, Clutton–Brock and Coulson 2002, Hebblewhite 2005, Hurley et al. 2011). To separate the effects of weather versus density, I used an IPM approach to identify the properties of mule deer populations that would suggest regulation by density dependence or limitation by weather. I estimated the effect of density with the addition of a density term on each of our measured vital rates, recruitment (fawn ratios in December), winter fawn survival, and adult female survival. I then added weather covariates identified as important in previous chapters to the time varying estimate of winter fawn survival to increase model fit and test if density dependence is evident in the populations or if weather was mimicking the effect of density dependence. In all chapters, my search for factors that regulate or limit mule deer population size provides tools for harvest management and increases understanding population ecology of a high value ungulate.

Throughout the rest of this Dissertation, I use the second-person voice, we, reflecting the highly collaborative nature of my Dissertation research. I recognize the contributions of my co-authors in each chapter. Moreover, each chapter is formatted for publication in a different peer-reviewed journal, and Chapter 2 is already published in *Philosophical Transactions of the Royal Society B*. Chapter 3 is formatted with the intent to submit to *Journal of Wildlife Management*, Chapter 4 for submission to Biology Letters, and Chapter 5 for submission to *Oecologia*.

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CHAPTER 2. FUNCTIONAL ANALYSIS OF NDVI CURVES REVEALS OVERWINTER MULE DEER SURVIVIAL IS DRIVEN BY BOTH SPRING AND FALL PHENOLOGY[1]

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INTRODUCTION

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A major challenge for the application of remote sensing to monitoring biodiversity responses to environmental change is connecting remote sensing data to large-scale field ecological data on animal and plant populations and communities (Turner et al. 2003). Large herbivores such as ungulates are an economically and ecologically important group of species (Gordon et al. 2004) with a global distribution and varied life-history responses to climate that are very sensitive to the timing and duration of plant growing seasons (Senft et al. 1987). Until recently, monitoring plant phenology and the nutritional influences on ungulate life histories have been impossible at large spatial scales due to the intense effort necessary to estimate even localized plant phenology. The remote sensing community has largely solved this issue with by partnering with ecologists to provide circumpolar remotely sensed vegetation indices, fueling the recent explosion of the integration of remote sensing data into wildlife research and conservation (Turner et al. 2003, Pettorelli et al. 2005c, Pettorelli et al. 2011). With satellites like AVHRR, MODIS, SPOT (Huete et al. 2002, Running et al. 2004), and growing tool sets for ecologists (Dodge et al. 2013), derived metrics are being commonly used to analyze the ecological processes driving wildlife distribution and abundance (Pettorelli et al. 2011). Indices such as the Normalized Difference Vegetation Index (NDVI) and the Enhanced Vegetation Index (EVI) strongly correlate with vegetation productivity, track growing season dynamics (Zhang et al. 2003, Zhao et al. 2005) and differences between landcover types at moderate resolutions over broad spatio-temporal scales (Huete et al. 2002). Indices extracted from NDVI correlate with forage quality and quantity (Hamel et al. 2009b, Cagnacci et al. 2011, Pettorelli et al. 2011) and thus have become invaluable for indexing habitat quality for a variety of ungulates (Hebblewhite et al. 2008, Hamel et al.

2009b, Ryan et al. 2012). For example, only this technology can track a landscape scale plant growth stage that ungulates often select to maximize forage quality (Fryxell et al. 1988). Because of this spatial and temporal link to forage quality, NDVI can be predictive of ungulate nutritional status (Hamel et al. 2009b), home range size (Morellet et al. 2013), migration and movements (Hebblewhite et al. 2008, Cagnacci et al. 2011, Sawyer and Kauffman 2011). An increasing number of studies have also linked NDVI to body mass and demography of a wider array of vertebrates. While there have been recent reviews of the link between NDVI and animal ecology (Pettorelli et al. 2011), few provided examples where fall phenology was considered. We conducted a brief review of recent studies to expose readers working at the interface of remote sensing and biodiversity conservation to the preeminent focus on spring phenology using a-priori defined variables. From the literature review we performed, 16 out of 22 case studies in temperate areas focused on spring, while 3 used a growing season average, and only 3 considered both spring and fall phenology (Table 2-1). Most studies were based on NDVI metrics describing the active vegetation period, such as; start, end, and duration of growing season (Table 2-1). Moreover, all but one (see Table 2-1, Tveraa et al. 2013) were based on a-priori defined NDVI metrics assumed to provide a reliable description of plant phenology through the growing season. From this empirical evidence so far reported (see Table 2-1 for details) spring phenology appears as an important period in temperate systems. However, recent field studies on ungulates emphasized the critical importance of late summer and fall nutritional ecology, suggesting vegetation conditions during this period will also influence population performance of large herbivores. Our brief review complements that of Pettorelli et al. (2011) and illustrates the importance of considering phenological dynamics over the entire growing season.

Despite this focus on spring phenology, the best existing approach is to use a number of standardized growing season parameters derived from NDVI describing the onset, peak, and cessation of plant growth. Unfortunately, these useful parameters are often highly correlated. In Wyoming for example, the start of the growing season was delayed and the rate of green-up was slower than average following winters with high snow cover (2013), but these ecologically different processes were highly correlated. Thus, an important barrier to understanding the complex influence of growing season dynamics on ungulate survival is how to disentangle correlated plant phenology metrics. Another underappreciated barrier is the challenge of harnessing the time series nature of NDVI data, which requires specific statistical tools; no previous study has attempted to describe how the NDVI function varies across an entire growing season or discriminates between sites. To fill this important gap, the joint use of functional analysis (Ramsay and Silverman 2005) to characterize seasonal variation in NDVI curves and path analyses (Shipley 2009) to assess both direct and indirect effects of plant phenology offers a powerful way to address entangled relationships of plant quality and their effects on population dynamics of ungulates.

Pioneering experimental work on elk (*Cervus elaphus*) (Cook et al. 2004)has led to a growing recognition that in temperate areas, late summer and fall nutrition are important drivers of overwinter survival and demography of large herbivores (Cook et al. 2004, Monteith et al. 2013). Summer nutrition first affects adult female body condition (Monteith et al. 2013), which predicts pregnancy rates (Cook et al. 2004, Stewart et al.

2005, Monteith et al. 2013), overwinter adult survival rates (Bender et al. 2007, Monteith et al. 2013), litter size (Tollefson et al. 2010), as well as birth mass and early juvenile survival (Lomas and Bender 2007, Bishop et al. 2009, Tollefson et al. 2010). The addition of lactation during summer increases nutritionally demand and thus is an important component of the annual nutritional cycle (Sadleir 1982, Simard et al. 2010). Nutrition during winter (energy) minimizes body fat loss (Bishop et al. 2009), but rarely changes the importance of late summer and fall nutrition for survival of both juveniles and adults (Cook et al. 2004). Winter severity then interacts with body condition to shape winter survival of ungulates (Singer et al. 1997, Monteith et al. 2013), and can, in severe winters, overwhelm the effect of summer/fall nutrition through increase energy expenditure, driving overwinter survival of juveniles.

Like most other large herbivores of temperate and northern areas, mule deer (*Odocoileus hemionus*) population growth is more sensitive to change in adult female survival than to equivalent change in other demographic parameters. Survival of adult female mule deer, however, tends to vary little (Unsworth et al. 1999, Hurley et al. 2011); see (Gaillard and Yoccoz 2003) for a general discussion. In contrast, juvenile survival shows the widest temporal variation in survival, often in response to variation in weather (Portier et al. 1998, Gaillard et al. 2000, Coulson et al. 2001) and population density (Bartmann et al. 1992). This large variation in juvenile survival, especially overwinter, often drives population growth of mule deer (Unsworth et al. 1999, Bishop et al. 2009, Hurley et al. 2011). Fawns accumulate less fat than adults during the summer, which increases their mortality because variation in late summer nutrition interacts with winter severity (White and Bartmann 1998, Unsworth et al. 1999). While previous studies have shown that spring plant phenology correlates with early juvenile survival in ungulates, summer survival is not necessarily more important than overwinter survival. Yet, to date, the effect of changes in fall plant phenology on overwinter juvenile survival remains unexplored.

Our first goal was to identify the annual variation of plant primary production and phenology among mule deer population summer range, measured using NDVI curves of the growing season. Second, with annual plant phenology characterized, we assessed both direct and indirect (through fawn body mass) effects of these key-periods on overwinter survival of mule deer fawns. We used a uniquely long-term (1998 – 2011) and large-scale dataset to disentangle plant phenology effects on mule deer survival, encompassing 13 different populations spread over the entire southern half Idaho, USA while most previous studies have focused only within 1 or 2 populations. These populations represent diversity of elevations, habitat quality, and climatological influences. We focused on overwinter fawn survival because previous studies (Unsworth et al. 1999, Hurley et al. 2011) have demonstrated that this parameter is the primary driver of population growth.

Mysterud et al. (2008) used a path analysis to separate independent effects of summer versus winter on body mass. We present a novel methodological framework in which we analyze NDVI measurements using functional principal component analysis to discriminate among study areas in Idaho with differing fall and spring phenology. We then use hierarchical Bayesian path analysis to identify factors of overwinter mule deer survival. Based on previous studies, we expected that plant phenology should be strongly associated with body mass of mule deer at 6 months of age, and that body mass and winter severity should interact to determine overwinter survival. We expected direct effects of plant phenology on winter survival to be weaker than winter severity because severe conditions may overwhelm nutritional improvements to fawn quality. We also expected early winter severity would affect overwinter fawn survival more than late winter (Hurley et al. 2010).

MATERIALS AND METHODS

(a) Study Areas

The study area spanned ~ 160,000km^2, representing nearly the entire range of climatic conditions and primary productivity of mule deer in Idaho. We focused on 13 populations with winter ranges corresponding to 13 Idaho game management units (GMUs); hereafter we use GMU synonymous with population (Figure 2-2). There are three main habitat types (called ecotypes hereafter) based on the dominant overstory canopy species on summer range; coniferous forests, shrub-steppe, and aspen woodlands. The populations were distributed among the ecotypes (Figure 2-2) with 5 populations in conifer ecotype (GMUs 32, 33, 36B, 39, 60A), 2 in shrub-steppe ecotype (GMUs 54, 58), and 6 in aspen (GMUs 56, 67, 69, 72, 73A, 76). Elevation and topographic gradients within GMUs affect snow depths and temperature in winter, and precipitation and growing season length in the summer, with elevation increasing from the southwest to the northeast. Conifer GMUs ranged in elevation from 1001 – 1928m, but most were <1450m. Winter precipitation (winter severity) varied widely (from 10 to 371mm) in coniferous GMUs. Coniferous ecotype summer ranges are dominated by conifer species interspersed with cool season grasslands, sagebrush, and understory of forest shrubs. Shrub-steppe GMUs ranged from 1545 to 2105 m, with winter precipitation from 24 to 105 mm. Summer range within shrub steppe ecotypes was dominated by mesic shrubs (e.g., bitterbrush (*Purshia tridentate*), sagebrush (*Artemisia* spp.*)*, rabbitbrush (*Chrysothamnus* spp.), etc.). Aspen ecotype GMUs were located in the east and south with winter use areas ranging from 1582 to 2011m, with 5 of the 6 GMUs above 1700m with early winter precipitation ranging from 25 to 146mm. In summer, productive mesic Aspen (*Populus tremuloides*) woodlands were interspersed with mesic shrubs.

(b) Mule deer monitoring

We radiocollared mule deer fawns at 6 months of age in the 13 GMUs (Figure 2-1), resulting in 2,315 mule deer fawns from 1998-2011. We captured fawns primarily using helicopters to move deer into drive nets (Beasom et al. 1980), but occasionally by helicopter netgun (Barrett et al. 1982) or clover traps (Clover 1954). Mule deer capture and handling methods were approved by IDFG (Animal Care and Use Committee, IDFG Wildlife Health Laboratory) and University of Montana IACUC (protocol #02-11MHCFC-031811). Fawns were physically restrained and blindfolded during processing with an average handling time of < 6 minutes. We measured fawn mass to the nearest 0.4 kilogram with a calibrated spring scale. Collars weighed 320 - 400 grams (≤ 2% of deer mass), were equipped with mortality sensors and fastened with temporary attachment plates or surgical tubing, allowing the collars to fall off the animals after approximately 8-10 months. We monitored between 20 and 34 mule deer fawns in each study area for a total of 185 to 253 annually from 1998-2011.

We monitored fawns with telemetry for mortality from the ground every 2 days between capture and 15 May through 2006, and then once at the 1st of each month during 2007-2011. We located missing fawns aerially when not found during ground monitoring. When a mortality signal was detected, we determined cause of death using a standard protocol (Wade and Bowns 1982). In addition, we kept a minimal annual sample of ~ 600 adult females with radiocollars, using the same capture techniques as fawns. We used the composite sample of monthly aerial and mortality locations over the entire study period from these deer to estimate mule deer population ranges.

(c) Defining Population Ranges of Mule Deer

We used the mule deer winter and summer ranges for each GMU as the main spatial units of analysis, and we extracted NDVI data from summer range and winter weather from winter range for each year from each population. We combined relocation points for all individuals and years in a single study site to estimate a 95% adaptive kernel home range for both summer and winter (Worton 1989) for mule deer captured within a population. All deer populations were migratory with an average winter range size of 430 km^2 and average summer range size of 3360 km^2. Migratory periods, 1 April to 1 June and 1 October to 15 November, were excluded from the home range estimates and remaining animal locations between 1 June and 30 September were used for summer, 1 December to 31 March for winter. Climate and habitat information was then summarized by the aggregate home range of radio-collared deer for winter and summer within each population.

(d) Functional Analysis of NDVI curves

We measured growing season phenology for each population-year using 1-km resolution, 7-day composite AVHRR NDVI data obtained from the NOAA-14,-16, and -17 AVHRR, and maintained by the USGS (http://phenology.cr.usgs.gov/index.php) (Eldenshink 2006). AVHRR NDVI data extends over the full temporal extent of our mule deer monitoring effort and has been shown to correspond well with MODIS NDVI data (Eldenshink 2006). Radiometric sensor anomalies, atmospheric effects, and geometric registration accuracies were previously accounted for according to Eldenshink (2006). Further, the data were accompanied by a cloud contamination mask, which was generated using an adaptation of the cloud clearing of AVHRR data (CLAVR) algorithm (Worton 1989). We then rescaled the processed data from the USGS 0-200 classification, with 100 corresponding to vegetated/nonvegetated threshold to the standard NDVI scale of -1 to 1, with 0 as the threshold. All cloud contaminated pixels were thus removed by applying this previously generated cloud contamination mask, and the resulting data gaps were infilled using a simple temporal interpolation method (Zhao et al. 2005). Finally, a minimum NDVI threshold value of 0 was applied to define periods of little to no photosynthetic activity and filter any pixels containing ice and snow from the analysis. Since phenological changes in NDVI only directly represent ungulate forage dynamics in non-forested vegetation types, we extracted NDVI values from only, grass and shrub vegetation types (not burned within 5 years), which we characterized using SAGEMAP landcover data (2005 USGS, Forest and Rangeland Ecosystem Science Center, Snake River Field Station, Boise, ID). Masking in this fashion directly parallels nutritional ecology as mule deer are adapted to feeding in open vegetation types and actively select these types during the growing season (Hamlin and Mackie 1989, Mackie et al. 1998, Thiel 2012). To encompass the entire growing season for each population-year, but excluding winter anomalies caused by varying snow condition, we restricted NDVI data to 15 March to 15 November. This time period provided a standardized measure of growing season while capturing the variability both within and between populations for comparing curves.

We first assessed among population-year variation in NDVI curves to test direct and indirect (i.e., through body mass) effects of changes in plant phenology on overwinter survival of fawns. In most previous studies (see table 2-1 for a review), ecologists have either used a-priori summary statistics of NDVI. Unfortunately, this approach has led to the use of only a few variables to define the growing season in any ecosystem, thus to more completely assess vegetation phenology, we proposed a new approach to identify the key-periods along the NDVI curve. Instead of defining these periods a priori, our approach is based on a multivariate functional analysis of variation in observed NDVI curves.

We used a functional principal component analysis (FPCA), a type of functional data analysis (FDA) to analyze among-population and among-year variation in NDVI curves. FDA is specifically designed to characterize information in multivariate time series (Ramsay and Silverman 2005). FPCA techniques are relatively recent (Ramsay and Silverman 2005) and surprisingly rarely used in ecology and remote sensing [but see (Embling et al. 2012)] even if they offer a very powerful way to analyze temporal ecological data such as NDVI time series. FPCA was applied to NDVI curves to identify spatiotemporal patterns of vegetation changes. While a-priori defined metrics estimated from NDVI data have occasionally been analyzed using PCA (Herfindal et al. 2006), standard PCA is not optimal for time series data. In PCA, weeks would be considered as independent vectors of values whereas FPCA explicitly accounts for the chronology of weeks by treating the statistical unit as the individual NDVI curve. This ensures that the patterns identified by FPCA are constrained to be temporal trends within the growing period (i.e., portions of the curve) and not due to few independent NDVI values. FPCA produces eigenvalues (measuring variation explained by each dimension) and principal component scores for sampling units (summarizing similarities among NDVI curves). However, eigenvectors are replaced by eigenfunctions (harmonics) that show the major functional variations associated to each dimension.

To facilitate the application of FPCA by ecologists and remote sensing scientists we provided in electronic supplementary materials the data and the full R code (based on the fda package) to reproduce the analysis performed in the paper. As these methods are poorly known in ecology and remote sensing, we also provided an expanded description of the mathematical theory but the reader could consult the original books (Ramsay and Silverman 2005, Ramsay et al. 2009) for additional information.

Sampling units (population-years) were partitioned using the k-means algorithm applied on the first two principal component scores. We computed the Calinski & Harabasz criterion for partitions between 2 and 10 groups and select the optimal number of clusters that maximizes the criterion. We also computed the amount of variation in the first two principal component scores (NDVI curves) that were explained by space (i.e., population) and time (year). This allowed us to understand which source of variation contributed most to differences in growing season dynamics. We then used principal component scores in subsequent analyses as explanatory variables of mule deer fawn mass and survival.

(e) PRISM Weather Data

We characterized winter (1 November to 31 March) weather conditions using 4km gridded PRISM observations of minimum monthly temperature and total monthly precipitation from 1995 – 2011 (Daly et al. 1997)(available from http://www.prism.oregonstate.edu). Temperature and precipitation data were averaged across the winter range for each population, and then summed (averaged) across months for precipitation (temperature) to produce climate covariates that represented measures of winter severity, respectively. We produced variables for early winter (November – December) and late winter (January-March) for both precipitation and temperature. These variables were highly correlated ($r > 0.4$), thus we selected the variable with the highest first order correlation to our response variable, overwinter survival of fawns, as our winter severity index.

(f) Environmental Effects on Body Mass and Overwinter Survival of Fawns

We estimated population- and year-specific estimates of overwinter fawn survival (from 16 December to 1 June) using staggered Kaplan-Meier non-parametric survival models. We then employed path analysis (Shipley 2009) to test the population-level effects of body mass and winter weather, and to tease apart the direct from the indirect effects (through fawn body mass, see Figure 2-3) of key periods of NDVI on overwinter survival. For the path analysis, we transformed our response variable with an empirical logit function (Warton and Hui 2010) because average survival for each population-year is a proportion bounded between 0 and 1 (Zar 1995). We used mass of female fawns in

December to measure the cohort quality of the birth year (Hamel et al. 2009a) and eliminate the effect of sexual size dimorphism (Hurley et al. 2011). A first, indirect, mechanistic link between environmental conditions early in life and overwinter survival could be that variation plant phenology and nutritional quality affects the body development of fawns, which in turn, drives overwinter survival. An alternative could be that variation in plant phenology is directly related to overwinter survival as a result of the availability and quality of winter forage. Because winter precipitation was recorded in November-December at the same time as the weighing of fawns, we could not test for an indirect effect of winter precipitation through body mass on overwinter survival. Our model included a population effect entered as a random factor on the intercept to account for the repeated measurements of overwinter survival in different years within a population.

We used a Bayesian framework to fit the path analyses to our data (Gelman and Hill 2007). We used non-informative normal (mean of 0 and a standard deviation of 100) and uniform (range between 0 and 100) priors for the regression coefficients and variance parameters respectively. Using JAGS (Plummer 2003), we generated 50,000 samples from Monte-Carlo Markov Chains (MCMC) to build the posterior distributions of estimated parameters after discarding the first 5,000 iterations as a burn in. We checked convergence graphically and based on Gelman's statistics (Gelman and Hill 2007). Estimated parameters were given by computing the mean of the posterior distribution, and the 2.5th and 97.5th percentiles of the distribution provided its 95% credibility interval. We considered a variable as statistically significant if the credibility interval of its posterior distribution excluded 0. We assessed the fit of the model by computing the squared correlation coefficient between observed and predicted values (Zheng and Agresti 2000). Finally, to compare the relative effect sizes of the explanatory variables on overwinter survival we replicated the analyses using standardized coefficients.

RESULTS

(a) Functional Analysis of NDVI Curves

Functional PCA analysis of NDVI data led to the identification of two independent eigenfunctions (hereafter FPCA components), which reflected contrasting patterns of plant phenology in spring and fall. Both FPCA components corresponded to continuums of increasing NDVI intensity, in early and late growing seasons, and were used as explanatory variables of overwinter survival of mule deer fawns.

The first FPCA component described the late season phenology, after peak value and accounted for 48.9 % of the total variation in NDVI curves. The second FPCA component represented the early season phenology and accounted for approximately half as much variation as the first FPCA component (27 %; Fig 2-1). FPCA components can be interpreted as the amount of deviation from the overall average NDVI curve in terms of overall primary productivity at different times within the growing season. For example, high FPCA component 1 scores mean both high primary productivity in open habitats in fall, but also a longer fall growing season compared to lower FPCA component 1 scores (Figure 2-1a, c). Similarly, positive values of FPCA component 2 reflect both higher spring primary productivity and early onset of plant growth (e.g., Fig 2-1b, c; Type 4 dark green).

Combining both continuums in a factorial plane allowed us to distinguish five NDVI types of curves in reference to the overall mean trend (Figure 2-1c). For example, NDVI in fall was close to the average for the NDVI curve type 2 (dark blue, Figure 2-1c) but NDVI in spring was the lowest of all curve types in Figure 2-1c. Conversely, NDVI curve type 3 (light green, Figure 2-1c) has NDVI values above average in both spring and fall. The NDVI curve type 1 (light blue, Figure 2-1c) has the highest NDVI in fall, while NDVI curve type 5 (red, Figure 2-1c) had lowest fall productivity. Generally, a given population displayed one NDVI curve type, with some extreme values belonging to a different type (Figure 2-2, Appendix A Figure 2-S1). Decomposition of the among-population and among-year variance in NDVI curves in fact shows that most (73.8 %) of the observed variation in NDVI curves was accounted for by population (i.e., spatial variation), and much less (20.8 %) by annual variation within a population, with a high degree of synchrony between populations within a year (only 5.4 % of the variation in NDVI curves is unexplained). This suggests that the 5 NDVI types we identified (Figure 2-1) strongly reflect the distribution of ecotypes and vegetation characteristics among populations (Figure 2-2).

(b) Environmental Effects on Body Mass and Overwinter Survival of Fawns

The average body mass of female fawns in December was 34.0 kg (SE = 2.55). In agreement with our hypothesis, body mass of 6-month-old fawns was positively related to NDVI in both spring and fall (Fig 2-3 & 2-4). From the estimated standardized regression coefficients, the effect of NDVI in fall (FPCA component 1) on autumn body mass of fawns (standardized $\beta = 0.694$, SE = 0.209) was greater the effect of NDVI in spring (FPCA component 2; standardized β =0.652, SE = 0.206). FPCA component in the fall explained more variance in body mass than traditional estimates of phenology such as, start, end or peak date of growing season (Appendix A Table 2-S3). The fall was thus of more importance to the body development of mule deer fawns at the onset of winter than spring (Fig 2-3 & 2-4).

The annual overwinter survival of mule deer fawns averaged 0.55 (SE = 0.24, range = 0 to 0.94) across populations. Our best model accounted for 44.5% of the observed variation in overwinter survival, including the additive effects of autumn body mass of female fawns, early winter precipitation, and of spring and fall NDVI. As expected when mean body mass reflects the average demographic performance of a given cohort, the annual overwinter survival of fawns was associated positively with the mean cohort body mass in late autumn (Figure 2-3 & 2-5A). Total precipitation during early winter from November to December (ranging from 11 to 372 mm) was associated with decreased fawn survival (Figure 2-3 & 2-5B). Once the effect of body mass and winter precipitations were accounted for, spring had negative impacts on the overwinter survival of fawns (Figure 2-3, 2-5D), so that survival was lower with higher NDVI during the spring plant growth season. Fall was not significantly related to overwinter survival beyond the positive effect on body mass. Winter precipitation has the greatest effect size on overwinter survival of fawns (standardized β = -1.138, SD = 0.200), followed by spring (standardized β = -0.587, SD = 0.217) and fall (standardized β =-0.369, SD = 0.247), while fawn body mass in fall has the smallest relative effect size (standardized β = 0.350, SD = 0.146). The observed relationships between environmental conditions and overwinter survival of fawns differed slightly among populations but differences were not statistical significance (Appendix A Figure 2-S2).

DISCUSSION

Our results linked variation in observed plant phenology to body mass and survival of juvenile mule deer during winter across populations and years, demonstrating the benefits of connecting remote sensing and biological information to understand consequences of environmental change on biodiversity. We used a new statistical approach to identify plant phenology from NDVI curves encompassing the entire growing season. Previous studies have reported effects of plant phenology on body mass and demographic parameters in several species of mammals and birds (see Table 2-1 for a review). However, all these studies but (Tveraa et al. 2013)'s one were based on a-priori defined metrics mostly focusing on indexes of spring phenology, thus spring metrics appear to explain population parameters, but the relative role of late plant growth season has rarely be investigated. Our approach provides a compelling example and motivation for functional analysis of remote sensing derived measures of plant growth as a first step to help identify plant phenological periods most affecting population dynamics of animals.

Our results emphasized that the relative role of spring versus fall phenology is unclear for ungulate species adapted to more arid environments. By defining the period's a-posteriori, we found that mule deer fawns survived better in populations with higher NDVI during fall, and thus longer fall growing seasons. The effect size of fall NDVI was stronger than the effect size of spring NDVI for predicting 6-month old body mass. Body mass was positively related to overwinter survival, but precipitation during early winter decreased survival with an effect size almost 3 times as strong as early winter body mass, similar to other studies of winter ungulate survival (Bartmann 1984, Bishop et al. 2005, Hurley et al. 2011). Previous studies on large herbivores reported an effect of the preceding winter conditions when the juvenile was in utero (Post et al. 1997, Herfindal et al. 2006, Mysterud et al. 2008, Tveraa et al. 2013), or an effect of spring conditions (Herfindal et al. 2006) on body mass. The patterns of variation in NDVI curves translated to spatial variation in plant growth during fall, and hence mule deer body mass and survival. First, we found almost twice as much variation in the NDVI curves occurred in the fall (FPCA component 1, Figure 2-1a) compared to spring (FPCA component 2, Figure 2-1a). Thus, plant phenology during the fall was more variable than spring in our semi-arid system. Second, we found almost three times the variation in NDVI curves was explained by spatial variation among populations in a given year compared to among-year variation. The high proportion of the variance explained among populations indicates that variation among NDVI curves within a population was consistent year-to-year and also synchronous between units within a year. These patterns of stronger variation during fall (vs. spring) and among populations (vs. among years) contributed to fall NDVI having double the effect size on body mass, and hence survival. Thus, the most variable period of the growing season (e.g. fall) had the strongest effect size on mass and survival. These results mirror results from studies of just the spatial variance in survival (Lukacs et al. 2009) and suggest that plant phenology may also synchronize population dynamics. With the recent focus on fall nutrition of elk (Cook et al. 2004), however, many ungulate managers in North America are focusing increasingly on fall nutrition. Our results emphasize that, at least for large herbivores, focusing a priori on just one season, spring or fall, without explicit consideration of the spatiotemporal variation in the entire curve of plant phenology could be misleading.

Forage availability for large herbivores varied by vegetation cover type, precipitation, and temperature during the growing season (Marshal et al. 2005, Stewart et al. 2005). Increased rainfall in summer, reflected in increased NDVI in fall, will promote growth of forbs (Marshal et al. 2005) a highly selected forage for mule deer (Hobbs et al. 1983, Marshal et al. 2005) and can promote new growth in fall germinating annual graminoids (e.g., Cheatgrass *Bromus tectorum*) and delay senescence, prolonging access to higher quality forage (Hebblewhite et al. 2008). Increased summer-fall nutrition improved calf and adult female survival, fecundity rates, and age of first reproduction in captive elk (Cook et al. 2004). Rainfall during the growing season also increases quality and quantity of winter forage (Marshal et al. 2005), which increases survival of fawns and adult female mule deer (Bishop et al. 2009). Tollefson et al. (2010) showed that summer forage has the greatest impact on mule deer juvenile survival and overall population growth rate in a penned experiment in eastern Washington, USA. In our study area, effects of climate and plant phenology certainly varied across our southeast to northwest gradient (electronic supplemental materials), but will require individual-level analyses of individual radiocollared mule deer to most clearly separate out local influences on overwinter survival. Therefore, especially in arid or semi-arid systems, we expect that future studies will identify strong signatures of fall NDVI and climate on demographic parameters of large herbivore populations, similar to our results.

One obvious difference between our arid study system and previous studies of NDVI and large herbivores is that NDVI curves were not a classic bell shape. Instead, plants in open-habitats had a left-skewed growth curve, with a rapid green up in spring, but then a long right tail in the NDVI distribution, and, occasionally, secondary growth peaks in late summer and fall (e.g., Figure 2-1c). Most other studies that examined NDVI curves found more symmetrical shapes, with a rapid plant green up and senescence (Herfindal et al. 2006, Pettorelli et al. 2007). However, (Martinez-Jauregui et al. 2009) found the classic bell-shaped NDVI curve for Norwegian and Scottish Red deer (*Cervus elaphus*), but a similarly earlier and flatter NDVI curve in southern Spain. We believe our right-skewed fall growing season dynamics may be characteristic of arid or semi-arid systems where precipitation and growing seasons cease during summer. Nonetheless, the variability among studies in the shape of the NDVI curves emphasize the importance of identifying key periods of the growing season a-posteriori.

One unexpected result from our study was the negative direct effects of spring NDVI on overwinter survival of mule deer fawns, in contrast to the stronger positive effect of both spring and fall NDVI on body mass, and of body mass on overwinter fawn survival. There could be several competing explanations for this puzzling result. First, despite the power of path analysis at disentangling complex relationships (Shipley 2009), there could still remain some confounding effects of body mass or winter severity. Although we attempted to control for spatial variability with random effects of study site, there could also be negative covariance between winter severity, which, because spring NDVI is correlated to winter severity of the preceding winter (Christianson et al. 2013), could lead to negative correlation between spring NDVI and subsequent winter severity. The effect of this general relationship may downscale to study site differently if snow depth passes a threshold where few fawns survive regardless of mass, as is the case sporadically in some of our higher elevation study sites (67, 69, 72) that typically display the most productive NDVI curve types. Mysterud and Austrheim (Mysterud and Austrheim 2013) provide a very plausible explanation based on the negative effect of a later spring (Axis 2) will increase winter survival through prolong access to high quality forage. Alternatively, viability selection operating on mule deer cohorts may explain this pattern (Fisher 1930). Counter-intuitively, if good spring growing conditions enhance summer survival, a large proportion of the cohort will survive until the onset of the winter, including frail (Vaupel et al. 1979) individuals that would experience increased mortality during winter (Wilson and Nussey 2010), and the opposite during harsh springs. As individual early mortality in populations of large herbivores is tightly linked with maternal condition (Gaillard et al. 2000), fawns surviving to the winter will be mostly high quality fawns enjoying high maternal condition. Those fawns would thus be expected to be robust enough to survive winter. Bishop et al. (Bishop et al. 2009) suggested this exact viability selection process for mule deer fawns in Colorado, supporting our interpretation of this counterintuitive spring NDVI effect. Viability selection could also be compounded through the interaction between winter severity and the preponderance of predator-caused mortality in winter (Hurley et al. 2011). There might also be negative covariance between neonate and overwinter survival (Bishop et al. 2009), driven as we suggest here by different spring and fall phenology patterns. Regardless, many plausible biological processes exist to explain the effect of early season plant growth on winter survival of fawns.

Functional analysis provides a powerful approach to identify the key-periods of the growing season from remote sensing data and to assess their differential effects on life history traits. Our functional analysis applied to year- and population-specific NDVI curves allowed us to identify two distinct components of variation that corresponded closely to contrasting spring and fall phenology. Of course, many remote sensing studies have used NDVI for decades to examine differences in spring and fall phenology (Huete et al. 2002). Yet despite the primacy of multivariate approaches in remote sensing, only a few studies have used even standard Principle Components Analysis (PCA) to examine spatial trends in NDVI (Hall-Beyer 2003) or identify NDVI anomalies (Lasaponara 2006). Functional analysis allowed us to identify phenological patterns a-posteriori and to summarize NDVI curves into only 2 independent components instead of 5-12 a-priori defined metrics that are strongly correlated (see Table 2-1). Moreover, our FPCA axes explained variation similarly or better than pre-defined parameters based on previous studies (e.g., Axis 1 versus senescence date, Appendix A Table 2-S3). Functional analysis provides a novel and powerful approach for studies of the ecological effects of plant phenology, and arose out of the productive collaboration between remote sensing scientists and ecologists. We anticipate the benefits of functional analyses to extend far beyond NDVI, to ecological analyses of variation in the other remotely sensed vegetation indices (e.g., fPAR, EVI), MODIS snow and temperature datasets, and aquatic measures like sea surface temperature, chlorophyll, and other important ecological drivers.

In conclusion, in large parts of world that are semi-arid or deserts, our results strongly show that it may not be just spring phenology that matters to ungulate population dynamics. Our new approach using functional analysis of the entire NDVI curve provides a powerful method to identify first key periods within the growing season and then disentangle their respective role on demographic traits when combined with hierarchical path analysis. Our approach thus allowed us to determine the most likely pathways that plant growth influenced mule deer overwinter survival of fawns. Finally, and perhaps most importantly, we demonstrated a novel approach to first identify different temporal components of remote sensing datasets that are the key drivers of large-scale population responses, aiding the broad objective of enhancing our ability to monitor responses of biodiversity to environmental change at global scales.

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TABLES

Table 2-1. A brief literature survey of the studies that investigated relationships between NDVI metrics and life history traits linked to performance and population abundance. The literature survey was performed using ISI web of knowledge using the key-words “NDVI and survival”, “NDVI and body mass”, “NDVI and body weight”, “NDVI and reproductive success”, “NDVI and recruitment”, “NDVI and population growth”, and “NDVI and population density”. Only studies performed on vertebrate species were retained. For each case study, the table displays the focal trait(s), the focal species, the NDVI metric(s) used, the outcome (“+”: positive association between NDVI and performance, “-” : negative association between NDVI and performance, “0”: no statistically significant association between NDVI and performance”), the reference, and the location of the study.

Trait	**Species**	**NDVI metrics**	**Outcome**	**Location**	**Reference**
Protein mass Body mass Carcass mass Body fat	Caribou *Rangifer tarandus*	Average NDVI in June	Protein mass: + Other traits: 0	Québec-Labrador (Canada)	(Couturier et al. 2008)
Birth mass Juvenile autumn mass	Caribou *Rangifer tarandus*	Average NDVI in June	+	Québec-Labrador (Canada)	(Couturier et al. 2008)
Population density Juvenile body mass	Semi-domesticated reindeer *Rangifer tarandus*	Summed NDVI over the breeding season	Juvenile mass: 0 Population density: + (in populations with poor winter ranges only)	Norway (across populations)	(Tveraa et al.) 2007
Population size	Lesser grey shrike *Lanius minor*	NDVI in May-June (breeding areas) NDVI in January-March (wintering areas)	+	France Spain (breeding areas) Kalahari (wintering areas)	(Giralt et al. 2008)

Reproductive performance (lamb/ewe in December)	Sheep *Ovis aries*	NDVI in March-May NDVI in May	NDVI in May: + NDVI in March-May: 0	North Western Patagonia	(Texeira et al. 2008)
Survival	African elephant *Loxodonta africana*	Seasonal maximum NDVI	Juvenile survival: + Adult survival: 0	Kenya	(Wittemyer 2011)
Parasite loading	Red-legged partridge *Alectoris rufa*	Yearly mean NDVI	+	Spain	(Calvete et al. 2003)
Body mass	Red deer *Cervus elaphus*	Monthly NDVI	Spring NDVI: + (Spain only) Other metrics/populations: 0	Europe (across population)	(Martinez-Jauregui et al. 2009)
Wing length Tail length Clutch size Body mass (Males and females)	Barn swallow *Hirundo rustica*	NDVI in December-February (wintering areas)	Male wing length, male and female tail length, clutch size: + Other traits: 0	Italy (breeding area) Africa (wintering areas)	(Saino et al. 2004)
Juvenile and adult Survival	White stork *Ciconia ciconia*	NDVI in October-November (Sahel) NDVI in December-February (Eastern southern Africa)	+	Eastern Germany Poland (breeding areas)	(Schaub et al. 2005)
Adult survival	Barn swallow *Hirundo rustica*	NDVI in September-November NDVI in December-February NDVI in March-May	+	Denmark	(Szép et al. 2006)

		(wintering areas in Africa)			
Conception rates	African elephant *Loxodonta africana*	Seasonal NDVI (wet vs. dry seasons)	+	Kenya	(Wittenmyer et al. 2007 ; Rasmussen et al. 2006)
Juvenile and adult survival	Egyptian vulture *Neophora percnopterus*	Yearly NDVI (wintering areas) NDVI in September-June (breeding areas)	+	Spain	(Grande et al. 2009)
Survival Reproductive success	Red-backed shrike *Lanius collurio*	NDVI in September-October (Sahel) NDVI in December-March (South Africa) NDVI in April (Germany)	Survival: + (NDVI in December to March) Reproductive success: + (NDVI in September-October)	Germany	(Schaub et al. 2012)
Juvenile survival	Greater sage grouse *Centrocercus urophasianus*	NDVI in May-August NDVI and Max NDVI in May, June, July, and August	+ (trends only) Strong co-variation among NDVI metrics	Idaho Utah (USA)	(Guttery et al. 2013)
Body mass	Red deer *Cervus elaphus*	NDVI in the 1st of May	+	Norway	(Pettorelli et al. 2005)
Juvenile body mass	Roe deer *Capreolus capreolus*	Summed NDVI in April-May Summed NDVI in August-October	+ (Chizé population) 0 (Trois Fontaines population)	France	(Pettorelli et al. 2006)
Kidney mass	Hystricognath rodents	Yearly NDVI (calculated from monthly NDVI)	-	South America (across species	(Diaz et al. 2006)
Body mass	Moose	7 NDVI metrics		Norway	(Herfindal et al.

	Alces alces	(PCA)	+		2006)
Body mass	Wild boar *Sus scrofa* Roe deer *Capreolus capreolus*	Summed NDVI over the growing season	Roe deer: 0 Wild boar: 0	Poland	(Mysterud et al. 2007)
Body condition	Raccoon dog *Nyctereutes procyonoides*	4 NDVI metrics (onset of spring, peak NDVI, Summed NDVI over the growing season, and rate of NDVI increase in spring)	Onset of spring: - Peak NDVI and Summed NDVI: + Rate of NDVI increase: 0	Finland	(Melis et al. 2010)
Juvenile body mass Reproductive success	Reindeer *Rangifer tarandus*	EVI (Enhanced Vegetation Index) Modelled using a double logistic function. Use of the parameters S (onset of spring), mS (rate of EVI increase), and mEVI (plant productivity)	S and mEVI on both mass and reproductive success: +	Norway	(Tveraa et al. 2013)
Juvenile body mass Pregnancy rate	Elk *Cervus elaphus*	NDVI correlated with bi-weekly forage biomass and quality over the previous growing season	Exposure to higher predicted forage quality : + juvenile body mass + female pregnancy	Canada	(Hebblewhite et al. 2008)
Juvenile mass	Sheep *Ovis aries* (2 breeds)	NDVI in late May Summed NDVI in June-August	NDVI in late May: + Summed NDVI in June-August: 0 or – depending on the breed	Norway	(Nielsen et al. 2012 ; Nielsen et al. 2013)
Population size	Common House-Martin *Delichon urbicum*	NDVI in December-February (wintering areas in	+	Italy	(Ambrosini et al. 2011)

	Common swift *Apus apus*	Africa)			
Juvenile body mass	Chamois *Rupicapra rupicapra*	5 NDVI metrics (NDVI slope in spring, NDVI maximum slope in spring, maximum NDVI, date of NDVI peak, Summed NDVI in March	+ (Summed NDVI in March the best predictor)	France	(Garel et al. 2011)
Juvenile growth Juvenile survival	Mountain Goat *Oreamnos americana* Bighorn sheep Ovis *canadensis* Alpine ibex *Capra ibex*	Summed NDVI in May Summed NDVI over the growing season Rate of NDVI change	Rate of NDVI change: - Other metrics: 0	Canada Italy	(Pettorelli et al. 2007)
Population abundance	American redstarts *Setophage ruticilla*	NDVI in December-March (wintering areas)	+	North America (breeding areas) Carribean – Cuba (wintering areas)	(Wilson et al. 2011)
Reproductive success Survival	White-tailed deer *Odocoileus virginianus*	Summed NDVI in May-August Rate of NDVI change between May and June Maximum change between May and June	Summed NDVI in May-August on reproductive success: + Rate of NDVI change and Maximum change on reproductive success: -	Anticosti Québec (Canada)	(Simard et al. 2010)

			Effects on Survival: 0		
Population density	Murine rodent *Akodon azarae*	Seasonal NDVI	+	Argentina	(Andreo et al. 2009)
Population rate of increase	Kangaroos *Macropus sp.*	NDVI for 6 months and 12 months	+ (but not better predictor than rainfall)	Australia	(Pople et al. 2010)

FIGURES

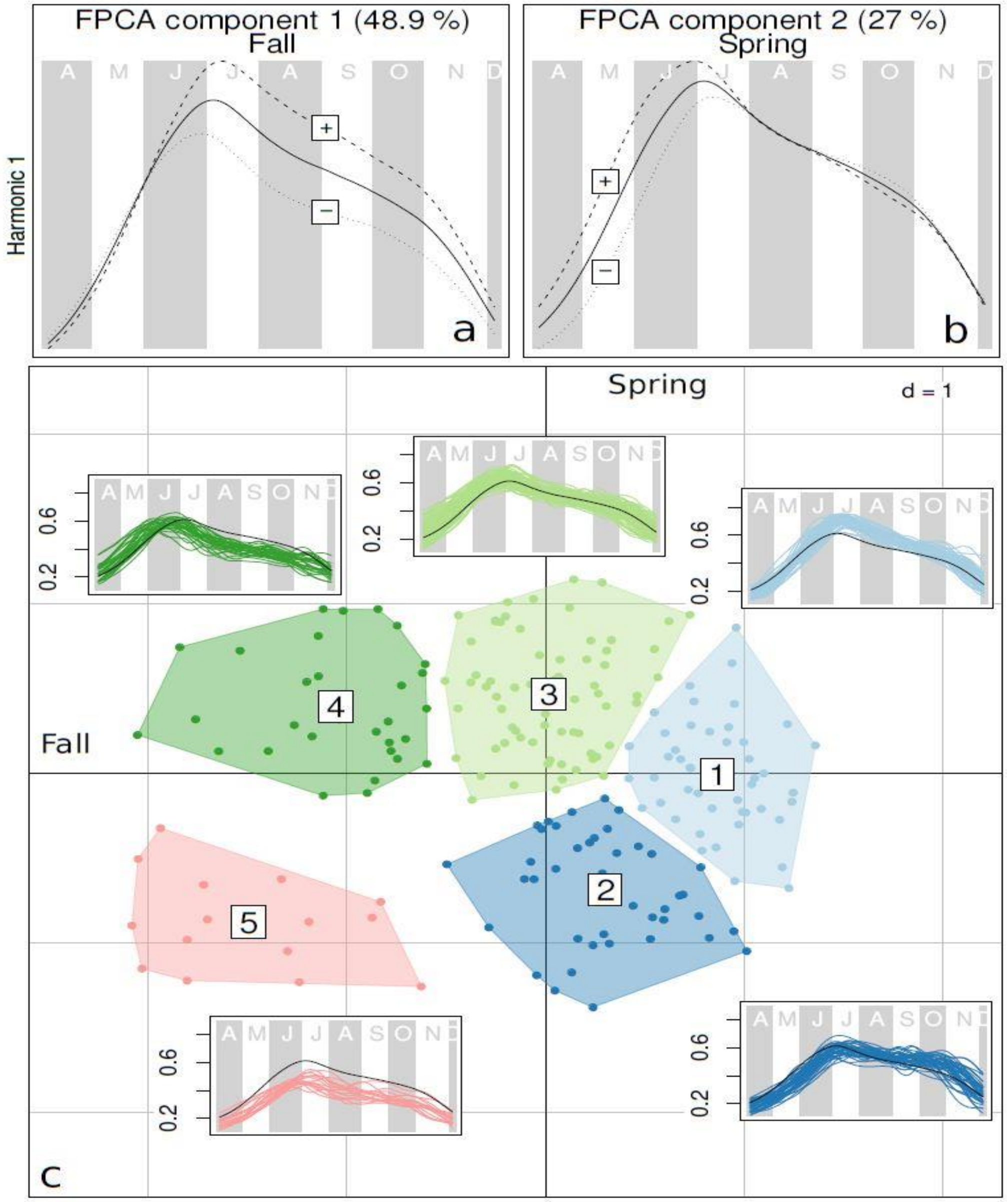


Figure 2-1. Results of Functional Principal Component Analysis of the typology of NDVI curves in Idaho, USA, from 1998-2011 from April (A) to November (N) for each population-year (dot) identifying two key periods, the spring (2nd FPCA component, the Y-axis) and the fall components (1st FPCA component, X-axis). a) Variation in NDVI

curves among populations and years was best explained by FPCA 1, which explained 48.9% of the variation, and characterized primary production from June to October (e.g., summer/fall). b) FPCA 2 (Y-axis) characterized primary production in May and June and explained 27% of the seasonal variation. c) NDVI typology was best characterized by 5 clusters, shown in different colors, that corresponded to different patterns of spring and fall primary production, compared to the mean NDVI curve across all of Idaho. For example, typology 5 was characterized by low NDVI intensity in both spring and fall, typology 3 by high NDVI intensity in both spring and fall, and typology 4 by high NDVI intensity in spring, but low in fall, etc.

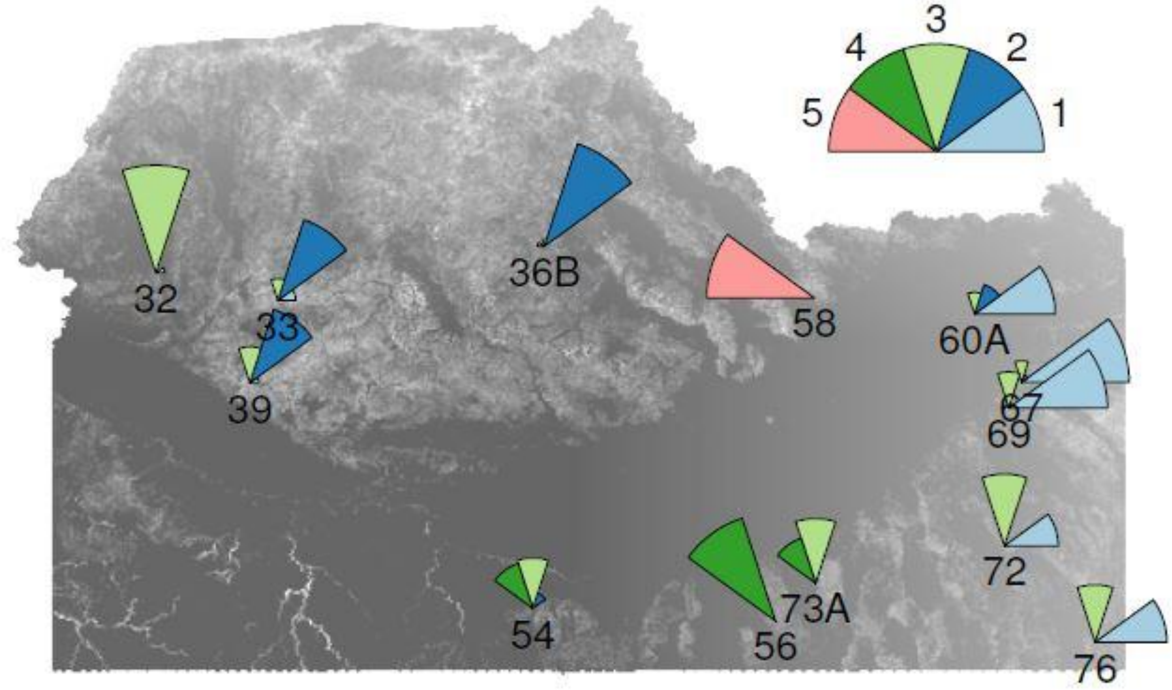


Figure 2-2. Distribution of the 5 NDVI typologies shown in Figure 1, with corresponding colors (inset) across the 13 mule deer populations (GMU's) in Idaho, USA, from 1998-2011. The size of the pie wedge is proportional to the frequency of occurrence of each NDVI typology within that mule deer population. For example, population 56 had all but one population-year occurring in NDVI typology 4 (Figure 2-1) indicating low primary productivity during spring but higher during fall.

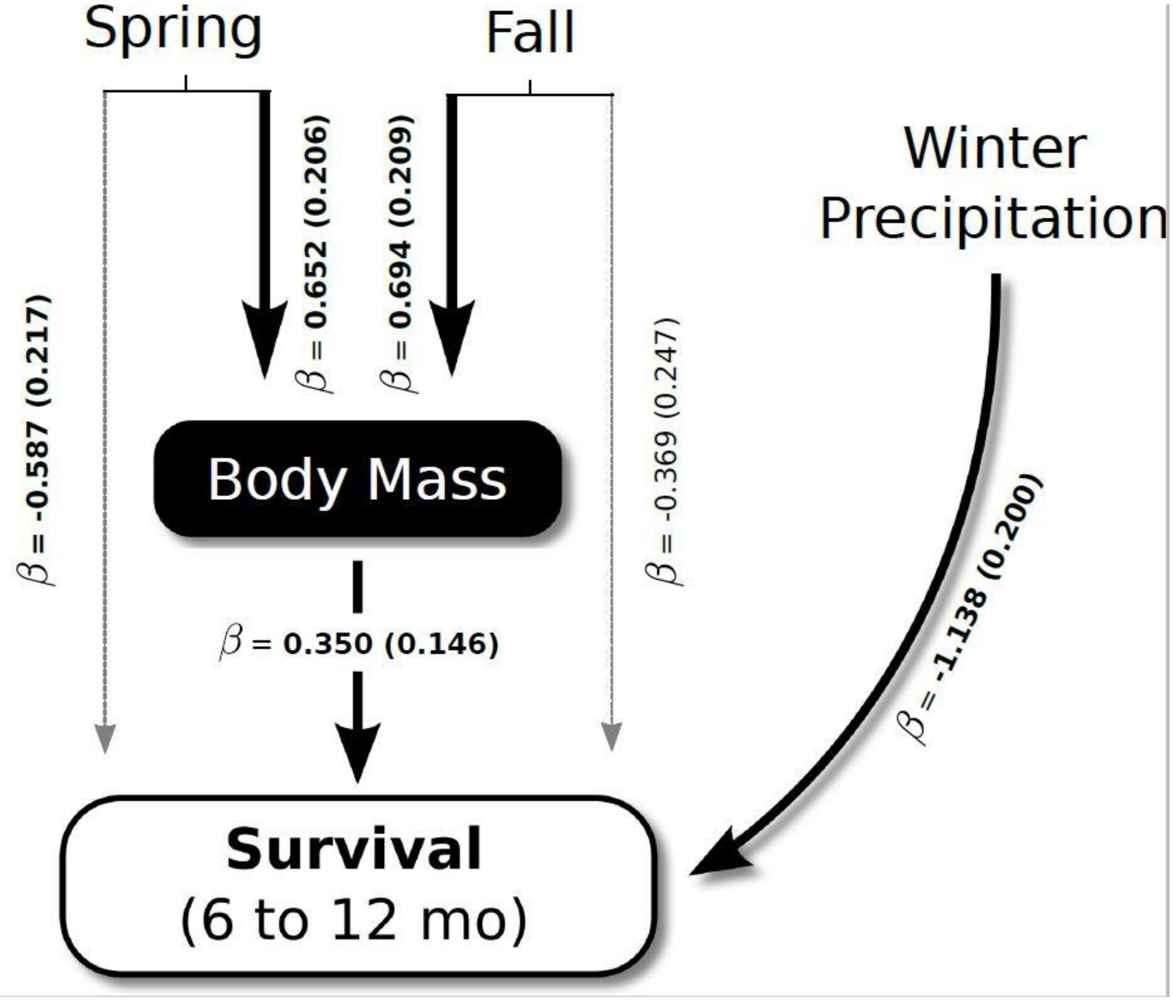


Figure 2-3. Hierarchical Bayesian Path Analysis of the effects of spring and fall growing season functional components (from Figure 1) and winter precipitation on mule deer fawn body mass and overwinter survival from 1998-2011 in Idaho, USA. This model explained 44.5% of the variation in survival. Beta coefficients and their standard deviation are shown, with solid lines indicating the indirect effects of NDVI on survival mass through their effects on body mass, and dashed lines indicate the direct effects of NDVI on survival.

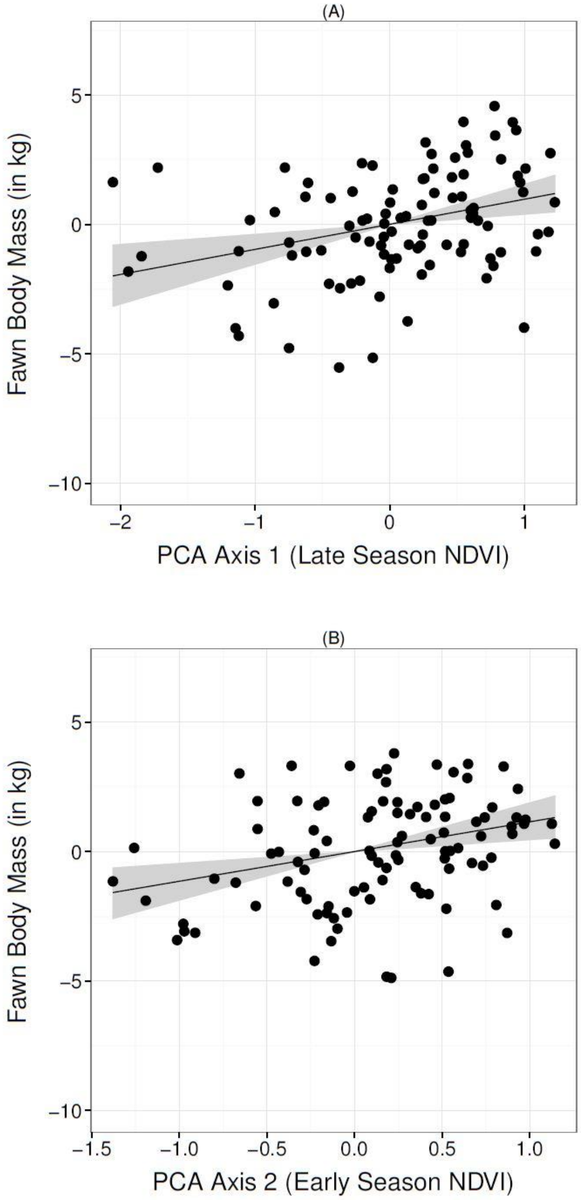


Figure 2-4. Results of hierarchical Bayesian path analysis showing the standardized direct effects of a) FPCA component 1 from the functional analysis (Fall NDVI), and b) FPCA component 2 (Spring NDVI) on body mass (kg) mule deer fawns in Idaho, USA, from 1998-2011.

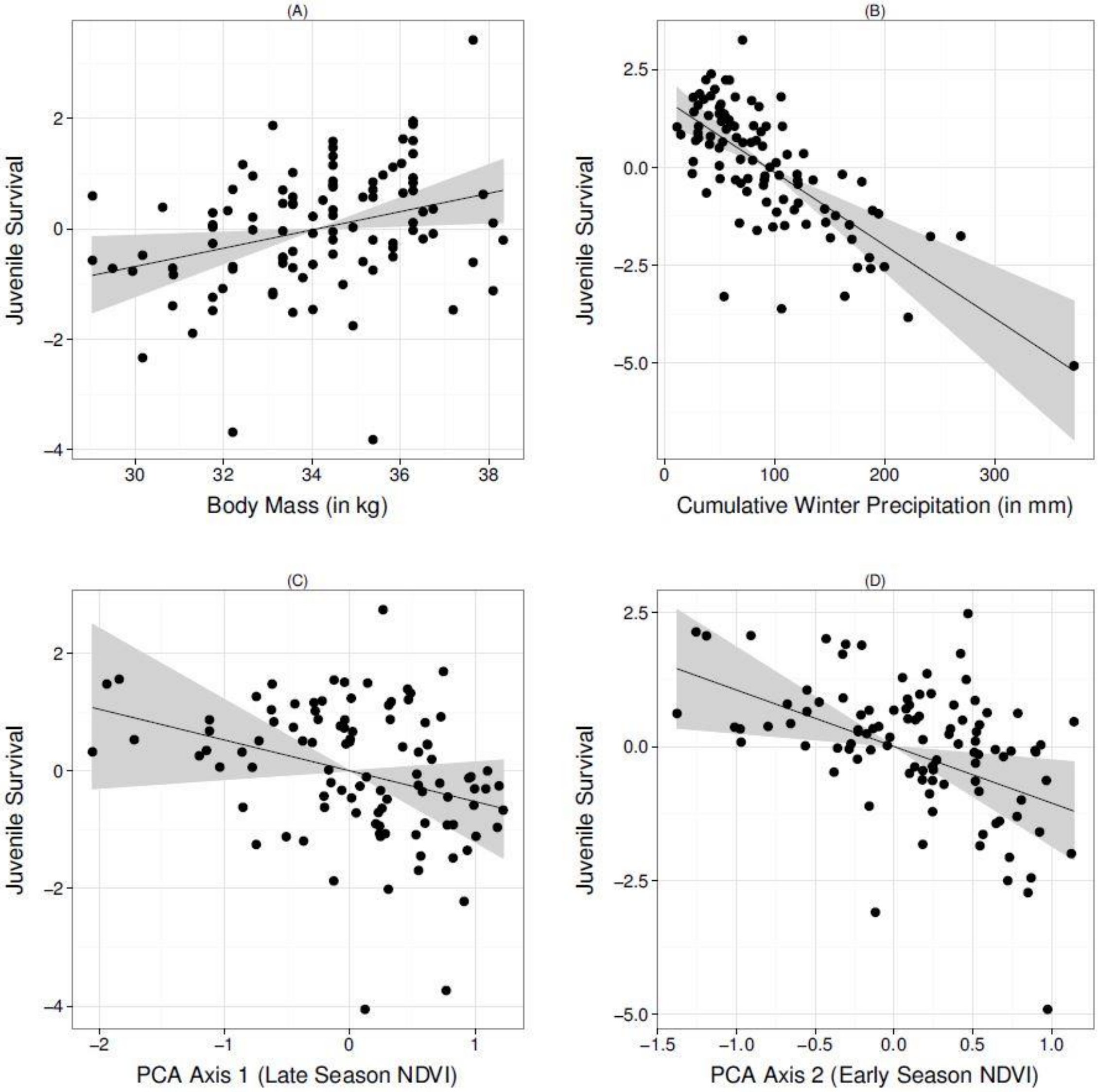


Figure 2-5. Results of hierarchical Bayesian path analysis showing standardized direct effects of a) body mass (kg), b) cumulative winter precipitation (in mm), c) FPCA component 1 from the functional analysis (Fall NDVI), and d) FPCA component 2 (Spring NDVI) on the overwinter survival of mule deer fawns in Idaho, USA, from 1998-2011.

APPENDIX A. SUPPLEMENTAL MATERIALS

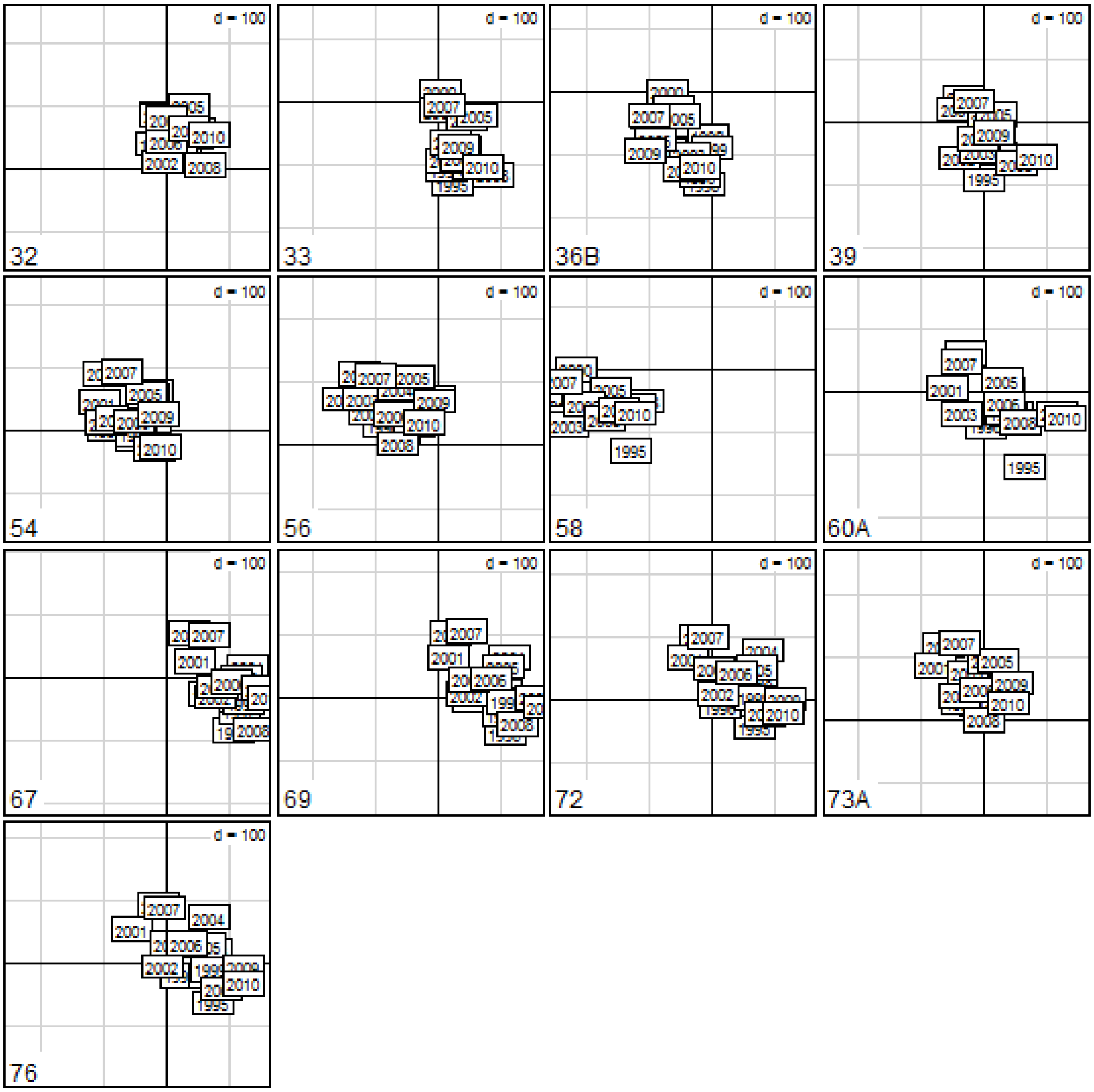
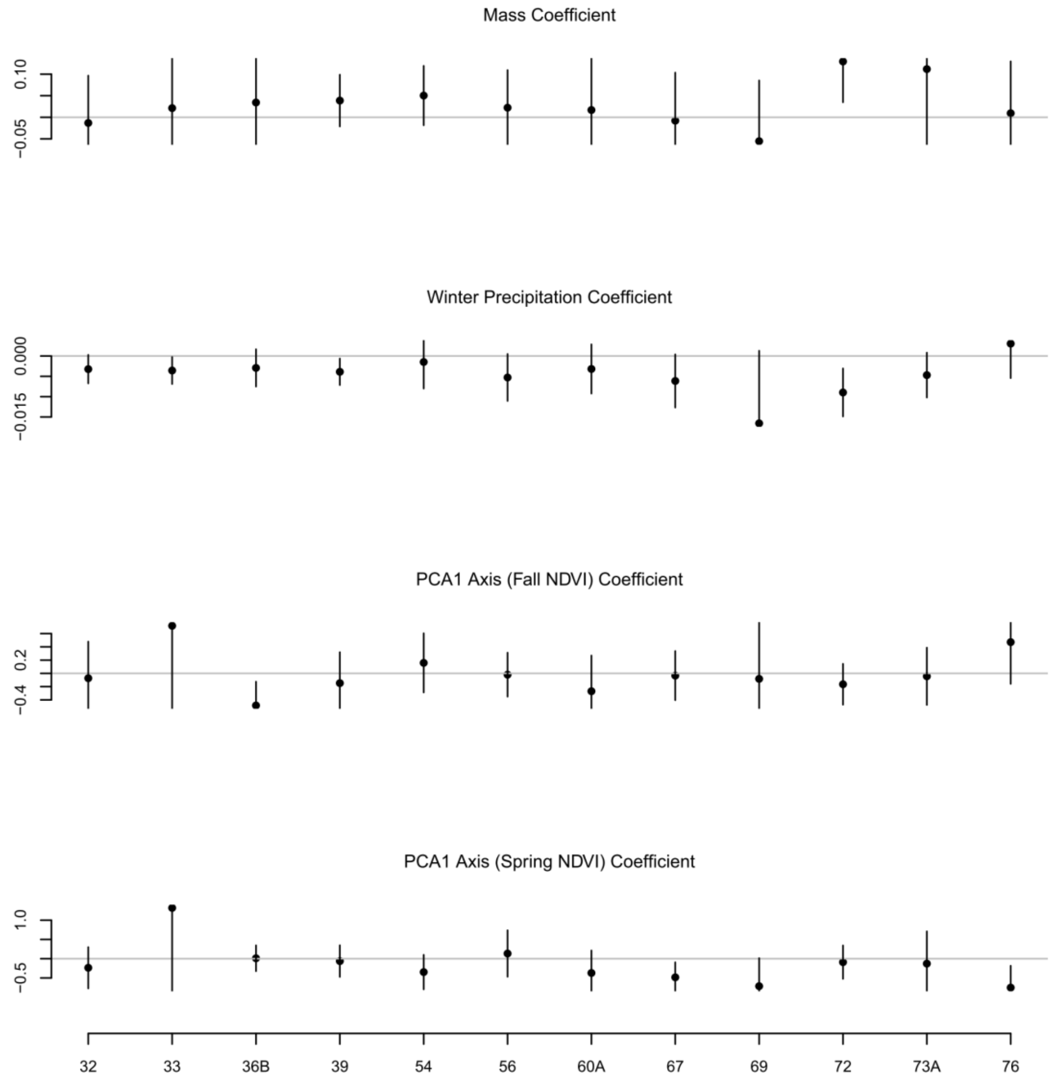


Figure 2-S1. Results of functional analysis of NDVI typology for each of the 13 mule deer populations (GMU's) in Idaho, 1998-2011. Individual population-years are shown along the same axes as in Figure 1 showing the spring (Y-axis) and fall (X-axis) growing season components of the NDVI growing season dynamics. For example, population unit 58 experiences the lowest primary productivity year round, but especially in fall.


Mass Coefficient

Winter Precipitation Coefficient

PCA1 Axis (Fall NDVI) Coefficient

PCA1 Axis (Spring NDVI) Coefficient

Figure 2-S2. Coefficients from Hierarchical Bayesian path analysis of individual mule deer populations (GMU’s) showing the effects of body mass, winter severity, and Fall and Spring NDVI on overwinter mule deer fawn survival in Idaho, 1998-2011.

Table 2-S3. Comparison of FPCA Axis 1 to traditional NDVI derived covariates for estimating vegetation phenology. Axis 1 is replaced by one of the traditional variables reported in other papers. We did not remove Axis 2 from the model because it was supposed to be linked to early season NDVI. To hold everything else constant, Axis 1 is replaced by each of the variables below one by one for survival and body mass.

Response	**Axis 1 replaced by...**	**Estimates**	**AIC (~ R^2)**
Survival	Axis 1	-0.0625 (0.0482), P=0.19	24.57
Survival	October precipitation	0.001 (0.001), P = 0.48	25.77
Survival	Petgreen	-0.001 (0.0007), P = 0.16	24.25
Survival	Petsenes	-0.004 (0.002), P = 0.09	**23.37**
Survival	Peakday	-0.001 (0.002), P = 0.53	25.89
Body mass	Axis 1	0.812 (0.346), P = 0.02	**519.13**
Body mass	October precipitation	-0.001 (0.011), P = 0.96	524.50
Body mass	Petgreen	0.013 (0.006), P = 0.04	520.04
Body mass	Petsenes	0.024 (0.021), P = 0.26	523.23
Body mass	Peakday	0.004 (0.555), P = 0.83	524.43

This table points to the conclusion that well defined variables are indeed easier to interpret but comes with the risk of being less general. The three variables tested are green up date, senescence date, and peak date calculated after Pettorelli et al. (2005). In our case, one local variable competes with Axis 1 but it is not the same for body mass (Petsenese) and survival (Petgreen). Axis 1 is the best or second best variable for both response variables.

2-S4: Technical description of the Functional Principal Component Analysis

Let y_{ij} be the NDVI value measured in the i-th sampling unit ($1 < i \leq n$) for the j-th week ($1 < j \leq p$). To compare NDVI curves by FPCA, these discrete values (y_{ij}) should be converted to a function x_i with values $x_i(t)$ computable for any value t. This step involves a smoothing procedure that requires defining a set of functional primary elements (basis functions) and then to set up a vector, matrix, or array of coefficients to define the function as a linear combination of these basis functions. Hence, the complete procedure consists in three main steps: 1) Definition of the basis functions, 2) smoothing of the observed curves, and 3) summarizing the variation in the curves. To define the basic functions, one uses a set of functional building blocks (basis functions) ϕ_k, $k = 1, \dots, K$ which are used to define a function $x_i(t)$ as linear combination:

$$x_i(t) = \sum_{k=1}^{K} c_{ik}\phi_k$$

We used cubic (i.e. four order) B-splines (i.e. piecewise polynomials of degree three) with 36 breakpoints so that K=38 (number of interior breakpoints + order). Second, to smooth the observed curves, one approximates discrete data from the function using a roughness penalty approach. The aim is to construct a model $y_{ij} = x_i(t) + \epsilon_{ij}$ so that the estimated curve gives a good fit to the data. In other words, we are looking for a coefficient vector $\mathbf{c}_i = \{c_{ik}, \dots, c_{ip}\}$ that minimizes the sum of square errors:

$$SSE(\mathbf{c}_i) = \sum_{j=1}^{p} \left(y_{ij} - x_i(t_j)\right)^2 = \sum_{j=1}^{p} \left(y_{ij} - \sum_{k=1}^{K} c_{ik}\phi_k\left(t_j\right)\right)^2$$

When K is high, this procedure tends to overfit (or undersmooth) the data. The roughness penalty approach solves this problem by imposing smoothness by penalizing some measure of function complexity. For instance, we used the integrated squared second derivative as penalty term ($PEN_2 = \int [D^2 x_i(t)]^2 dt$) so that the model fitting leads to minimize $SSE(\mathbf{c}_i) + \lambda \cdot PEN_2$. The smoothing parameter λ was set to 1. Finally, to summarize the variation between the smoothed curves, we now replace the original data with the *n* functions $x_i(t)$ representing the temporal evolution of NDVI for the different sampling units. As in standard PCA, data are centred ($z_i(t) = x_i(t) - \bar{x}(t)$, where $\bar{x}(t)$ is the functional mean) so that FPCA will focus on deviations to the average trend. FPCA seeks for a function $\xi_1(t)$ maximizing:

$$\mu_1 = \frac{1}{n}\sum_{i=1}^{n}\left(\int \xi_1(t) z_i(t) dt\right)^2 \text{ with } \int \xi_1(t)^2 dt = 1$$

In FDA terminology, $\mu_1$is the first eigenvalue and $\xi_1(t)$ is the first weight function (or harmonic) that describe the major variational component. The principal component scores (i.e., positions of the sampling units on FPCA axes) are given by $\int \xi_1(t) z_i(t) dt$. Hence, FPCA finds a score for sampling units, linear combination of smoothed curves with maximal variance (i.e. that reveals the most important types of variations among the curves). As in standard PCA, subsequent eigenfuctions $\xi_2(t)$, $\xi_3(t)$, $\xi_l(t)$ (associated to eigenvalues $\mu_2 > \ \mu_3 > \mu_l$) maximize the same criterion with an additional constraint of orthogonality:

$$\int \xi_l(t) \xi_k(t) dt = 0 \text{ for } k \neq l$$

2-S5: R code for Bayesian Hierarchical data analysis

Model specification using JAGS language used to produce Figure 3, 4 and 5.

```
model

{

# Variable definition
# N : number of site and year estimates of overwinter
survival (integer)
# Y : observed overwinter survival, arcsin-square root
tranformed (covariate)
# GMU : categorical variable (range from 1 to 13)
# mass : body mass of female fawns in late autumn
# winP : average winter precipitation in November –
December
# axis1 : first axis scores of the functional PCA
# axis2 : second axis scores of the functional PCA

# Estimated parameters are alphas (from 1 to 13, plus
alpha_mass) and betas (from 1 to 6)

     for(i in 1:N) {

             Y[i] ~ dnorm(mu[i], tau)
 # Declare response variable as normal
 #for survival

 # Direct effects of body mass, winter precipitation, axis
1 and axis 2 of the functional PCA.
          mu[i] <- alpha[GMU[i]] + beta1 * mass[i] + beta2
* winP[i] +
                             beta3 * axis1[i] + beta4 *
axis2[i]


                 mass[i] ~ dnorm(mu_mass[i], tau_mass)
# Declare response variable

# for body mass

                 # Indirect effects of NDVI on body mass
```

```
                mu_mass[i] <- alpha_mass + beta5 *
axis1[i] + beta6 * axis2[i]

     }



         # From dispersion to standard deviation
     sigma <- 1 / sqrt(tau)

     sigma_mass <- 1 / sqrt(tau_mass)


        # Declare non-informative priors
        tau ~ dgamma(0.001, 0.001)

        tau_mass ~ dgamma(0.001, 0.001)

        for (j in 1:J){

       alpha[j] ~ dnorm(0.0, 1.0E-6)

     }

        alpha_mass ~ dnorm(0.0, 1.0E-6)

        beta1 ~ dnorm(0.0, 1.0E-6)

        beta2 ~ dnorm(0.0, 1.0E-6)

        beta3 ~ dnorm(0.0, 1.0E-6)

        beta4 ~ dnorm(0.0, 1.0E-6)

        beta5 ~ dnorm(0.0, 1.0E-6)

        beta6 ~ dnorm(0.0, 1.0E-6)
```

CHAPTER 3: GENERALITY AND PRECISION OF REGIONAL-SCALE SURVIVAL MODELS FOR PREDICTING OVERWINTER SURVIVAL OF JUVENILE UNGULATES[2]

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INTRODUCTION

Interest in improving ecological prediction has recently surged because of the growing need to project the effects of land use and climate change (Mouquet et al. 2015). In wildlife ecology and management, prediction has played an increasingly important role, for example in predicting the spatial location of suitable habitat for species reintroductions (Mladenoff et al. 1999, Boyce and Waller 2003), identifying spatial human-wildlife conflict areas (Bradley and Pletscher 2005), predicting spatial wildlife-vehicle collisions (Hurley et al. 2009), nutritional condition and pregnancy of ungulates (Cook et al. 2004), spatial models of wolf abundance (Rich et al. 2013), and spatial nest success and survival of birds based on habitat (Aldridge and Boyce 2007). Wildlife applications have commonly focused on developing technology for spatial predictions, while rigorous attempts to predict population dynamics and harvest are limited (Jenouvrier et al. 2009). An exception is perhaps the much-lauded North American waterfowl program that formally integrates predictions about population size into an adaptive harvest management framework (Nichols et al. 2007).

While there have been some attempts to formally predict future population dynamics in harvested ungulates with statistical models (Freddy 1982, Peek et al. 2002, White and Lubow 2002), prediction is rare in the population management of ungulates, although the relevance to state wildlife agencies for harvest management programs is undeniable. One challenge in development of predictive statistical models for survival is the complexity of dealing with integrating survival data across populations that are hierarchically structured in space and time (e.g., Lukacs et al. 2009). As wildlife survival studies have increased scope and spatial range, pooling data across multiple populations has increased model complexity from single season, single population models (Bartmann and Bowden 1984, White et al. 1987), to populations across multiple years, populations and ecological regions (Griffin et al. 2011, Brodie et al. 2013). The recent growth of hierarchical modeling in ecology has furthered the use of Bayesian methods for wildlife ecologists to enable the development of spatially structured, hierarchical and flexible statistical models (Royle and Dorazio 2006, Kery and Schaub 2012). Bayesian models are inherently well-suited to prediction as well, with many recent examples in the ecological and wildlife literature about prediction of spatially and temporally hierarchical phenomenon such as epidemiology, animal movements and population ecology (Heisey et al. 2010a, Geremia et al. 2014, Mouquet et al. 2015). A remaining challenge in prediction is that not all models can be all things to all needs at all times. Levins (1966) was amongst the first ecologists to point out that modeling of any sort inherently requires trade-offs between variance/precision, bias, and generality (the ability of a model to predict accurately across a range of conditions) and that any model cannot maximize all three.

In most recent wildlife survival analyses, the best model is usually selected using a model selection criterion, such as a maximum-likelihood (e.g., Akaike Information Criteria, AIC) or a Bayesian (e.g., BIC, DIC) approach (Barker and Link 2015). The entire purpose of model selection methods is hence to select the best statistical model that approximates performance in out-of-sample prediction. Unfortunately, evaluating future predictions with independent data is rarely done, but is needed to produce robust predictive models. Some researchers (Franklin et al. 2000, Frair et al. 2007, Hebblewhite and Merrill 2011) have evaluated the predictive performance of climate or habitat-based ungulate survival models using data that were used to build the statistical model, essentially model goodness-of-fit, but not with out-of-sample data sets. Assessing the predictive power of a model in this fashion, however, often provides an optimistic view of the model's forecasting ability (Hastie et al. 2001). This lack of external validation is undoubtedly because of the expense and difficulty in collecting survival data.

Survival is especially difficult to measure in the field, but the ability to predict future survival of ungulates would greatly improve population dynamics modeling and thereby, management prescriptions of harvested populations. Vital rates have varying importance to populations. For example, juvenile survival often drives population dynamics for large and long-lived species because it is the most variable rate in space and time (Gaillard et al. 2000). This life-history model has prompted wildlife managers to prioritize juvenile survival and recruitment monitoring as a means to predict changes in ungulate population dynamics (White and Bartmann 1998b, Morellet et al. 2007, Lukacs et al. 2009). Unfortunately, for many species affected by overwinter juvenile survival, estimates are not available until after harvest regulations are developed. Thus, wildlife managers do not have the information needed at the time of season setting to make the best management decisions (Figure 3-1). It would be ideal if wildlife managers had some reliable way of predicting future overwinter survival based on other drivers of survival, such as weather variables or habitat characteristics, without the need to capture and monitor animals.

As a test case, we used a unique data set of mule deer juvenile survival in Idaho to evaluate the predictive performance of large-scale survival models, from simple to complex, with the ultimate objective of integrating them into harvest management policies. We aimed to test the predictive performance of overwinter survival models for mule deer fawns subjected to a large range of habitat quality, climate and predation regimes in Idaho. We evaluated both model fit (within sample or internal validation) to identify the main drivers of survival and to assess our capacity (out-of-sample or external validation) to develop a model that best predicts survival from these drivers. Our goal was to develop predictive models based on readily available climate and forage productivity covariates that would enable wildlife managers to predict overwinter survival, and thus population dynamics and harvest, without having to radiocollar juveniles.

First we develop models to estimate survival based on freely available remote sensed weather data. We developed hierarchical Bayesian (H-B) survival models (Lukacs et al. 2009, Kery and Schaub 2012) that integrate spatial and temporal variation in summer and winter weather (Hurley et al. 2014), across 11 years and 11 population management units for mule deer. These models include individual body mass because of the overwhelming importance of body mass to overwinter survival in juvenile mule deer repeatedly reported (Bartmann et al. 1992, Unsworth et al. 1999, Bishop et al. 2009, Hurley et al. 2011, Hurley et al. 2014). We then remove body mass to build predictive models that do not require animal capture to evaluate the loss of information without mass. We expanded upon Hurley et al. (2014) by measuring snow cover (MODIS SNOW) and depth (SNODAS) during three winter periods, early winter (November – December), winter (January – March) and late winter (April). Increased snow values in each of these periods should increase energy expenditure and thereby deplete stored fat, thus decreasing survival. We also incorporate the effect of previous growing season with functional analysis of NDVI (Hurley et al. 2014) to evaluate the effect of early and late season nutrition, which should positively correlate with subsequent winter survival.

Second, to test the predictive capacity of large-scale survival models, we conduct both within and out-of-sample validation. We evaluated predicted population-level survival using in-sample cross-validation (internal validation) by comparing modeled survival with a non-parametric Kaplan-Meier survival (Kaplan and Meier 1958) estimated with the same empirical data. We use Kaplan-Meier as a base for this comparison because it is a widely used metric of survival estimation in wildlife management agencies and, being non-parametric and non-distributional, is the simplest descriptive estimator for survival.

We then validated our best empirical models with out-of-sample data to reliably predict overwinter survival for years not used to fit the model. We test the ability of each of these models to make predictions across populations and years to evaluate the precision/generality trade-off in relation to complexity. Specifically, we hypothesized that if climate-alone drives overwinter mule deer fawn survival, then models of survival only based on climate covariates should reliably predict observed survival across populations. Alternately, if unmeasured variables, such as predation or habitat quality, play a crucial role, not including habitat-climate interaction should weaken the predictive capacity of climate-only survival models. Therefore, we subset our regional survival model into three ecotype-specific survival models to test if both predictive performance and predictors of survival differed at the regional and ecotype levels (Hurley et al. 2014).

STUDY AREA

Our study area covered a wide climatic, predation and habitat gradient of mule deer range in Idaho. We monitored overwinter survival of fawns in 11 Population Management Units (PMU) across central and southern Idaho that were themselves comprised of 28 different Game Management Units (GMU's; Figure 3-2). In Idaho, GMUs are nested within PMU's that are grouped together to represent ecological (interbreeding) populations, which form the basis for management. Through a hierarchical cluster analysis we classified GMUs into three groups and identified common habitat characteristics of these groups (called ecotypes hereafter) based on the dominant canopy species on summer range; coniferous forests, shrub-steppe, and aspen woodlands (Figure 3-2; Appendix B Figure 3-S1). We then assigned the PMUs to an ecotype classification based on the classified GMUs. GMUs within PMUs were of the same ecotype with the exception of one PMU, Mountain Valley, subsequently split into respective shrub and conifer ecotypes for analysis (Figure 3-2). Elevation and topographic gradients within PMUs affect snow depths and temperature in winter, and precipitation and growing season length in the summer, with elevation increasing from the southwest to the northeast. Areas used by mule deer in the winter in conifer ecotypes ranged in elevation from 1001 to 1928m, but most were <1450m. Winter precipitation (winter severity) varied widely (from 10 to 371mm) in coniferous GMUs. Coniferous ecotype summer ranges are dominated by conifer species interspersed with cool season grasslands, sagebrush, and understory of forest shrubs. Semi-desert Shrub-steppe PMUs ranged from 1545 to 2105m, with winter precipitation from 24 to 105mm. Summer range within shrub-steppe ecotypes was dominated by mesic shrubs [e.g., bitterbrush (*Purshia tridentata*), sagebrush (*Artemsia* spp.), rabbitbrush (*Chrysothamnus* spp.)]. Aspen ecotype PMUs were located in the east and south with winter use areas ranging from 1582 to 2011m, with two of the three PMUs above 1700m with winter precipitation ranging from 25 to 146mm. In summer, productive mesic aspen (*Populus tremuloides*) woodlands were interspersed with mesic shrubs.

METHODS

(a) Capture and Survival Monitoring

We modeled survival probability of 2,529 fawns within 11 Population Management Units in southern Idaho, 2003–2013 (Table 3-S1). We varied capture methods depending on winter range density of deer. In concentrated winter ranges, we used helicopters to herd deer into drive nets as our primary capture method (Thomas and Novak 1991), but in dispersed winter ranges we captured fawns with a netgun fired from a helicopter (Barrett et al. 1982) or clover traps (Clover 1954). Fawns were physically restrained and blindfolded during processing with an average handling time of < 6 minutes. Two types of radio-collars were used: expandable collars (Telonics model 500 with CB-5 Telonics Inc. 932 E. Impala Avenue, Mesa, AZ) and belt collars (Lotek model LMRT-3, Lotek Wireless Inc., 115 Pony Drive Newmarket, Ontario Canada). Collars weighed 320–400 grams, were equipped with mortality sensors, and fastened with temporary attachment plates or surgical tubing allowing the collars to fall off the animals after approximately 8–10 months. We measured fawn mass to the nearest 0.4 kilogram with a calibrated spring scale to assess early winter body size and condition. An Idaho Department of Fish and

Game (IDFG) veterinarian or veterinary technician was on site during most captures to assist with sampling and assure animal welfare. Animal capture protocols were approved by the Animal Care and Use Committee, IDFG Wildlife Health Laboratory, Caldwell, Idaho, USA, and University of Montana IACUC (protocol #02-11MHCFC-031811). Fawns were monitored with telemetry for mortality from the ground every 2 days between capture and 1 June. If radio signals could not be detected from the ground within 1 week, animals were located via aircraft. When a mortality signal was detected, the fawn was located and cause of death was determined using a standard protocol (Wade and Bowns 1982). Animals that lost radio-collars or with radiocollars that failed were removed (censored) from the analysis at the point of failure.

(b) Defining Seasons and Herd Unit Home Ranges

Because we wanted to associate individual deer to the weather and spatial covariates associated with its seasonal range, we estimated within-GMU level seasonal ranges across all 11 PMU's (Figure 3-2). Deer were captured within each PMU in each primary winter range within a GMU (range 1–6 different winter ranges) in proportion to the distribution of deer and abundance (*IDFG unpublished data*) in each GMU within the PMU. To exclude migratory periods from the seasonal home range estimates we only used locations between 1 June and 30 September for summer ranges and between 1 December and 31 March for winter ranges (Sawyer et al. 2005). We created combined seasonal 95% kernel density utilization distributions using a bandwidth of H = 0.05 to minimize the inclusion of unused habitat (Worton 1989). We used all telemetry and mortality locations collected, 1999–2013 (median = 96, range = 21 to 876) to create winter and summer utilization distributions for each GMU in the study areas. Climate and habitat information was then summarized within the seasonal home ranges of radio-collared deer for winter and summer within each GMU, the basis of the spatial covariates.

(c) Survival Variable Development

Individual covariates

Previous studies in Idaho reported only little between-sex differences in overwinter survival of mule deer fawns (Unsworth et al. 1999, Bishop et al. 2005a, Hurley et al. 2011). In contrast, the overwinter survival of mule deer fawns strongly increases with their body mass (Hurley et al. 2011). Thus, we included body mass (kg) of mule deer fawns at capture, as the only individual covariate for comparison purposes.

Spatial forage and weather covariates

We used remotely sensed and modeled measures of summer plant productivity [Normalized Difference Vegetation Index, NDVI (Pettorelli 2013)] and winter snow conditions (Snow cover and SNODAS) as spatial covariates for assessing the effects of climate and habitat on fawn winter survival. We chose remotely sensed spatial measures of these covariates because remotely sensed data are spatially explicit and generally available to wildlife managers with a shorter delay than PRISM data, allowing a rapid integration into harvest management programs.

We calculated NDVI from 16-day composite MODIS (Moderate Resolution

Infrared Spectroscopy) obtained from the MOD13Q1 NASA (250m^2) data product (from the NASA Land Products Distributed Active Archive Center LPDAAC, https://lpdaac.usgs.gov/) (Huete et al. 2002). Radiometric sensor anomalies, atmospheric effects, cloud contamination and geometric registration accuracies were corrected using a simple temporal interpolation method (Zhao et al. 2005). We used a minimum NDVI threshold value of 0 to define periods of little to no photosynthetic activity, and filtered pixels containing ice and snow data flags from the analysis. Since phenological changes in NDVI directly represent ungulate forage dynamics only in non-forested vegetation types, we extracted NDVI values from only open canopied grass and shrub vegetation types (not burned within five years), which we characterized using SAGEMAP land cover data (2005 USGS, Forest and Rangeland Ecosystem Science Center, Snake River Field Station, Boise, ID, USA, described in the supplemental materials). We also restricted NDVI data to 15 March to 15 November to encompass the entire growing season for each population-year, and excluded winter anomalies caused by varying snow conditions.

We then used a Functional Analysis to assess the shapes of the growing season curves for each population-year according to the methods of Hurley et al. (2014). However, unlike Hurley et al. (2014) who performed this Functional Analysis on NDVIg from the AVHRR (Advanced Very High Resolution Radiometer) / NDVI gimms dataset (Zeng et al. 2013) from 1998-2011, here we used MODIS NDVI. This was because MODIS NDVI is available at a finer resolution (250m) than AVHRR and is available to present, where the NDVI gimms dataset ends in 2011, allowing us to include additional data. Functional analysis was based on a multivariate functional analysis of variation in observed NDVI curves of NDVI values over time. We used the first two principal component scores of the NDVI curves, which accounted for 74% of the variance and could be interpreted as a measure of annual fall (post NDVI peak) and spring plant growth (early growing season). Each of the remaining three other PC scores accounted for 10% or less of the variance and provided little additional information to explain the NDVI phenology curves.

To measure winter snow cover, critical for determining energy expenditure and limiting access to forage, we used two different remotely sensed snow products from the MODIS satellite platform, and the Snow Data Assimilation System, SNODAS (Hall et al. 2002, Barrett 2003). The MODIS (MOD10A2) snow data product measures complete snow coverage in 8-day composites at a 250m resolution. We measured snow cover during three winter periods, early winter (November – December), winter (January – March) and late winter (April), in two different ways. First, we estimated the percentage of each winter period each pixel was covered by snow as a measure of fractional snow cover. Second, we used the number of weeks > 90% of the winter use area was covered by snow. As another measure of snow effects on survival, we used two measures of SNODAS, which predicts snow depth at 1km^2 daily resolution. SNOWDAS is a numeric model prediction based on air temperature, relative humidity, wind speed and precipitation downscaled from broad 13km^2 scales to the 1-km^2. The two measures were average depth during the period and the cumulative daily measures through the period. The final variables for the survival models included the following remotely-sensed variables; functional analysis principal components for fall (FPC), functional analysis principal components for spring (SPC), mean % snow cover in November and December (ND%snow), mean % snow cover in

January to March (W%snow), mean % snow cover in April (A%snow), number of weeks with >90% snow cover in November and December (FWeeks), number of weeks with >90% snow cover in January to March (WWeeks), number of weeks with >90% snow cover in April (AWeeks), average and cumulative snow depth in November and December (FDepth, FCum), average and cumulative snow depth in January – March (WDepth, WCum), average and cumulative snow depth in April (ADepth, ACum).

Our goal was to develop a small set of predictive covariates and because these covariates were derived from similar data sources, we expect them to be highly correlated. Ideally we wanted to keep the best predictive covariate from each period. To accomplish this, we screened all covariates for collinearity and retained the individual covariates of collinear pairs with significant relationship ($P < 0.05$) to simple discrete time, known-fate models of overwinter fawn survival. Using these two criteria, we removed seven covariates from our analysis and retained seven spatial covariates ecologically related to mule deer ecology and survival; FPC, SPC, ND%snow, W%snow, A%snow, FWeeks, and WDepth. None of the retained seven covariates had a correlation coefficient > 0.7 (Appendix B, Table 3-S2).

(d) Survival Modeling

We used Bayesian hierarchical survival models (Royle and Dorazio 2006, Kery and Schaub 2012) to estimate overwinter fawn survival from 16 December to 1 June, including covariates at the appropriate spatial and temporal resolution for each hierarchical level: individual, seasonal range (GMU, j=1….j), and Population

Management Unit (PMU, k=1…k; Figure 3-2). We treated survival in a known-fate (with detection probability = 1 with radio-collars), discrete-time formulation (Murray and Patterson 2006) in 24 weekly (7-day) intervals from 16 December to 1 June, and accommodated left and right staggered entry (capture) and exit (mortality, censor) common in wildlife studies (Pollock et al. 1989). Overwinter survival was estimated as the product of each weekly interval, seasonal study area, and PMU following the discrete-time survival paradigm using a generalized linear model with a logit-link function following:

$$logit\left(\widehat{\emptyset}_i\right) = \mu + \varepsilon_i \qquad \text{Eq. 1}$$

where $logit\left(\hat{\phi}\right)$ is the overwinter survival (0, 1) of individual mule deer i=1…n that is a function of a linear combination of covariates (see Eq. 2 for how we specify covariates), μ, and Bernoulli distributed error ε. Here, we added hierarchical structure to the survival estimator with different covariate effects hypothesized to manifest at the individual GMU by season and PMU levels. First, we considered body mass in full models by adding the individual body mass for each individual mule deer to Eq. 1. This provided us with a way of measuring the difference in predictive performance between models with and without body mass. Next we considered the hierarchical spatial structure of seasonal ranges nested within PMUs using hierarchical random effects (Lukacs et al. 2009, Zuur et al. 2009). We considered a fixed-intercept difference in survival between GMUs to be nested within a random-intercept difference in survival at the PMU level. We chose to place the random intercept at the PMU, not GMU level because ostensibly spatial forage and weather covariates were already incorporated at the GMU level, but a random intercept at the PMU level allowed for the effect of these GMU-level covariates to vary across PMUs

(Zuur et al. 2009). Next we included a random intercept for year to allow for temporal variation. We then included a combination of our spatial climate covariates measured at the seasonal-range (GMU) scale. Finally, some covariate effects likely differed between GMUs in a manner consistent with random coefficients. However, because of computational difficulty, we only explored one random coefficient at a time in models for the strongest covariate measured by effect size and precision. Thus, the most complex formulation for our hierarchical survival model was:

$$logit(\,\hat{\phi}_{ijk|t}) = \beta_{0j} + \zeta_{0t} + \zeta_{0k} + \beta_1 Mass_i + \left[\mathbf{BX}_{\boldsymbol{ij}}\right] + \zeta_{1k} * x_{ij} + \varepsilon_{ijk|t}$$

Eq. 2

where $\hat{\phi}_{ijk|t}$ is survival of individual mule deer i=1…n in seasonal GMU area j=1…j in PMU k=1…k in year t=1…11 and μ in Eq. 1 = $\beta_{0j} + \zeta_{0t} + \zeta_{0k}$ that we define here; β_{0j} is the fixed-effect (intercept) of each seasonal range at the GMU level; ζ_{0t} is the random intercept of year t; ζ_{0k} is the random intercept of PMU; β_1 is the coefficient of individual body mass; $\left[BX_{ij}\right]$ is the vector of seasonal range-level spatial climate covariates (FPC, SPC, W%snow, etc.) at GMU j; ζ_{1k} is the random coefficient (slope) at the PMU level on the GMU-level covariate x_{ij}; and $\varepsilon_{ijk\vee t}$ is the error at the level of individual, GMU and PMU in year t. We assumed all random effects were distributed with mean equal to zero and unknown variance, e.g., ~ Normal(0, σ^2).

As a final step to estimating unbiased PMU-level survival, $\hat{\phi}_{k\vee t}$, for evaluation of predictive capacity at the PMU-level, we applied a weighting scheme to the estimate obtained with Eq. 2 to weight GMU-level sampling variation in sample sizes according to the estimated mule deer population size (IDFG, unpublished data, Chapter 5) at the PMU level. Thus, we estimated $\hat{\phi}_{k|t}$ following:

$$\hat{\phi}_{k|t} = \frac{\widehat{n_j}}{n_k} * \hat{\phi}_{ijk|t} \qquad \text{Eq. 3}$$

where n_j = the number of individual mule deer in GMU j (Chapter 5) that is nested in PMU k.

We fit Bayesian hierarchical survival models with JAGS (Plummer 2003) using a Metropolis-Hastings Gibbs Markov chain Monte Carlo algorithm (Gelman et al. 2014). We used non-informative prior distributions for all covariates in Eq. 2 and centered and scaled (e.g., standardized) all covariates with mean = 0. We ran each model across three different chains for 20,000 iterations each, with a burn-in of 5,000 iterations (Plummer 2003, Gelman et al. 2014), and obtained posterior distributions, means and medians for all estimated parameters.

(e) Model Development

Taking advantage of our unusually large sample sizes, we relied on out-of-sample predictive performance for model selection. We also calculated commonly used metrics including the Deviance Information Criteria (DIC), the mean Deviance (over all retained simulations) and the pD, a Bayesian measure of the effective number of parameters (Gelman et al. 2014). Thus, for each model, we report cross-validation R^2_{CV}, the out-of-sample external validation R^2_{EV}, DIC, Deviance and pD, but strongly favored R^2 diagnostics for model selection.

We developed a limited candidate set of models considering both summer and winter seasons for a total of 13 models. We developed models for all animals in the data set (hereafter overall models), and then partitioned the animals by ecotypes (i.e. ecotype models for aspen, conifer and shrub-steppe included only data from those PMUs within each ecotype). We also developed two models (early prediction) using data available prior to 1 January to assess our ability to predict survival prior to winter, one with a random effect of FWeeks and one without. For candidate model development, we first fit a model with all seven covariates (including mass, herein called the full model). We then removed mass to evaluate a set of prediction-only models. From the full model without mass we proceeded to remove the least informative parameters, based on credible intervals overlapping 0 and effect size of the standardized covariates, in a purposeful backward stepwise fashion (retaining each successive model) until reaching a reduced model where all parameters were highly informative (Gelman et al. 2014). Because of the high diversity of the climate and of the habitat across our study area, we then added a random effect (coefficient) for slope for each of the covariates identified in the reduced model as the most informative parameters (only one for each model) to the full models and reduced models. Random effects of covariates were not applied to ecotypes models because covariate effects were expected to be similar within ecotypes. Our final step was to predict survival with data collected prior to 1 January as a truly predictive model for practical use in the harvest season setting process. We evaluated early prediction models comprised of the most important covariates identified during overall model development.

(f) Evaluating the Precision, Accuracy and Generality of Survival Models

We evaluated models using both internal validation and external validation for our overall set of models, prediction-only models (e.g., no body mass), and ecotype models (Hastie et al. 2001). We considered internal validation as a measure of the model's goodness-of-fit and external (e.g., out-of-sample) validation as the strongest measure of a model's generality, accuracy and precision (Hastie et al. 2001), as well as the ultimate model selection diagnostic (Hooten and Hobbs 2015). We first predicted the expected survival for each animal given a set of covariates using Eq. 2, using all data for internal cross-validation. We conducted internal validation for all models (overall, ecotype, etc.). Second, we conducted external validation withholding all survival data for 2007 and 2008 to estimate predictive performance. We did not externally validate ecotype models due to small sample sizes, but compared ecotype models' internal validation to our overall models to evaluate if using finer-scale ecotype models would increase explanatory power of survival models.

We compared predicted survival rates from each Bayesian survival model against observed survival rates within each year and PMU. Observed survival rates were estimated using the simple non-parametric, non-distributional Kaplan-Meier (K-M) estimator (Kaplan and Meier 1958):

$$\widehat{S_{t,k}} = \prod_{i=1}^{t,k} \left(\frac{n_i - d_i}{ni}\right) \qquad \text{Eq. 4}$$

and $\hat{S}_{t,k}$ is the estimated survival of mule deer in year i=1…t, and PMU k=1…k, n_i is the number of animals starting each weekly interval, d_i is the number of deaths, and the product of the weekly survival rates provides the non-parametric estimator of survival.

We used Pearson's correlation coefficient between observed and predicted survival to estimate precision (R^2). We also assessed the bias of the regression between observed and predicted (i.e., a slope of 1 indicates equality of both) using spline curves. The JAGS code for our hierarchical survival models is presented in Appendix B (Table 3-S4).

RESULTS

(a) Observed survival

We captured and monitored a total of 2,529 fawns, averaging ~ 30 fawns/year/PMU (range 14 to 75) per year from 2003–2013 to develop survival models (Appendix B, Table 3-S1). Statewide survival of fawns ranged from 0.32 (SE = 0.032) to 0.71 (SE = 0.034) during 2003–2013, and mean survival for all years varied across PMUs (Figure 3-2b; Appendix B, Table 3-S1, for PMU-year specific KM estimates).

(b) Covariate and random effects for overall model

Male fawns were heavier than females (mean = 37.1 kg vs. 34.2 kg, $t = -13.1$, $P \leq 0.005$) and survival increased with mass in the full overall Bayesian survival model (standardized coefficient, $\beta = 0.457$, SE = 0.037). In our overall models, winter survival increased with higher fall plant productivity later in the fall (Figure 3-3, Appendix B, Table 3-S2). Higher snow cover during January through March and higher number of weeks in autumn with >90% snow cover both decreased fawn survival (Figure 3-3, Appendix B, Table 3-S2). Survival also increased with higher spring functional analysis values but this effect was more variable between models than the effects of plant productivity in fall (Figure 3-3, Appendix B, Table 3-S2) and thus SPC was not included in the final model. Winter snow depth and snow cover in April had minimal relationship to winter fawn survival for the overall models (Figure 3-3, Appendix B, Table 3-S2).

The high spatial heterogeneity of the study area was highlighted by the strength of both random intercepts and random slopes (Figure 3-2c, Appendix B, Table 3-S2). There was support for variation between PMUs in overall survival and also in the effects of winter on survival (Table 3-1, Figure 3- 4) as all the top five models in terms of internal validation included random slopes of one other most influence top three covariates (Table 3-1). However, these models add complexity and parameters thus were not considered amongst the top models according to DIC or validation diagnostics. Covariate effects also varied considerably across PMUs. For example, the influence of winter snow cover on survival varied across PMUs, with the strongest influence in the high elevation southeastern PMUs and least in the low elevation western PMUs (Figure 3-2c**).**

(c) Overall survival model validation, prediction, and complexity

Ranking overall survival models using internal validation, external validation or DIC produced contrasting perspectives on what is the ‘best’ model. The best-supported overall survival model in terms of internal explanatory capacity ($R^2cv = 0.814$) was a model including all covariates (excluding body mass) with a random effect (slope) for winter percent snow cover (Table 3-1, Figure 3-4). If we were to rank models using DIC, however, a model with all covariates including mass was most supported (Table 3-1), despite the substantially lower explanatory capacity ($R^2cv = 0.695$).

Overall model predictions correlated well with the Kaplan-Meier survival estimates for the external validation, when 403 mule deer fawns from 2007-2008 were left out (Figure 3-5). Although the highest R^2_{CV} was obtained with the most complex model with a random effect of snow cover in winter, the R^2_{EV} was substantially lower when these two validation years were including in the re-parameterization of this top model (Figures 4 & 5, $R^2 = 0.814$ for all years vs. 0.698 with 2007 and 2008 excluded and predicted). Without mass included, the most parsimonious model with the highest external predictive power ($R^2_{EV} = 0.704$) was a function of three covariates, winter percent snow cover, fall NDVI, and the number of weeks with complete snow cover in November and December (Table 3-1, Figure 3-5). The most supported early prediction model (only covariates before 1 January) included three covariates with a random slope for Fall Weeks with > 90% snow cover with high explanatory capacity ($R^2cv = 0.818$), but low external predictive power ($R^2_{EV} = 0.590$).

The reduced model produced a slightly lower R^2 (0.785) between KM and modeled estimates, suggesting a trade-off between generality and precision when predicting survival. Although, the R^2 of the model fit must increase as covariates are added, the opposite was true in the validation (Figure 3-4 vs. 3-5). Validation of these models suggested that the best performing model in terms of predictive power was not necessarily the best explanatory model. Interestingly, the top model that did not include mass ranked by DIC was also the best non-random effects survival model to successfully predict out-of-sample mule deer survival (Figure 3-5). Our most parsimonious model predicted better than the more complex models, likely due to overfitting the data with the additional parameters included by DIC. This suggests that for generality of true prediction, the more complex models were becoming more and more overfit. Thus, the absolutely best model from an external validation and prediction perspective in this case was the simplest function of three covariates (model 2 in Table 3-1).

(d) Ecotype survival models and covariate effects

Model selection results were similar among vegetative ecotypes as the top models from a DIC perspective in all ecotypes were the full models including mass (Table 3-2, Figures 3-3 to 3-6). In the aspen ecotype, there was a perfect correspondence between the ‘best’ model selected from a traditional DIC perspective and the internal validation (Table 3-2). However, the best model from DIC in the conifer ecotype had the poorest predictive performance. The overall predictive performance of the shrub-steppe models was lower than conifer or aspen, and the top predictive model had two fewer covariates than the best-selected model from DIC. The covariate effect of body mass was similar in each ecotype model where it was retained in to the overall survival model reported above; β= 0.504, SD = 0.071 in aspen, β= 0.429, SD = 0.046 in conifer, and β= 0.397, SD = 0.095 in shrub-steppe. Mass only improved predictive performance for aspen. Inclusion of mass in conifer resulted in the worst predictive performance, and in shrub-steppe, mass reduced prediction again. The models we would select to predict ecotype survival without mass would be model 5 in aspen with two covariates; model 5 in conifer, and model 1 in shrub-steppe (Table 3-2).

Models without mass had equivalent predictive performance as other, more complicated models (e.g., R^2_{CV} of 0.859 for aspen model 2 with seven covariates versus R^2_{CV} of 0.853 for the two covariate model). Internal validation R^2_{CV} of all aspen models were > 0.851, suggesting an improved fit over the most parsimonious overall model (Table 3-1, Figure 3-4). The best internally validated model for conifer ecotype was the full model, excluding Mass (Table 3-2, Figure 3-6). This conifer model explained 0.803 of the variance in overwinter fawn survival. The best internally validated model for shrub-steppe was the 6-covariate model, excluding Mass and WDepth, accounting for 60.4% of the variance (Table 3-2, Figure 3- 6). The effect of summer range quality did not have the strength in ecotype specific model as in the overall likely due to similar values within the ecotype, whereas winter snow conditions will be more site-specific. Our prediction of lower performance in more carnivore-driven systems is supported by both the lower R^2 of the top conifer model than the aspen and our survival prediction consistently biased low when predicting high survival in the conifer models versus the aspen models.

DISCUSSION

By combining Bayesian hierarchical survival models with spatio-temporal data on forage and winter conditions derived from remote sensing, we successfully developed powerful explanatory mule deer survival models across most of the state of Idaho. This supports our general working hypothesis that climatic variation and primary production are the major determinants of juvenile mule deer overwinter survival. Our overall models were able to externally predict out-of-sample survival with R^2_{EV} values that ranged from 0.59 – 0.71 across time and space. This is a novel approach because there have been few if any tests of the predictive capacity of such a large-scale model to predict the survival of a key demographic trait for a harvested species. The modeling approach we advocated should enable wildlife managers to estimate the key vital rate of a population in a large range of ecological contexts. The first step should be to identify this critical vital rate. As recruitment is often the most important vital rate for ungulates (Gaillard et al. 2000), the key component should be either the summer or the winter juvenile survival. In mule deer, like in other ungulates living in northern temperate areas such as bighorn sheep (King et al. 2006, Eacker 2015), identifying the drivers of overwinter survival might allow reducing the need to capture and monitor ungulates annually. Instead, a monitoring system incorporating survival prediction with periodic monitoring for model calibration would save considerable funds with minimal loss in accuracy. Our most general survival model predicted overwinter survival of mule deer fawns through Idaho’s wide variety of vegetation, climate, and predator communities with easily obtainable remote-sensed data pertaining to vegetation quality and winter snow estimates.

The success of our approach based on Bayesian hierarchical models requires matching the spatial or temporal scale of covariates to the appropriate survival period (Heisey et al. 2010a, Heisey et al. 2010b, Heisey 2012). In this case we measured MODIS-based NDVI and snow covariates derived from MODIS and SNOWDAS products defined by the fawn habitat use in the population of interest in specific summer and winter ranges. In addition to these spatiotemporal remote sensing covariates, we also accounted for variation related to large-scale processes, such major vegetative differences through the use of random-effect terms for these unmeasured, but important, latent variables. PMUs in Idaho were developed from movement data of radio-collared animals representing putatively interbreeding populations that overlapped in their distribution on summer and fall ranges (Idaho Mule Deer Management Plan 2008). These PMU designations did not necessarily consider differences in vegetation quality, winter severity, and predation risk between specific summer and winter ranges. Allowing these effects to vary across winter ranges (GMU scale) within PMUs and across PMUs allowed covariates to account for the biological processes involved while minimizing the noise of inherent differences in PMUs. Our Bayesian hierarchical survival models provided an efficient means to capture this mix of measured and unmeasured drivers of overwinter fawn survival across scales.

The importance of scale to regional hierarchical models was best exemplified by the inconsistent importance of body mass in the survival models. Body mass is a very strong predictor of juvenile ungulate survival across a multitude of studies (Bartmann and Bowden 1984, Unsworth et al. 1999, Pettorelli et al. 2002, Bishop et al. 2009, Griffin et al. 2011, Hurley et al. 2014). Increased mass-at-capture strongly increased overwinter survival of mule deer fawns as expected. However, our best overall survival models that included mass (Table 3-1, models 9 and 11) had poorer predictive power than even our simplest survival models, accounting for ~ 10% less variation. We suggest this disparity is caused by spatial differences in vegetation quality and winter severity that were effectively captured by remotely-sensed measures of habitat. For example, fawn mass in the Palisades PMU was generally higher (39.5 kg, SE = 2.46) than elsewhere in the state because of high quality spring and summer range that also enabled higher body growth rates through the summer. However, winter snow cover and depth was often also the highest in this region (Figure 3-2b), resulting in high fawn mortality and overriding the benefit of higher mass arising from higher summer forage. In contrast, Boise River PMU fawn body mass was generally the lower (Male mean = 36.1kg, SE=1.52) because of poorer quality spring/summer forage and low precipitation. Despite these lower 'quality' fawns, the Boise River PMU experienced the least snow and mild winters; thus, perhaps counter-intuitively, survival was often high in this PMU without the low survival experienced in the higher elevation PMUs during severe winters. This contrast between summer and winter determinants of overwinter survival is interesting, but not ultimately why we think mass performed more poorly as a predictive covariate at our broadest scale of winter models. When averaging across different PMUs with high and low fawn body mass, body mass could not ultimately predict survival as well as PMU-level spatial and temporally varying covariates which ultimately drove differences in both starting body mass at the beginning of winter (e.g., summer forage) and the response, e.g., mortality or hazard rate of fawns in response to winter severity. This discussion also highlights that viability selection (Fisher 1930), whereby the lightest individuals are more likely to die either summer or winter, especially in lower quality habitat, may also be operating and another reason why body mass predicts individual overwinter survival well, but loses predictive strength at the population-level. Viability selection normally operates strongest on summer (neonatal) survival, reducing poor quality individuals before winter, but can also operate on the remaining cohort entering winter. Our weather covariates and the Bayesian hierarchical modeling framework will control for most of these differences, but extreme conditions may decouple the relationship when applied within the same model.

The importance of spatial variation in forage and winter snow cover influencing overwinter survival was also displayed in the top explanatory model (Table 3-1). This model included a random slope for winter snow instead of body mass, and accounted for the highest proportion of variance in our overall model set (R^2_{CV} =0.814). For example, in Boise PMU there was no effect of winter (Figure 3-2c), whereas in all the southeastern PMUs (e.g., Bannock, Caribou, and Palisades), the strength of the winter snow effect was nearly double that of those in the central conifer PMUs (Figure 3-2c, Central Mountains, Island Park, Smoky/Bennett, Weiser/McCall). We interpret that the random coefficient accounted for some of the variation at the PMU or GMU-level in the hazard rate caused by winter snow, which reflects spatial variation across PMUs in the realized effect body mass had on overwinter survival. For example, in the Bannock, Caribou, and Palisades PMUs, fawns with relatively high body mass often experienced greater overwinter mortality not because of a stronger effect of winter snow per se, but merely because of absolute winter severity, which was almost double the amount of snow as other PMUs (Figure 3-2c). However, even this random coefficient could not predict out-of-sample survival as well as the most parsimonious model that simply included the spatial variation in three key covariates directly. This discussion highlights that inferences from our Bayesian hierarchical survival models will vary depending on the scale of application, and also the challenges of interpreting random coefficients in complex models, again, emphasizing a parsimonious approach (Bolker et al. 2009, Zuur et al. 2009).

There was additional evidence in our survival modeling that ecotypes provided a biologically relevant scale for considering mechanisms affecting survival. Differences in snow cover between PMUs followed the ecotype divisions based solely on vegetation cluster analysis (Figure 3-2). This suggests that ecotype could be a strong driver of survival through nutrition or predator habitat and good partitioning metric. This is similar to a recent continental-scale synthesis of elk calf recruitment (which includes overwinter survival) reporting that ecotype differences accounted for more observed variation in recruitment than state-level or administrative boundaries (Lukacs et al. *In Review*). Moreover, in contrast to the overall mule deer survival models, body mass was included in the top ecotype models for all three ecotypes, aspen, conifer and shrub-steppe (Table 3-2) with a consistent positive effect between ecotypes on survival.

The ecotype-specific effects of summer/fall forage and winter snow on mule deer overwinter survival varied between ecotypes in ways that corresponded to important differences between PMUs. This is similar to many previous studies of mule deer, and other ungulates, that used a variety of different measures of forage and winter severity (Bishop et al. 2005a, Bishop et al. 2009, Hurley et al. 2011). Our approach evaluated the same consistent set of predictors across a wide geographical gradient and revealed important between-ecotype differences. For example, fall phenology (FPC) was observed to be important in the conifer communities, but not in the eastern aspen communities where only Nov-Dec weeks with complete snow and winter snow cover predicted survival quite closely (R^2_{CV}=0.853, Table 3-2, Figure 3-4). Yet, winter snow cover had similar magnitude effects on fawn survival in both aspen and conifer (Figure 3-3), but Nov-Dec snow cover only negatively affected survival in conifer. The forage production and quality of shrub-steppe communities was highly influenced by precipitation, more so than communities with canopy tree (aspen or conifer) cover as evidenced by the positive relationship of most types of precipitation (including snow) and summer phenology to survival. It appears that in these xeric shrub-steppe ecotypes, any moisture, except early winter snow (which we interpret as indicating the end of the fall growing season), will have a positive effect on survival in this ecotype as these open areas may require winter snow moisture for plant growth in early spring. In general across all ecotypes, vegetation phenology as measured by NDVI had much weaker effect sizes than the two primary snow covariates (W%snow and Fweeks, Figure 3-3). Snow accumulation is a more fine-scale process than vegetation phenology because minimal changes in temperature and aspect will change snowfall to rain. This may explain why FPC and SPC were important in the statewide models, but lose importance in the aspen ecotype model. Phenology is similar across this region, limiting its effectiveness to differentiate survival among PMUs within ecotypes. In the aspen ecotype, snow depth was important, likely due to the higher elevation areas and increased average snow depth. The full model including mass was the best fitting model for aspen, again suggesting that mass is a finer-scale process and related to snow conditions.

The regional variation we found in remotely-sensed measures of winter snow may also reflect differences in spatial resolution. For example, the higher resolution of the MODIS data at 250m as opposed to SNODAS at 1km may likely explain greater importance of snow cover compared to snow depth. The higher resolution may more accurately capture the effect of elevation and aspect in our topographically variable winter ranges by reflecting the snow free areas of a winter range at lower elevation. Regardless of which remotely sensed measure of winter severity was retained in our survival models, both allowed spatial variation in the measure of snow to improve predictions of overwinter survival.

Our challenge in producing predictive models of survival was to balance the precision, bias, and generality trade-offs (Levins 1966) while using readily obtainable covariates that describe the complexity of our spatially diverse system. This approach allowed us to select the most parsimonious model that maximized generality across large regional areas while minimizing model complexity (i.e. our simplest model has higher out-of-sample predictive capacity as our most complex model). This simple model with just three covariates, one summer vegetation quality and 2 two winter snow measures, should be general enough to estimate overwinter fawn survival in much of the arid west, given the data for model development was obtained from the diverse vegetation types. Interestingly, the inclusion of body mass decreased predictive capacity across ecotypes, likely because mass is related to individual survival, but the random sample of mean mass as used when predicting survival is a weaker measure of population level effects. The flexibility of a general model is important because Bishop et al. (2005) observed winter survival of fawns was not spatially synchronous even in adjacent winter ranges and cautioned that extrapolating survival to other populations can lead to erroneous population estimates, a problem we solved with our modeling approach.

Beyond statistical reasons, the potential discrepancies between predictions and observations might involve predation, which could also result in lower than predicted survival. We exclusively used vegetation quality and snow covariates to model survival, but this may not successfully capture predation-related drivers of fawn survival over the winter. For example, in our system, 21% (10% - 60%) of the fawns are killed by predators during winter (M. Hurley, *unpublished data*). Thus we only modelled 79% of the variation in overwinter survival when ignoring predation. Moreover, the interaction of weather conditions and habitat may influence fawn survival through predation risk (Griffin et al. 2011). Our predictive models also ignored possible density-dependence (Bonenfant et al. 2009). Understanding the mechanism by which forage-risk trade-offs translate to mortality may be the last critical step needed to integrate density and predation into survival models. While including covariates representing density and predation appeals ecologically, from a practical viewpoint, wildlife managers often will not have access to this information over large regions. Instead, as our ecotype-scale models demonstrate, some of this potential bias between observed and predicted survival seems to be diminished in the ecotype-scale models with lower predictive performance occurring in our highest predation risk ecotype, conifer.

We conclude that wildlife population studies should put more effort into testing the predictive performance of their models to understand their generality. Previous large-scale demographic syntheses of neonatal elk calf survival (Griffin et al. 2011), adult female elk survival (Brodie et al. 2013), and calf:cow ratios (Lukacs et al. 2015) all developed relatively parsimonious models to explain spatio-temporal variation of vital rates over large regions, far greater than our study. For example, Griffin et al. (2011) predicted 90-day elk calf survival using a fairly basic model of the number of predator species, previous summer precipitation, and May precipitation. This model accounted for a reasonable percentage of the variation (42%), but the out-of-sample predictive performance had never been tested so far. Conversely, many study-area specific survival models tend to often be so highly parameterized that we can question their predictive potential in other systems. Very few wildlife survival studies address any aspect of either internal or external validation. Internal validation may be limited by methodology because to date, discrete time survival modeling approaches still do not provide any measure of goodness-of-fit for evaluating internal model fit from a known-fate survival model (White and Burnham 1999).

MANAGEMENT IMPLICATIONS

We have developed models to predict mule deer fawn overwinter survival from 16 December to 1 June in Idaho’s semi-arid intermountain habitats. The models exclude information related to cause-specific mortality and mass of deer because this information is not commonly available to managers. Once these models are validated or modified for different vegetation communities, mule deer managers will realize extensive cost savings if winter fawn survival is now included in their monitoring program (radiocollared fawns). Modeling winter fawn survival with periodic fawn captures to empirically estimate fawn survival and calibrate the models can be included within integrated population models for harvest prescriptions. We suggest using the reduced overall model as the generality will likely transfer to different environments. Using the early prediction models will provide managers the ability to predict survival in the current winter, prior to harvest season development. Survival predictions can then be verified with the overall models for the entire winter season. We invite mule deer managers and researchers to evaluate performance of our models against their current monitoring program as further validation.

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TABLES

Table 3-1. Model selection results for the overall, overwinter Hierarchical Bayesian survival model for mule deer (*Odocoileus hemionus*) fawns based on 2529 individuals from 2003-2013 in Idaho, USA. The overall models contain data from all Population Management Units (PMU) and all years, and the full models contain all of the covariates. For each model, we report the model structure with covariates, Deviance Information Criterion (DIC), Difference from lowest DIC (ΔDIC), Effective Number of Parameters (pD), Deviance, and validation metrics. We conducted two forms of model validation; cross-validation within the observed data (R^2cv) and external validation (R^2_{EV}) with withheld survival data collected on n = 403 mule deer fawns in years 2007-2008 in the same study areas. The best model identified by each of the criteria (ΔDIC , R^2cv , R^2_{EV}) are bolded. Covariates include mean snow cover in November and December (ND%snow), mean snow cover in January to March (W%snow), mean snow cover in April (A%snow), functional analysis principal components for fall (FPC), functional analysis principal components for spring (SPC), number of weeks with >90% snow cover in November and December (FWeeks), and average snow depth in January – March (Depth).

Model		ΔDIC	DIC	pD	Deviance	R^2_{CV}	R^2_{EV}
1	W%snow(random)+FPC+FWeeks	122.9	11197.6	2409.1	8788.4	0.806	**0.705**
2	W%snow+FPC+FWeeks	71.4	11146.1	2358.0	8788.1	0.785	0.704
3	Full with random % W%snow	162.6	11237.3	2451.0	8786.3	0.814	0.698
4	ND%snow+W%snow+A%snow+FPC+SPC+FWeeks+Depth	228.8	11303.5	2517.6	8785.8	0.795	0.677
5	ND%snow +W%snow+A%snow+FPC+SPC+FWeeks	101.1	11175.8	2391.4	8784.4	0.796	0.675
6	ND%snow +W%snow+A%snow+FPC+FWeeks	228.7	11303.4	2515.0	8787.5	0.789	0.671
7	Full with random FWeeks	186.4	11261.1	2473.9	8789.1	0.808	0.667
8	W%snow+FPC(random)+FWeeks	123.3	11198.0	2415.1	8779.9	0.800	0.649
9	Full with random W%snow + Mass	176.3	11251.0	2650.4	8600.6	0.719	0.644
10	Full with random FPC	162.1	11236.8	2454.9	8781.8	0.806	0.628
11	ND%snow+W%snow+A%snow+FPC+SPC+FWeeks+Depth+Mass	**0.0**	11074.7	2472.1	8602.6	0.695	0.620
12	FPC+SPC+FWeeks (early prediction)	174.8	11249.5	2480.6	8768.9	0.816	0.620
13	FPC+SPC+FWeeks(random) (early prediction)	176.5	11251.2	2478.1	8773.0	**0.818**	0.590

R^2_{CV} = Cross validation; R^2_{EV} = Validation with external data

Table 3-2. Model selection results for the ecotype specific, overwinter Hierarchical Bayesian survival models for mule deer (*Odocoileus hemionus*) fawns based on 2529 individuals, including all years of data from 2003-2013 in Idaho, USA. The full models contain all of the covariates. For each model we report, the model structure with covariates, Deviance Information Criterion (DIC), Difference from lowest DIC (ΔDIC), Effective Number of Parameters (pD), Deviance, and validation metrics (Cross validation R^2). The best model identified by each of the criteria (ΔDIC , R^2cv) are bolded. Covariates are; mean snow cover in November and December (ND%snow), mean snow cover in January to March (W%snow), mean snow cover in April (A%snow), functional analysis principal components for fall (FPC), functional analysis principal components for spring (SPC), number of weeks with >90% snow cover in November and December (FWeeks), and average snow depth in January – March (Depth).

Model		Δ DIC	DIC	pD	Deviance	R^2_{CV}
Aspen model						
1	ND%snow +W%snow+A%snow+FPC+SPC+FWeeks+WDepth+Mass	**0.0**	2982.3	674.4	2308.0	**0.895**
2	ND%snow +W%snow+A%snow+FPC+SPC+FWeeks+WDepth	67.5	3049.8	672.6	2377.2	0.859
3	W%snow+A%snow+FPC+FWeeks+WDepth	56.9	3039.2	663.0	2376.2	0.856
4	W%snow+FWeeks+WDepth	92.9	3075.2	696.3	2378.9	0.854
5	W%snow+FWeeks	54.0	3036.3	655.1	2381.2	0.853
6	ND%snow +W%snow+A%snow+FPC+FWeeks+WDepth	113.3	3095.6	717.5	2378.1	0.852
7	W%snow+FPC+FWeeks+WDepth	60.3	3042.6	663.3	2379.3	0.851
Conifer model						
1	ND%snow+W%snow+A%snow+FPC+SPC+FWeeks+WDepth	118.8	6635.5	1367.5	5268.1	**0.803**
2	ND%snow+W%snow+A%snow+FPC+SPC	140.9	6657.6	1333.0	5324.7	0.799
3	ND%snow+W%snow+A%snow+FPC+SPC+WDepth	124.7	6641.4	1317.5	5323.9	0.797
4	ND%snow+W%snow+FPC+SPC	94.2	6610.9	1288.5	5322.4	0.796
5	ND%snow+W%snow+FPC	214.2	6730.9	1408.6	5322.2	0.795
6	ND%snow+W%snow+A%snow+FPC+SPC+FWeeks+WDepth+Mass	**0.0**	6516.7	1354.5	5162.2	0.762
Shrub-steppe model						
1	ND%snow+W%snow+A%snow+FPC+SPC+FWeeks	8.0	1285.0	154.3	1130.7	**0.604**
2	ND%snow+W%snow+A%snow+FPC+SPC+FWeeks+WDepth	18.0	1295.0	166.0	1129.0	0.596
3	ND%snow+W%snow+A%snow+FPC+SPC+FWeeks+WDepth+Mass	**0.0**	1277.0	165.0	1112.1	0.575
4	W%snow+A%snow+FPC+SPC+FWeeks	17.3	1294.3	165.2	1129.1	0.539
5	A%snow+FPC+SPC+FWeeks	96.2	1373.2	242.7	1130.4	0.535
6	W%snow+A%snow+FPC+FWeeks	6.3	1283.3	152.9	1130.4	0.507
7	FPC+SPC+FWeeks	48.5	1325.5	191.3	1134.2	0.411

FIGURES

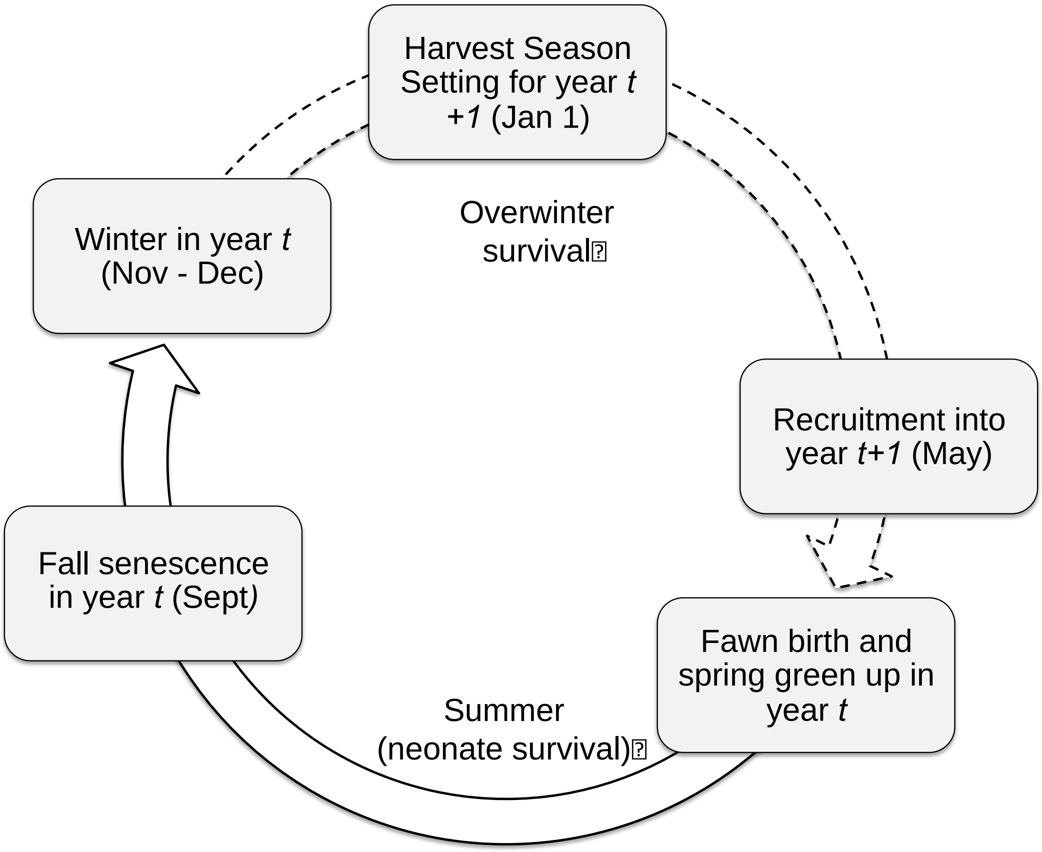
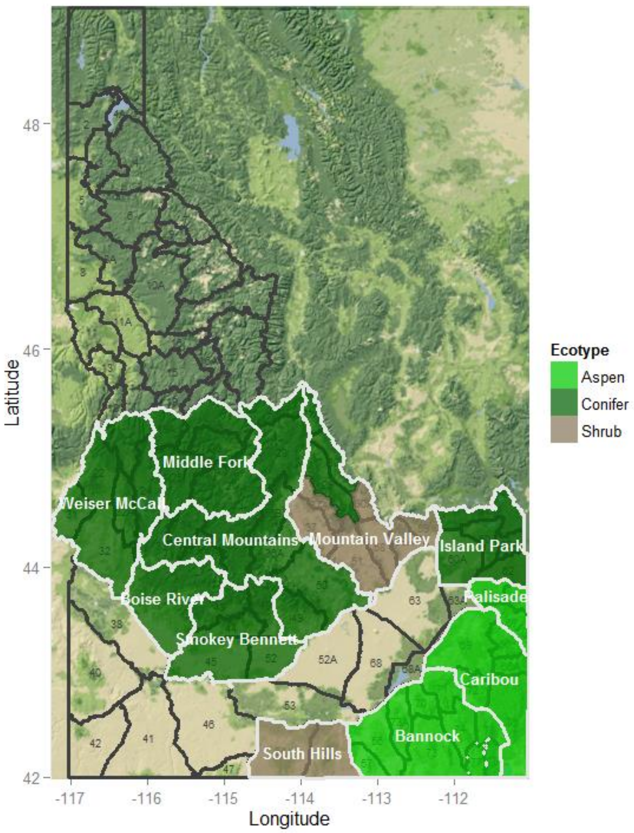


Figure 3-1. Annual survival cycle for mule deer (*Odocoileus hemionus*) fawns in year t from birth, through summer and winter survival to recruitment into the population in relation to the management setting of mule deer harvest in year t+1 in Idaho, USA. Winter begins in November or December and winter fawn survival is measured from 15 December to June 1 (dashed line). Season setting for harvest management begins in early January and final seasons are set in early March of each year.


Middle Fork
Weiser McCall
Central Mountains
Mountain Valley
Island Park
Palisades
Boise River
Smokey Bennett
Caribou
Bannock
South Hills
Ecotype
🟩 Aspen
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🟫 Shrub
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44
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Latitude
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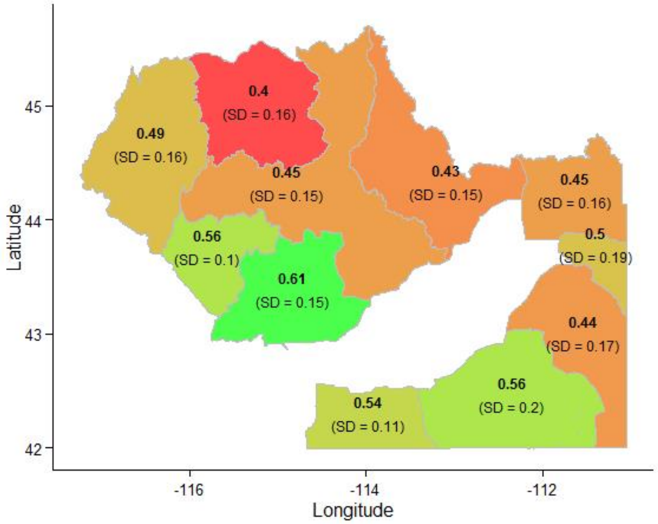
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(SD = 0.15)
0.45
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0.5
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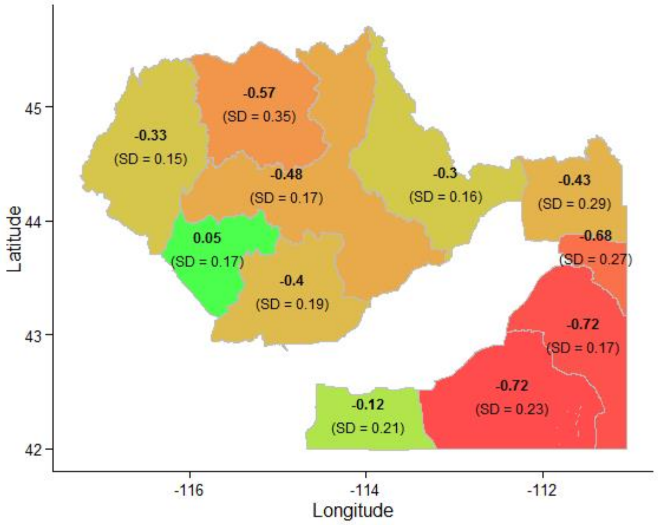
44
43
42
Latitude
-116
-114
-112
Longitude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(SD = 0.35)
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(SD = 0.15)
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(SD = 0.17)
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Latitude
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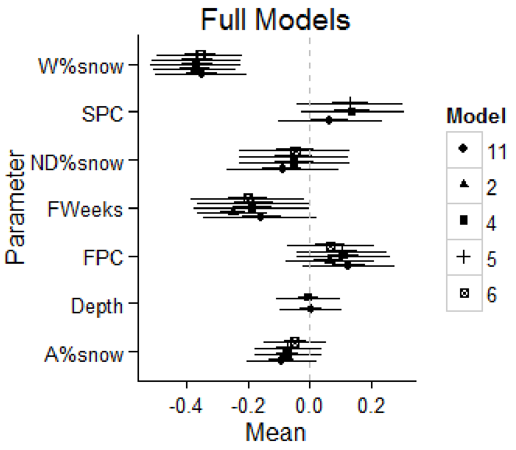
Figure 3-2. (left panel) Hierarchical relationship between Mule deer (*Odocoileus hemionus*) seasonal summer and winter ranges within the deer sampling unit at the Game Management Unit (GMU) and the larger-scale Population Management Unit (PMU), and largest-scale Ecotype in central and southern Idaho, USA, years 2003–2013. Spatial covariates for weather (summer precipitation, NDVI, snow-cover) were extracted from seasonal ranges estimated from radio telemetry data during summer and winter, and then associated with individual mule deer within each GMU, nested within each PMU. Expected overwinter survival of fawns in each PMU estimated from the mean of the annual posterior distributions (top right). Parameter estimate for the random effect of winter snow cover for the best fitting random effect model (bottom right, Table 1). Green colors denote minimal effect of winter and orange to red colors denote increasing effect of winter.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ND%snow
FWeeks
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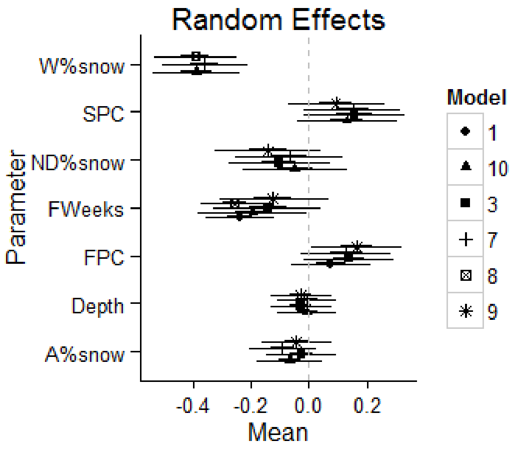
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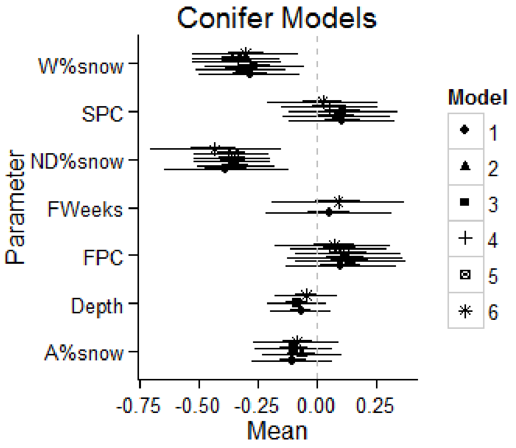
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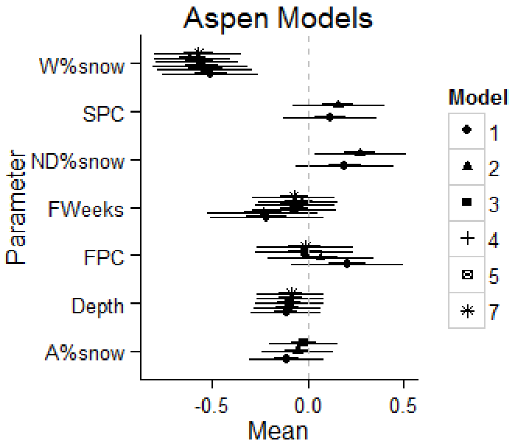
Aspen Models
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SPC
ND%snow
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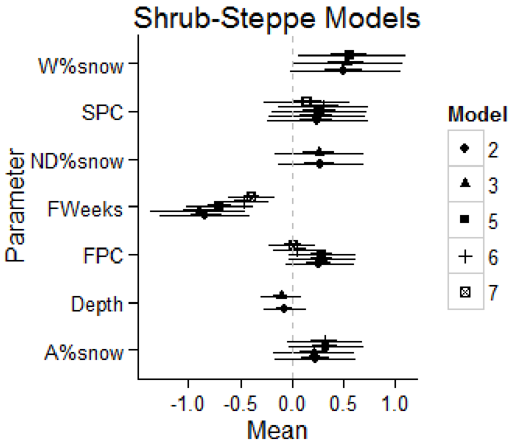
Shrub-Steppe Models
Parameter
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SPC
ND%snow
FWeeks
FPC
Depth
A%snow
-1.0
-0.5
0.0
0.5
1.0
Mean
Model
2
3
5
6
7

Figure 3-3. Effects of covariates on mule deer (*Odocoileus hemionus*) overwinter survival in Idaho, 2003-2013, from the top six Bayesian hierarchical models showing the mean, 75% and 95% Bayesian credible intervals for the following covariates: mean snow cover in November and December (ND%snow), mean snow cover in January to March (W%snow), mean snow cover in April (A%snow), functional analysis principal components for fall (FPC), functional analysis principal components for spring (SPC), Number of Weeks with >90% snow cover in November and December (FWeeks), and average snow depth in January – March (Depth).

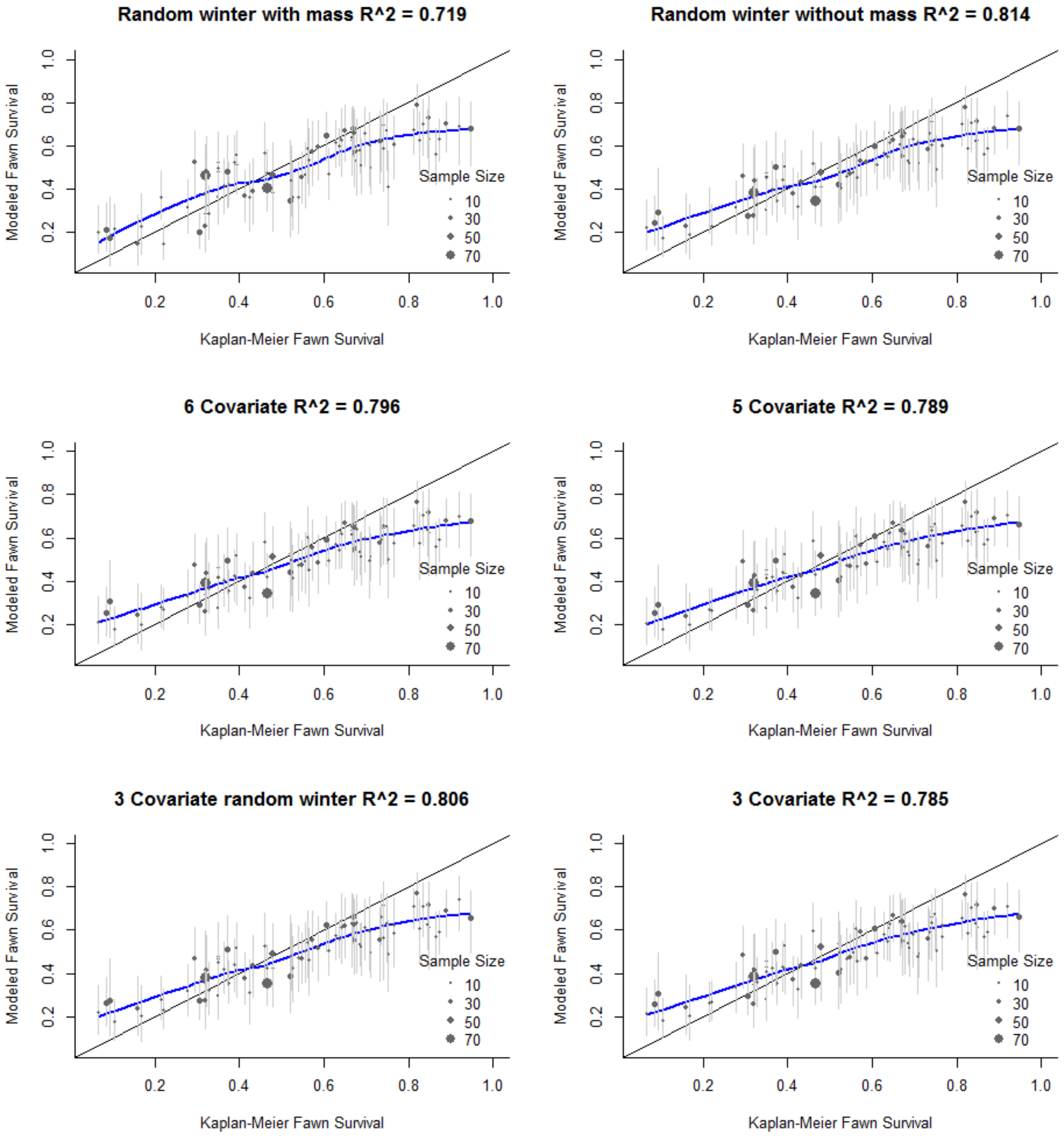


Figure 3-4. Observed (Kaplan-Meier survival, x axis) versus predicted (modeled y axis) overwinter survival of 6-month old mule deer (*Odocoileus hemionus*) fawns in southern and central Idaho for each PMU, 2003-2013. Survival was predicted for 2529 mule deer fawns using a hierarchical Bayesian survival model that accounted for spatial and

temporal variation in covariates. Panel figures for the numbering scheme of Table 1 a) Model 10, b) Model 1, c) Model 6, d) Model 5, e) Model 3, f) Model 9. The first model is the only model that includes mass. The blue line is a spline fit to illustrate bias of modeled survival estimates from observed estimates.

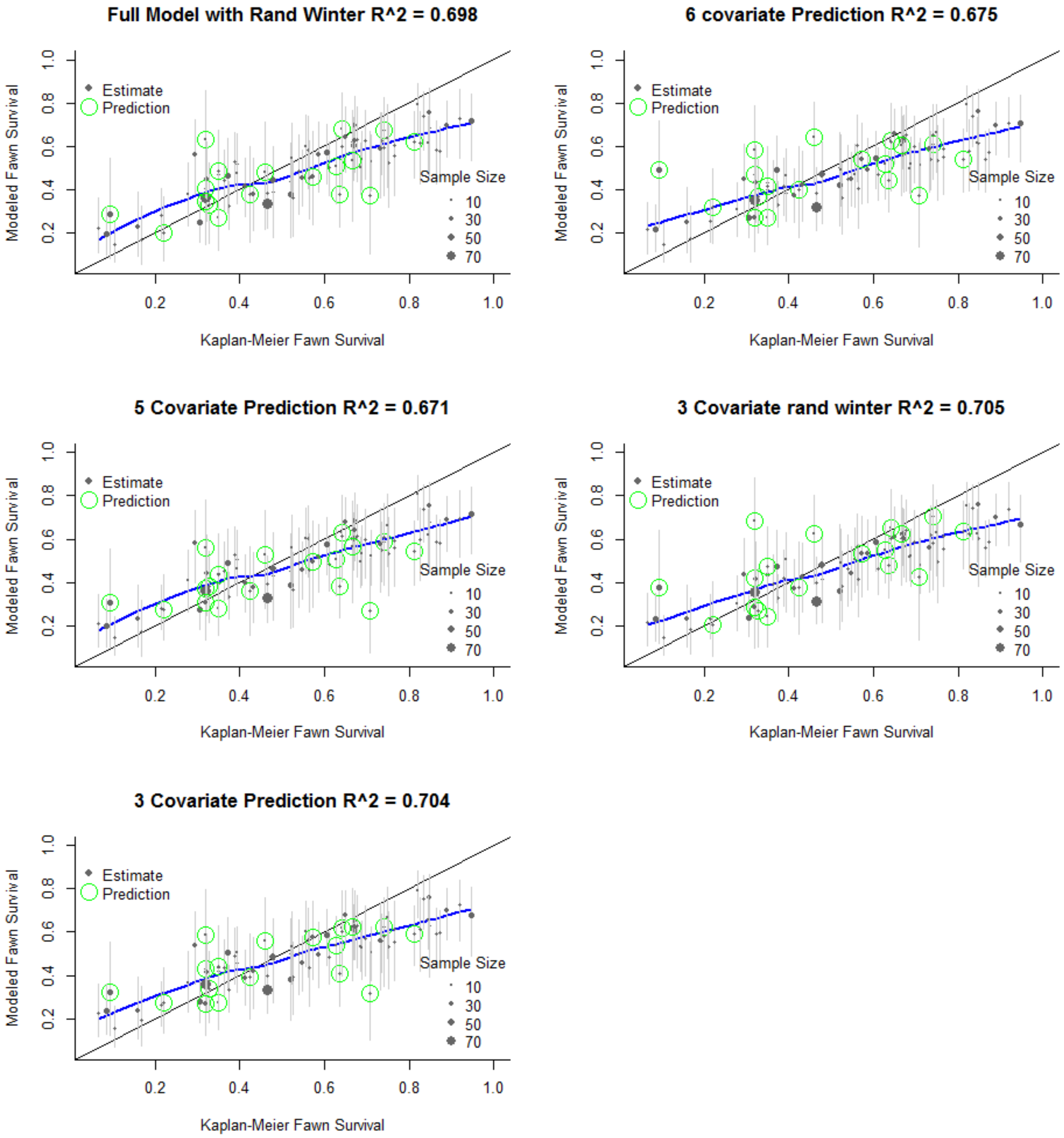


Figure 3-5. External validation of the overall models of mule deer (*Odocoileus hemionus*) fawn survival in Idaho, 2003-2013. We conducted external validation by withholding survival data collected on 403 mule deer fawns in years 2007-2008. We used the models to predict survival of fawns and then compared the estimate (green circle) to observed survival (Kaplan-Meier estimate) in the same study areas. The first and 4th models

include a random effect of winter % snow cover the others only random intercept and correspond to model numbers in Table 1. The blue line is a spline fit to illustrate bias of modeled survival estimates from observed estimates.

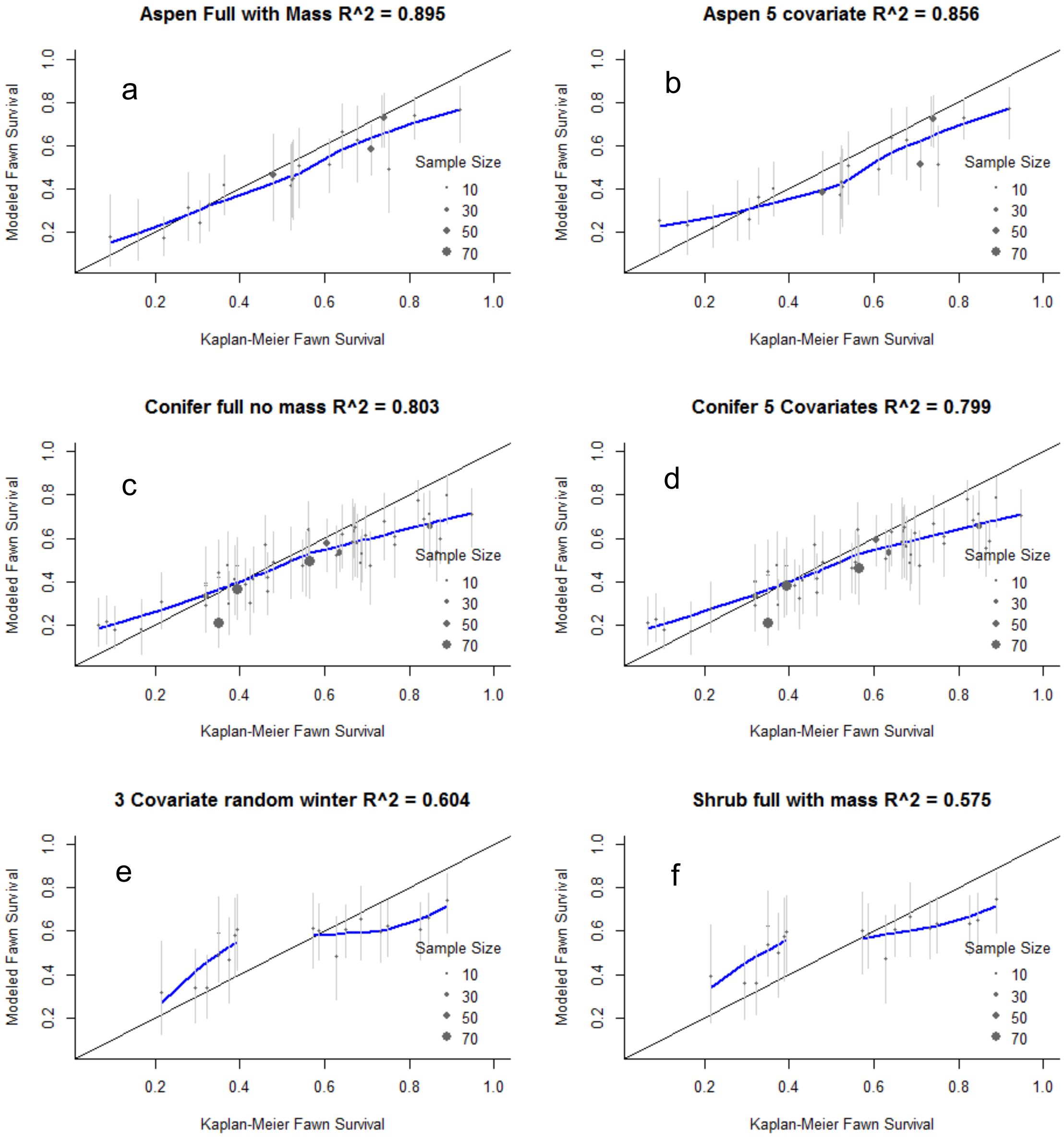


Figure 3-6. Observed (Kaplan-Meier x axis) versus predicted (modeled y axis) overwinter survival of 6-month old mule deer (*Odocoileus hemionus*) fawns within a, b) Aspen c, d) Conifer, and e, f) Shrub-Steppe ecotypes in southern Idaho, 2003-2013. The two most supported models are presented.

The blue line is a spline fit to illustrate bias of modeled survival estimates from observed estimates.

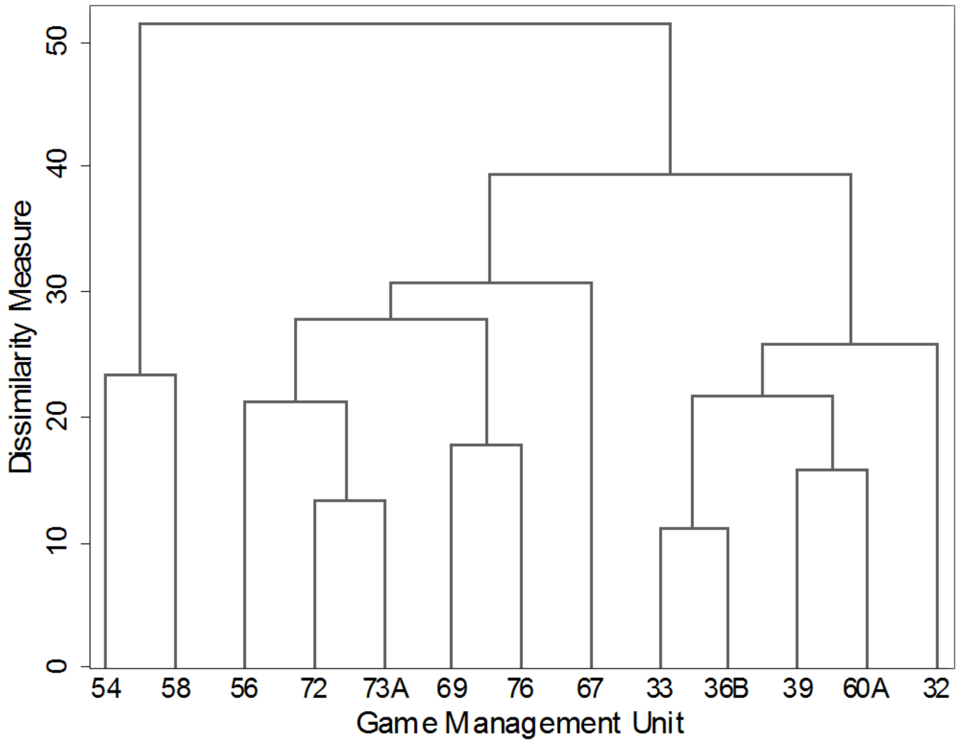
APPENDIX B. SUPPLEMENTAL MATERIALS

December 26, 2015

> Hurley, M., Hebblewhite, M., et al. 2015. Generality and precision of regional-scale survival models for predicting overwinter survival of mule deer fawns Journal of Wildlife Management, In Review.

3-S1: Summer Range Ecotype Classification

We used summer range as the basis for clusters as these season ranges show the greatest potential variance is nutritional quality and vegetation types. Vegetation variables were developed from the SAGEMAP vegetation layer (2005 USGS, Forest and Rangeland Ecosystem Science Center, Snake River Field Station, Boise, ID). The layer contained 126 land cover classes with a minimum mapping unit (MMU) of approximately 1 acre (0.4 ha). We reclassified the image into 18 vegetation classes with importance to mule deer ecology. These vegetation classes included; aspen woodland, riparian, other deciduous woodland, juniper woodland, mahogany woodland, coniferous forest, deciduous shrub land, mesic sagebrush shrub land, xeric sagebrush shrub land, wet meadow, mesic grassland, xeric grassland (includes Conservation Reserve Program lands), invasive grassland, agriculture, recent burn, open water, developed, and unavailable. The weighted mean accuracy assessment of the reclassification was 84.4%. We used a hierarchical weighted means cluster analysis based on summer range vegetation types within summer home ranges used by the wintering herd unit (Figure 3-S1) to identify vegetation community clusters. Defining differences identified in the three primary clusters were % conifer (>40%), %aspen (6 to 13%), and % mesic sagebrush (>60%) on summer range. The GMUs were distributed among the ecotypes with five in conifer ecotype (GMUs 32, 33, 36B, 39, 60A), two in shrub-steppe ecotype (GMUs 54, 58), and six in aspen (GMUs 56, 67, 69, 72, 73A, 76). PMUs were assigned to group depending on the designation of GMUs in each PMU.



Supplement Figure 3-S1. Hierarchical weighted means grouping of GMUs based on percent of vegetation types within deer sub-population summer range.

Table 3-S1. Winter survival rates and standard errors (SE)^a of radio-collared mule deer fawns in central and south Idaho. Note that 2007 and 2008 KM estimates were excluded for the out-of-sample validation of the Bayesian survival models.

PMU	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013
Bannock	NA	0.48 (0.099)	NA	NA	0.74 (0.092)	0.33 (0.093)	0.36 (0.071)	0.71 (0.082)	NA	NA	NA
Boise River	0.56 (0.099)	0.35 (0.099)	0.74 (0.092)	0.52 (0.100)	0.46 (0.103)	0.71 (0.104)	0.77 (0.092)	0.76 (0.084)	0.48 (0.099)	0.67 (0.096)	0.70 (0.096)
Caribou	0.74 (0.063)	0.53 (0.106)	0.52 (0.099)	0.31 (0.055)	0.81 (0.054)	0.22 (0.072)	0.28 (0.076)	0.61 (0.092)	NA	NA	NA
Central Mountains	0.35 (0.099)	0.32 (0.099)	0.67 (0.086)	0.10 (0.044)	0.64 (0.059)	0.42 (0.114)	0.39 (0.092)	0.87 (0.060)	0.47 (0.076)	0.61 (0.085)	0.47 (0.091)
Island Park	NA	0.85 (0.071)	NA	NA	NA	0.32 (0.093)	0.56 (0.111)	0.68 (0.109)	0.07 (0.057)	NA	NA
Middle Fork	NA	NA	NA	NA	NA	0.24 (0.103)	NA	NA	NA	NA	NA

Mountain Valley	NA	0.57 (0.103)	0.89 (0.047)	0.17 (0.076)	0.63 (0.112)	0.35 (0.112)	0.39 (0.106)	0.69 (0.075)	0.22 (0.076)	0.39 (0.083)	0.37 (0.080)
Palisades	0.92 (0.054)	0.54 (0.098)	0.68 (0.094)	0.16 (0.073)	0.64 (0.096)	0.09 (0.087)	0.52 (0.109)	0.75 (0.097)	NA	NA	NA
Smokey-Bennett	NA	NA	NA	NA	NA	0.32 (0.099)	0.67 (0.090)	0.83 (0.076)	0.37 (0.093)	0.82 (0.067)	0.85 (0.063)
South Hills	0.75 (0.089)	0.83 (0.079)	0.73 (0.087)	0.32 (0.105)	0.57 (0.126)	0.35 (0.107)	0.30 (0.113)	0.85 (0.071)	NA	0.65 (0.101)	0.59 (0.113)
Weiser-McCall	0.64 (0.096)	0.41 (0.070)	0.95 (0.051)	0.43 (0.094)	0.67 (0.111)	0.32 (0.101)	0.86 (0.074)	0.55 (0.084)	0.09 (0.052)	0.67 (0.086)	0.69 (0.082)

[a] Survival rates and SEs were calculated following Pollock et al. (1989).

Table 3-S2. Correlation matrix of weather covariates 2003 to 2013. Covariates included MODIS snow, SNOWDAS, and NDVI. Snow covariates were developed from the time periods; November-December, January-March, and April.

	AFD	FC	AWD	WC	AAD	AC	FW	WW	F%	W%	A%	FPC	SPC
Ave. Fall Depth (AFD)	1	0.96	0.63	0.63	0.39	0.48	0.48	0.27	0.52	0.41	0.40	0.28	-0.14
Fall Cumulative Snow (FC)	0.96	1	0.64	0.64	0.44	0.53	0.52	0.32	0.54	0.45	0.45	0.27	-0.12
Ave. Winter Depth (AWD)	0.63	0.64	1	0.98	0.59	0.69	0.36	0.55	0.4	0.63	0.40	0.26	-0.02
Winter Cumulative Snow (WC)	0.63	0.64	0.98	1	0.61	0.69	0.36	0.55	0.4	0.63	0.40	0.26	-0.02
Ave. April Depth (AAD)	0.39	0.44	0.59	0.61	1	0.95	0.26	0.22	0.28	0.35	0.49	0.22	-0.13
April Cumulative Snow (AC)	0.48	0.53	0.69	0.69	0.95	1	0.27	0.26	0.27	0.38	0.52	0.20	-0.14
Fall Weeks(FW)	0.48	0.52	0.36	0.36	0.26	0.27	1	0.57	0.69	0.58	0.35	0.31	-0.10
Winter Weeks (WW)	0.27	0.32	0.55	0.55	0.22	0.26	0.57	1	0.51	0.91	0.36	0.25	0.12
Fall %Snow Cover (F%)	0.52	0.54	0.40	0.40	0.28	0.27	0.69	0.51	1	0.63	0.39	0.38	-0.18
Winter %Snow Cover (W%)	0.41	0.45	0.63	0.63	0.35	0.38	0.58	0.91	0.63	1	0.46	0.32	-0.02
April %Snow Cover (A%)	0.41	0.45	0.40	0.40	0.49	0.52	0.35	0.36	0.39	0.46	1	0.28	-0.09
FallPC (FPC)	0.28	0.27	0.26	0.26	0.22	0.20	0.31	0.25	0.38	0.32	0.28	1	-0.04
SpringPC (SPC)	-0.14	-0.12	-0.02	-0.02	-0.13	-0.14	-0.10	0.12	-0.18	-0.02	-0.09	-0.04	1

Table 3-S3. Coefficients for full overall, aspen, conifer, and shrub-steppe models. Posterior parameter estimates that credible intervals do not overlap 0 are bolded. Covariates are centered and scaled (standardized).

	Model			
Parameter	Overall	Aspen	Conifer	Shrub Steppe
Random Intercept				
Bannock	**4.157**	**4.484**		
Boise River	**3.700**		**3.708**	
Caribou	**3.987**	**4.279**		
Central Mountains	**4.297**		**4.338**	
Island Park	**4.256**		**4.128**	
Middle Fork	**4.088**		**3.967**	
Mountain Valley	**4.283**		**4.111**	**3.582**
Palisades	**4.056**	**4.135**		
Smokey-Bennett	**3.961**		**3.869**	
South Hills	**4.056**			**4.294**
Weiser-McCall	**3.591**		**3.483**	
Early Winter % Snow Cover (Nov-Dec)	-0.088	0.193	**-0.434**	0.269
Winter % Snow Cover (Jan – Mar)	**-0.349**	**-0.507**	**-0.300**	**0.499**
April % Snow Cover	-0.092	-0.112	-0.085	0.223

Fall NDVI (FPC)	0.127	0.204	0.072	0.261
Spring NDVI (SPC)	0.065	0.118	0.025	0.237
Fall Week With > 90% Snow (Nov-Dec)	**-0.156**	-0.217	0.091	**-0.832**
Winter Snow Depth (Jan- Mar)	0.005	-0.115	-0.044	-0.072
Fawn Mass	**0.454**	**0.505**	**0.429**	**0.397**

Table 3-S4. Example of JAGS code for hierarchical model structure in Hurley et. al 2016

```
## This is the Full model with random effect of winter % snow cover

## JAGS code starts here

cat( "model {

     ## Likelihood for survival (individual level 1)
       for( i in 1:nAnimal ){
         for( j in 1:dead[i] ){
            eh[i,j] ~ dbern( S[i, j] ) # eh = individual encounter history
            S[i,j] <- 1/( 1+exp(-z[i, j]) )
            z[i,j] <- a0[year[i], GMU[i]] + e[year[i],GMU[i],j]  # index intercept on id and GMU
          }
       }

     ## Random effect for time
               for(i in 1:nYear) {
                    for( j in 1:nGMU ){
                         for( k in 1:nOcc ){
                              e[i,j,k] ~ dnorm(muGMU[j],tau)T(-5,5)
                         }
                    }
               }
     ## Modelling GMU level variables (level 2)
             for( i in 1:nYear ){
               for( k in 1:nGMU ){
```

```
                    a0[i, k] <- alpha0[PMUlevel3[k]] + alpha1 * fallCenter[i, k]
                    + alpha2[PMUlevel3[k]] * winterCenter[i, k]
                    + alpha3 * aprilCenter[i, k] + alpha4 * fallPCC[i, k] + alpha5 * springPCC[i, k]
                    alpha6 * fallWeeksCenter[i, k] + alpha7 * winterDepthC[i, k]
                                              }
                }

## Metaparameters for random effects (level 3)
       for( p in 1:nPMU ){
          alpha0[p] ~ dnorm(muPMU, tauPMU)
          alpha2[p] ~ dnorm(muCov1, tauCov1)
  }

## Get predicted values at the PMU level
                          for(i in 1:nPMU){
                                  for(k in 1:nYear){
                                          for(l in 1:nOcc){
                                                  for( m in 1:nGMU ){
                                                   tempProb[i,k,m,l] <- (1/( 1+exp(- (a0[k,m ] + e[k,m,l]))))
                                                  }
                                                  phiPMUOcc[i,k,l] <- tempProb[i,k,,l]%*% weightGMU[i, , k] # weighting
                                                                          #occasion specific survival by GMU sample size

                                  }
                          }
                  }

                          for(i in 1:nPMU){
                                  for(k in 1:nYear){
```

```
                        phiPMU[k,i] <- prod(phiPMUOcc[i,k, ])  # PMU estimate of survival
                    }
                }



    ## GMU random effect means
                for(i in 1:nGMU ){
                    muGMU[i] ~ dnorm( 0, tauGMU )T(-5,5)
                }

## Distribution of priors

    alpha1 ~ dunif(-10, 10)
    alpha3 ~ dunif(-10, 10)
    alpha4 ~ dunif(-10, 10)
    alpha5 ~ dunif(-10, 10)
    alpha6 ~ dunif(-10, 10)
    alpha7 ~ dunif(-10, 10)


    muPMU ~ dunif(-10, 10)
    muCov1 ~ dunif(-10, 10)
    tau ~ dunif(0, 10)
    tauPMU ~ dunif(0, 10)
    tauGMU ~ dunif(0, 10)
    tauCov1 ~ dunif(0, 10)

    }", file="jagsOuputSurvival.txt"
```

```
                 )
##
## JAGS model code ends
##

############## JAGS input variables
sp.data <- list( eh=eh, nAnimal=nAnimal, dead=dead,
                 year = year, nOcc = 24, nYear = nYear, nGMU = nGMU, nPMU = nPMU,
                 GMU = as.numeric(GMU),
                 fallCenter = fallCenter,
                 aprilCenter = aprilCenter,
                 winterCenter = winterCenter,
                 fallPCC = fallPCC,
                 springPCC = springPCC,
                 fallWeeksCenter = fallWeeksCenter,
                 winterDepthC = winterDepthC,
                 PMUlevel3 = PMUlevel3,
                 weightGMU = weightGMU
                  ) # data

sp.params <- c(#"a0",

                 "alpha0",
                 "alpha1",
                  "alpha2",
                 "alpha3",
                 "alpha4",
                 "alpha5",
                 "alpha6",
```

```
                    "alpha7",
                    "phiPMU",
                    "tau"
                    ) # parameters to track

sp.inits <- function() { # starting values
beta1guess <- runif( 1, 0, 1 )
alphaGuess <- runif(11, 0, 1)
gammaGuess <- rep(0, 11)
Tauguess <- runif( 1, 0, 1 )
Muguess <- runif( 1, 0, 1 )
list(alpha1 = beta1guess, alpha2 = alphaGuess, alpha3 = beta1guess,
          alpha4 = beta1guess, alpha5 = beta1guess, alpha6 = beta1guess, alpha7 = beta1guess,
          muPMU = Muguess, muCov1 = Muguess,
          tauPMU = Tauguess, tauCov1 = Tauguess, tau = Tauguess)
}

surv.res <- jags(sp.data, sp.inits, sp.params, "jagsOuputSurvival.txt",
          n.chains=3, n.iter=20000, n.burnin=5000, n.thin=1)
```

CHAPTER 4: HABITAT-MEDIATED DENSITY DEPENDENCE IN NEONATAL SURVIVAL OF MULE DEER FAWNS[3]

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INTRODUCTION

Resource limitation is the primary mechanism governing the process of density dependence (Sinclair 1989, Bonenfant et al. 2009). In most species including large herbivores, both pattern- (through the analysis of time series of counts) and process- (through direct analysis of life history traits in response to change in density) oriented approaches have demonstrated evidence of density-dependence as populations approach or exceed nutritional carrying capacity (Abrahams and Dill 1989, Saether et al. 1998, Gaillard et al. 2000, Bergman et al. 2015). A decrease of the per capita food resources has been cited as the key mechanism involved in density-dependence. However, at the individual level, behavioral responses to disturbance and especially the avoidance of

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predation should modify the per capita resource availability by shifting habitat selection, and thereby change the strength of density-dependence. Current theory of risk-sensitive foraging predicts that a tradeoff should occur between fitness benefits through nutrition and fitness costs through predation (Abrahams and Dill 1989, Hebblewhite and Merrill 2009) when habitats with greater forage quality or biomass are more risky. If prey are distributed in an ideal free manner, increasing density should also reduce the strength of selection for high-quality patches because of density-dependent competition for food (Fretwell and Calver 1969, McLoughlin et al. 2010). Density-dependent changes in habitat selection are thus expected to drive population dynamics through an overall decrease in survival. In contrast, prey displaying despotic distribution may exclude conspecifics from high quality habitat thereby creating segments of the population with disparate resource selection and population demography. For example, White and Warner (2007) observed density-dependence in mortality mediated by habitat based on refugia within corral for reef fishes as mortality increased when refugia were filled. Yet for many large herbivores, our understanding of density-dependent mortality arising from this interaction between space and predation is unknown (Bonenfant et al. 2009, McLoughlin et al. 2010).

Differential vulnerability of life-history stages to predation could also provide a mechanism for such density dependent predation mortality. Indeed, for many species, it is the juvenile life-history stage where the first signals of density dependence occur (Bonenfant et al. 2009). For example, a juvenile survival sink may be created if the maternal female is forced into lower quality habitats with lower forage quality and higher risk. This habitat selection may reduce the population productivity rate as total adult female numbers increase. In the case of large herbivores like mule deer (*Odocoileus hemionus*), juveniles remain with their mothers throughout the first year of their life, and so are dependent on the habitat selection strategies of their mothers (Shallow et al. 2015). If a mule deer fawn survival sink is driving density-dependent survival, we would expect that neonate mule deer mortality would be positively related to the predation risk from their main predators, coyotes (*Canis latrans*; Hurley et al. 2011). Under the classical model of density dependence where density is driven by food competition, we predict that overall fawn mortality will increase with increasing density (Bonenfant et al. 2009). However, if density dependence is driven instead by predator-mediated risk in lower quality habitat, we would instead predict that only predator-related fawn mortality will be density-dependent, and that overall fawn mortality need not be necessarily related to density. This might arise because non-predator related mortality is compensatory (White and Bartmann 1998).

To test these predictions of density-dependent mortality, we monitored neonatal survival and cause-specific mortality of mule deer fawns for the first 6 months of life. We took advantage of an ongoing management experimental reduction in coyotes (Hurley et al. 2011) in one of two adjacent populations of mule deer in southern Idaho, and compared response to both changes in density and coyote abundance in neonatal mortality. First, to test whether fawn mortality occurred because of the habitat use of lower quality, higher coyote predation risk areas at higher density, we developed a spatial model for coyote predation risk (Hebblewhite et al. 2005). We then tested whether higher coyote predation risk was correlated with fawn survival using Cox-proportional hazards survival models (Hebblewhite and Merrill 2011). Finally we tested for density-dependence in survival (mortality) of mule deer fawns with increasing density, and then, just coyote-caused fawn survival for the study area as a whole and each unit individually to assess the influence of lower coyote density due to coyote removal. If risk-sensitive foraging was driving neonatal mortality, then we predicted a decline in overall mortality at high density in the experimental coyote removal treatment, but not necessarily a decline in coyote-caused mortality. In contrast, in the reference population, we predicted no relationship between mortality and density, but a stronger (than the coyote removal area) relationship between coyote caused mortality and mule deer density (*sensu* Sinclair and Arcese 1995).

MATERIALS AND METHODS

(a) Data collection

We monitored neonate mule deer (*Odocoileus hemionus*) fawns in Game Management Units (GMU) 56 (2,338 km^2) and 73A (1,128 km^2) from 1998–2002 in southeastern Idaho. These two GMUs are within the Bannock mule deer population management unit used in Chapters 3 and 5. Elevations ranged from 1,350 m to 2,666 m. Each GMU encompassed a mountain range in its entirety and provided suitable yearlong habitat for a distinct subpopulation of deer with minimal interchange between the two GMUs. As methods for another management experiment conducted by Idaho Fish and Game (IDFG), coyotes were actively removed from GMU 73A (herein after removal area) and GMU 56 was designated a reference area (reference), see Hurley et al. (2011) for a detailed description of study areas and coyote removal treatments. We used aerial surveys via a Bell 47 helicopter to estimate mule deer population size from late March to mid-April each year from 1997 to 2003. We captured neonate fawns from 1 June to 18 June by observing fawning behavior of adult females (for details of capture methods see Hurley et al. 2011). Fawns were fitted with brown or black expandable radio collars designed to break away 6 to 8 months after capture. Animal capture protocols were approved by the Animal Care and Use Committee, Idaho Department of Fish and Game Wildlife Health Laboratory, Caldwell, Idaho, USA, and University of Montana IACUC (protocol #02-11MHCFC-031811). We monitored telemetry signals for mortality of neonate deer via aerial (fixed-wing aircraft) or ground telemetry at 1 to 2 day intervals during summer and twice weekly throughout autumn until collars were shed. We identified the cause of death within 24 hours using criteria developed by Wade and Bowns (1982), and categorized mortalities as coyote, mountain lion, bobcat, unknown predator, malnutrition, natural, other, and unknown.

We developed a spatial model of coyote predation risk (the main cause of mortality, see results) using a resource selection function (RSF; Manly et al. 2002), framework based on coyote scat transects (e.g., Hebblewhite et al. 2005). We conducted coyote scat surveys annually to estimate coyote occurrence or absence (Knowlton 1985). Eighty 1-mile transects were randomly selected in each GMU and surveyed from May to June 1998–2002 (Figure 1) the key temporal window for most neonatal fawn mortality (Shallow et al. 2015). Landcover types were defined from the SAGEMAP vegetation (Chapter 3). From the 126 land cover classes with a minimum mapping unit (MMU) of approximately 1 acre (0.4 ha), we identified 18 habitat types based on mule deer ecology, leading to a weighted mean accuracy of 84.4%. We placed a 1,000 m buffer around coyote transects and intersected the resulting polygon with the cover type and digital elevation models using a Geographical Information System (ArcGIS ver. 9.3.1, ESRI Inc. 2009). We then measured the proportion of each habitat type within the buffer.

(b) Statistical analysis

We first estimated survival of mule deer neonates in each year using non-parametric Kaplan-Meier survival estimation (Kaplan and Meier 1958, Hosmer and Lemeshow 1999). We used left- and right- staggered entry to account for different capture times and losses due to emigration or collar malfunction. We used estimated birth date as beginning at risk time (origin), then enter the analysis on capture date (enter the risk set), and end time at death or censored from shed collar or end of study (30 November; see Hurley et al. 2011,for details). Next, we estimated cause-specific mortality rates using cumulative incidence functions in a competing risks format (Heisey and Patterson 2006).

Second, we developed our model of coyote predation risk estimated using a used-unused resource selection probability function (RSPF) design with a random intercept accounting for intra-annual variation and dependency within transects (Manly et al. 2002, Gillies et al. 2006). The sample unit was the coyote transect, and the dependent variable, presence or absence, was modeled using logistic regression. This approach assumes predation risk is driven by the relative abundance of coyotes, which has been borne out in studies of other canids preying on ungulates (Hebblewhite and Merrill 2009). Coyote scat transects were conducted in both GMU 56 and 73A, as well as neighboring GMU's (Hurley et al. 2011). We treated year as a random effect to control for year-to-year variance in coyote use of transects and non-independence of repeated trials of transects each year (Gillies et al. 2006). Models were developed with purposeful forward and backward stepwise variable selection (Hosmer and Lemeshow 1999). We compared models with and without the random effect using AIC_c (Burnham and Anderson 1998) and validated the most supported coyote RSPF model with k-folds cross validation (Boyce et al. 2002). We developed coyote predation risk models based on the landcover model, a digital elevation model for elevation, and a measure of terrain ruggedness (Sappington et al. 2007).

We measured probability of presence of coyotes from our predation risk model at the neonate fawn capture site buffered by 500 m and included the probability as a covariate in Cox-proportional hazards models (Hosmer and Lemeshow 1999, Hebblewhite and Merrill 2011) to test the influence of coyote predation risk on fawn survival. We regressed mortality against mule deer density in each year (previous spring survey) using linear regression to test the first prediction of the classic hypothesis of density dependence. We next tested the relationship between the percent of marked fawns killed by coyotes and mule deer population density in both GMUs to test the hypothesis of a coyote predation-mediated density-dependence in mule deer.

RESULTS

Mule deer population size fluctuated substantially over the study period, increasing from 2,810 (GMU 56= 1878, 73A = 932) in 1998 to 4,695 in 2001 (GMU 56= 2932, 73A = 1763) and then decreased to 3,067 (GMU 56= 1496, 73A = 1571) in 2002 due to severe climatic conditions. We captured 251 neonatal fawns from 1998–2002, median 58 / year in total, evenly distributed between GMUs. Cause-specific mortality rates of these fawns were 0.13 in GMU 56 and 0.11 in 73A due to coyotes, 0.11 in GMU 56 and 0.07 in 73A due to mountain lions, 0.08 in GMU 56 and 0.05 in 73A due to unknown predation, and the remainder due to all other causes (see Hurley et al. 2011). Thus, coyotes were the leading cause of mortality. Overall neonatal survival rates (1 – mortality) varied from 0.20 – 0.74, consistent with previous studies of neonatal mule deer fawn survival (Pojar and Bowden 2004).

Coyote scats were recorded on 527 of 1035 coyote scat transects, providing a balanced used versus unused logistic regression based RSPF. The random intercept model had a lower AIC_c than the best logistic regression without random effects ($\Delta\mathrm{AIC}_c = 25.5$) or the full model ($\Delta\mathrm{AIC}_c = 34.2$). Coyotes selected habitat with low elevation and mesic sage and avoided high elevation and aspen habitats (Table 4-1, Figure 4-1). The top model was validated with a 5-fold cross validation which yielded a mean $r_s = 0.829$, indicating the model performed well at predicting coyote presence.

Mule deer fawn mortality increased with our coyote predation risk model ($\beta = 0.938$, $\chi^2 = 4.0$, $P = 0.045$). The spatial distribution of mule deer fawns with respect to coyote presence was markedly bimodal, opposing locations with rare (< 0.05) vs. abundant (> 0.3, Figure 4-2) coyote probability of presence. The hazard ratio for the effect of coyote presence on neonate mortality was 2.56 (95% CI = 0.993 to 6.58) indicating fawns with 100% probably of coyotes would die at 2.56 times the rate of fawns born in areas of 0% probability of coyote presence. Applying this ratio to the range of predicted probability of coyote presence in our study (0.014 to 0.72) suggests neonates were about as likely to die if born in habitats highly frequented by coyotes (Figure 4-2).

To test our first prediction of density dependence for the entire study area, we found no clear or strong relationship between mule deer fawn mortality and population density when both GMUs were treated as one study area for mortality and population density (Fig. 4-3a; $\beta = 0.008$, $F_{1,3} = 0.001$ $p = 0.98$, $R^2 = 0.0001$). Our second prediction of habitat mediated density dependence provided a clear signal as the contribution of coyote predation to fawn mortality increased significantly with mule deer density ($R^2 = 0.90$) when the 2 GMUs were treated as one population (Fig. 4-3b; $\beta = 0.328$, $F_{1,3} = 27.2$ $p = 0.01$, $R^2 = 0.90$).

We also observed no clear relationship between mule deer fawn mortality and population density when the GMUs were separated in GMU 56 ($\beta = 0.11$, $F_{1,3} = 0.19$, $p = 0.69$, $R^2 = 0.06$, Figure 4-4a), and a negative, but weak, relationship in GMU 73A ($\beta = -0.540$, $F_{1,3} = 1.67$ $p = 0.29$, $R^2 = 0.36$, Figure 4-4b), suggesting total fawn mortality was declining with density in the coyote removal area. Again, our second prediction of density dependent predation risk, was borne out when GMUs were separated. The pattern persists and coyotes killed more fawns as the population density increased, even though the overall mortally was constant or slightly decreasing (Figure 4-4a). The relationship was stronger in GMU 56 ($\beta = 0.251$, $F_{1,8} = 5.74$, $p = 0.09$,, $R^2 = 0.65$; Figure 4-4b), but still positive in GMU 73A ($\beta = 0.125$, $F_{1,8} = 0.86$, $p = 0.42$, $R^2 = 0.21$; Figure 4-4b) where coyotes were actively removed.

DISCUSSION

We have demonstrated differential survival of neonate mule deer fawns based on an interaction of mule deer behavior and resource selection and resource selection by their primary predator, coyotes. We observed a density-dependent increase in mule deer fawn mortality caused by coyotes with increasing mule deer density, but, critically, not an increase in overall mortality (e.g., Figure 4-3a, 4-3b). This supports our hypothesis that predation interacting with mule deer behavior may be the mechanism generating the density-dependent signature of observed in these populations (Chapter 5). We suggest that predation interacting with competition for space, not competition for food, may be the primary mechanism limiting these same populations at lower density as in Chapter 5. This is especially likely because we saw some evidence for declining overall mortality with increasing densities, whereas coyote-caused mortality increased. More generally, this supports the importance of density-dependent trade-offs between risk and forage in driving patterns of density-dependence in large herbivores (Sinclair and Arcese 1995, Hebblewhite and Merrill 2011).

The next step would be to directly test whether female mule deer resource selection follows the same avoidance pattern of resource selection for higher coyote predation risk. Previous studies have shown that mule deer select aspen habitats for fawn rearing in direct contrast to our coyote resource selection (Hurley, unpublished data). However, these habitats occur at higher elevations with lower primary prey density for coyotes. In these systems, primary prey for coyotes are not mule deer, but lagomorphs (Mills and Knowlton 1991). Resource use by coyotes and resulting density has been linked to lagomorph abundance and the differential density by habitat type is likely related to resource use of their primary prey, lagomorphs. To successfully breed, coyotes must be holding a territory prior to denning season in April and most of the aspen habitats are covered in deep snow at that time (Chapter 2), whereas, white-tailed jackrabbits (*Lepus townsendii*) are most abundant in the mid-elevation mountain shrub communities (mesic sage) in our study area. Accordingly, we observed higher survival of neonates and lower probability of coyote use in aspen habitats than in mesic sage. Our results are similar to Byers (1997) who reported pronghorn antelope (*Antilocapra antilocapra*) maternal behaviors are driven by anti-coyote behaviors, and that in turn, coyote foraging is driven by small mammal abundance. The differential mortality of neonatal mule deer as a function of coyote predation risk suggests that neonate fawns are alternate prey in this system, and are killed opportunistically and coyotes do not move to the higher quality aspen habitats, with higher deer density, to forage.

Aspen is a rare cover type in the study area, comprising 5% of the total landscape with 72% of the adult females selecting this habitat at low densities in 1998 at study initiation (Hurley, unpublished data). Females actively exclude conspecifics from fawn rearing habitat as observed in this study and by Taylor (2013), thereby limiting subdominant females' use of the highest quality cover types for fawn rearing (Shallow et al. 2015). Mountain shrub cover types may provide adequate maternal nutrition in some years with adequate precipitation, but senescence of forage will be earlier in the summer than the higher elevation aspen and conifer types (Chapter 2). Mortality of neonates may increase in these habitats through nutrition, disease, contact with livestock, or increased predation risk. We suggest that the decrease in mule deer productivity as populations increase may be related to fill of the high quality habitat and the resulting increased use of lower quality, high predation risk habitat. We conclude that the appearance of density dependent effects were the result of mule deer behavior and not forage biomass limitation.

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TABLES

Table 4-1. Parameter estimates of the top coyote (*Canis latrans*) resource use model in southern Idaho, 1998–2002, used to estimate exposure of neonatal mule deer (*Ocodoileus hemionus*) fawns to coyote predation risk.

Vegetation Type	Coef.	z	P>|z|	95% CI	
Intercept	2.48	2.75	0.006	0.714	4.25
Aspen	-2.48	-2.54	0.011	-4.40	-0.569
Other Deciduous	-3.59	-1.33	0.182	-8.87	1.688
Elevation	-.002	-2.83	0.005	-0.002	-0.0005
Mesic sage	.870	4.02	0.000	.446	1.294
Mesic grass	-50.3	-2.11	0.035	-96.88	-3.65
Developed	6.88	1.99	0.046	0.117	13.63

FIGURES

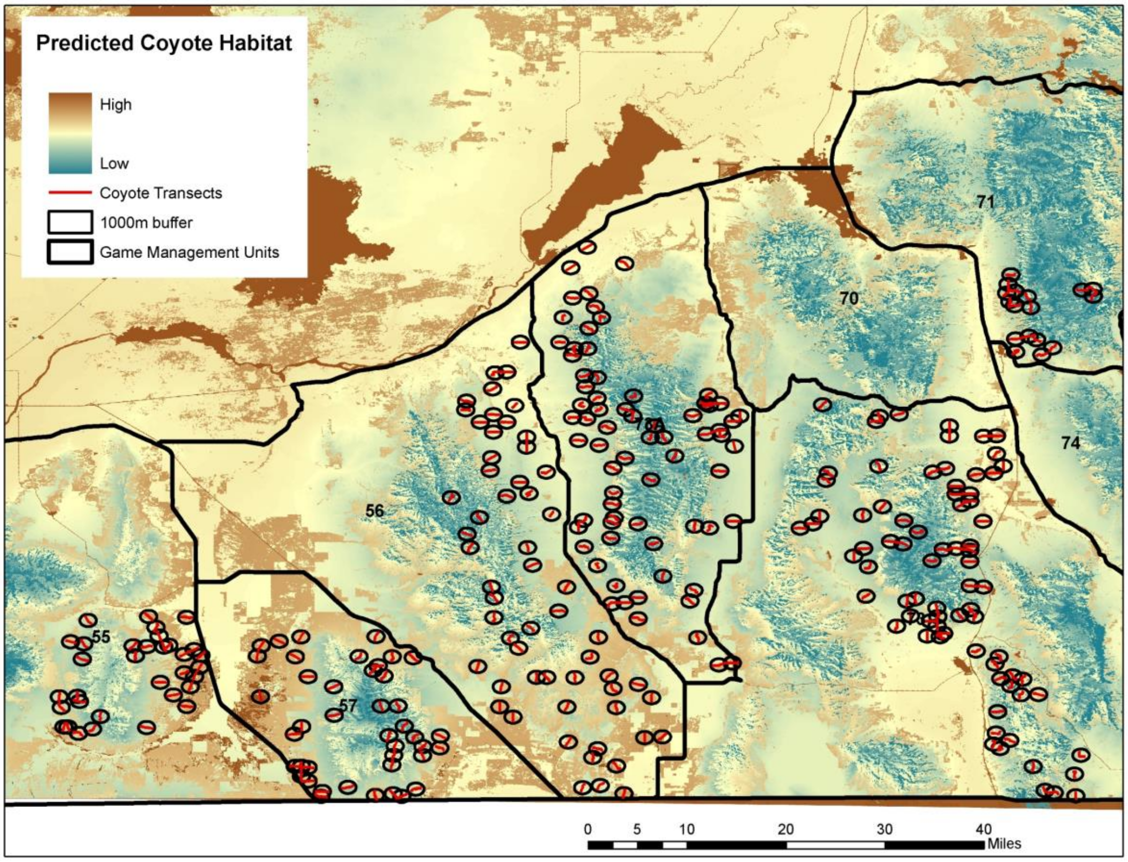

Figure 4-1. Spatial predictions from the resource selection function based model of coyote (*Canis latrans*) predation risk for mule deer (*Odocoileus hemionus*) neonatal predation risk in southern Idaho, 1998–2002, showing the two Game Management Units 56 and 73A where neonatal mule deer were monitored. The spatial distribution of coyote transects used to develop the model in a wider spatial area are depicted by black circles.

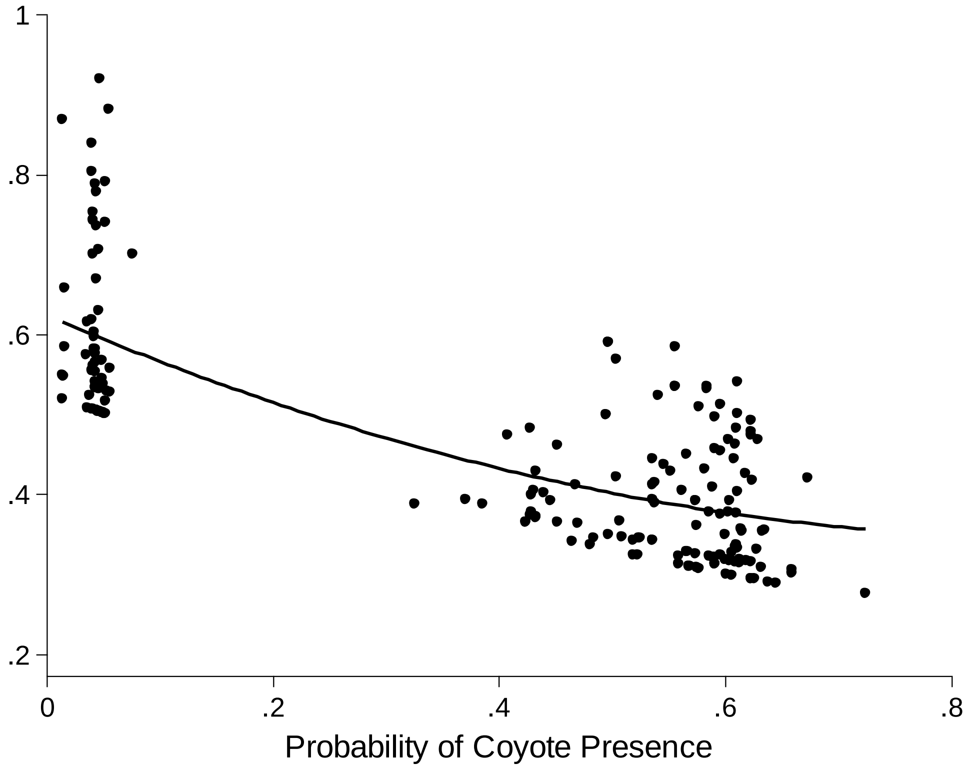

Figure 4-2. Relationship between coyote (*Canis latrans*) predation risk (estimated from a resource selection functions based on scat transects) and mule deer (*Odocoileus hemionus*) fawn survival (estimated with Cox-proportional hazards models) in mule deer in southern Idaho, 1998–2002.

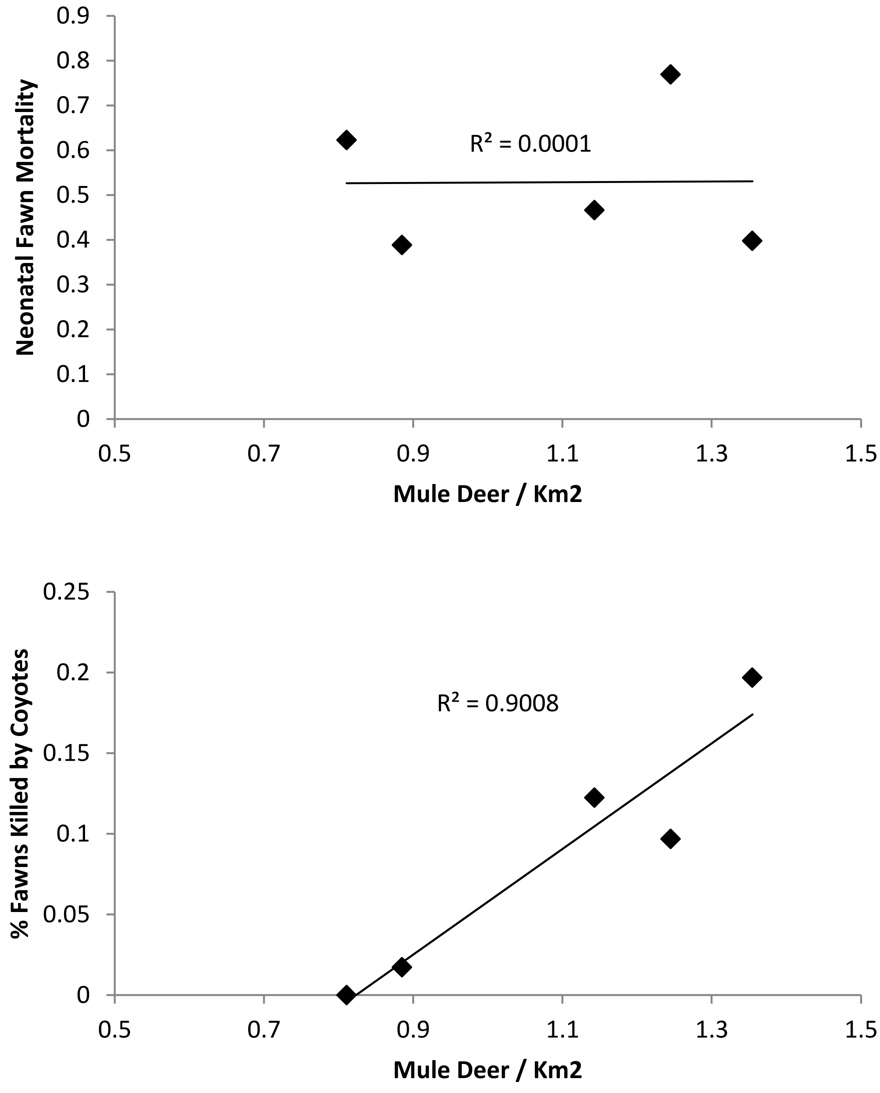

Figure 4-3. Relationship between mule deer (*Ocodoileus hemionus*) density and overall fawn mortality rates (top panel) and fawn mortality caused by coyotes (*Canis latrans*) including average density and mortality (bottom panel) for two Game Management Units (GMU 56, 73A) in southern Idaho, 1998–2002.

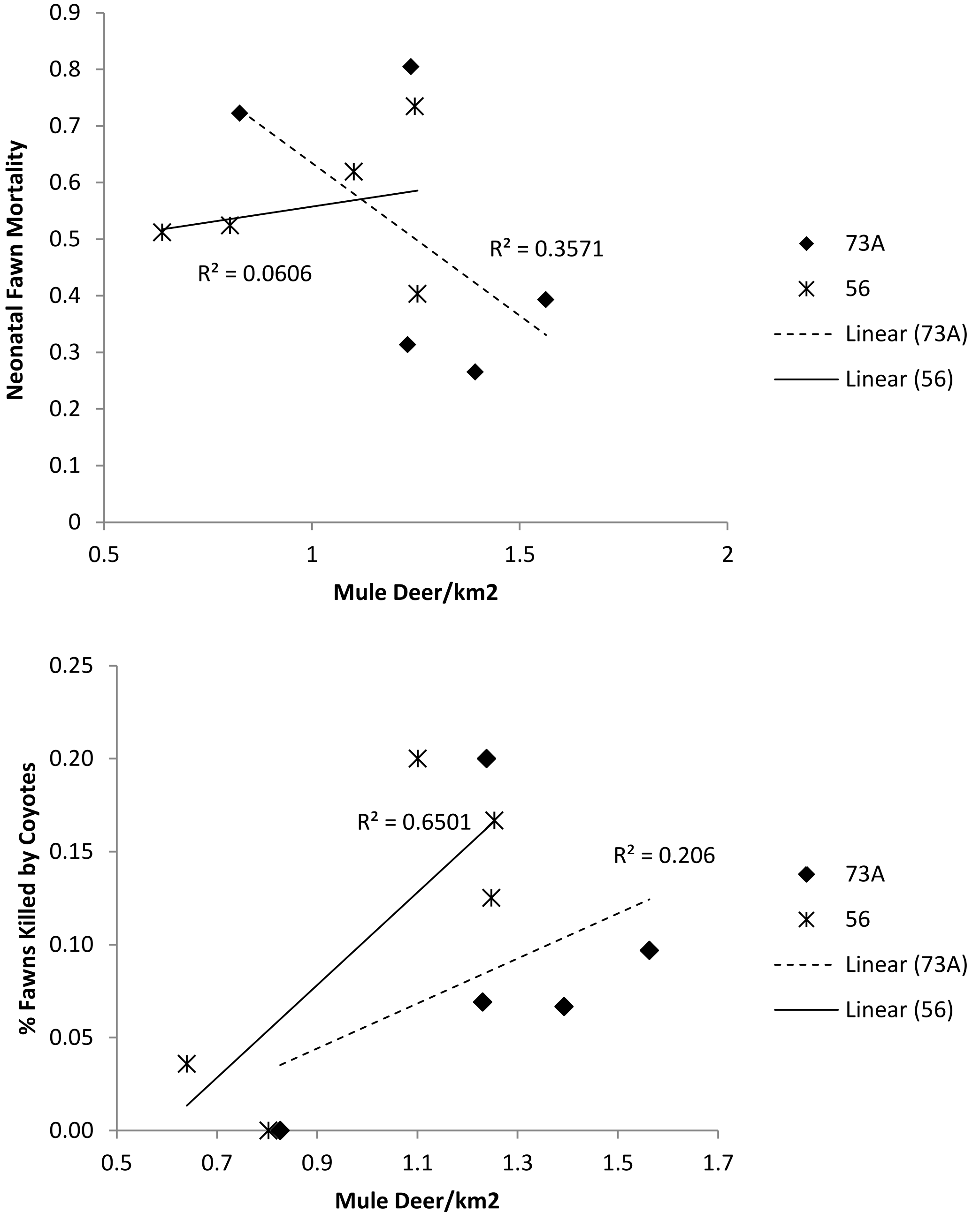

Figure 4-4. Relationship between mule deer (*Ocodoileus hemionus*) population size and a) overall fawn mortality rates (top panel) and b) fawn mortality caused by coyotes (*Canis latrans*) including independent measures of density and mortality (bottom panel) in 2 Game Management Units (GMU 56, 73A) in southern Idaho, 1998-2002.

CHAPTER 5: DISENTANGLING CLIMATE AND DENSITY-DEPENDENT EFFECTS ON UNGULATE POPULATION DYNAMICS[4]

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INTRODUCTION

The search for density-dependence in population dynamics is one of the fundamental questions of ecology (Andrewartha and Birch 1954, Krebs 1994). Without limits to growth, populations are predicted to grow exponentially and quickly surpass ecological carrying capacity. Thus, understanding the strength and mechanisms of density-dependence in population growth is a primary effort for population ecologists. In this paper, we view of density-dependence based on the logistic growth model that predicts linear density-dependence driven by intraspecific competition for resources (space, food, etc.) with increasing density (Krebs 1994). Density-dependence need not only be linear, and can either be concave (strong response only at low density) or convex (at high density) by extending the logistic model to the theta-logistic model (Krebs 1994). Regardless of form, the strength of density-dependent feedbacks to population growth are generally expected to be stronger, and more convexly non-linear, in large, longer-lived species, compared to smaller, more r-selected species (Fowler 1981, Caughley and Krebs 1983). Life-history strategies, pace of life, and other factors often reduce the generality of this continuum, but empirical evidence supports stronger density-dependence in large mammals (Fowler 1981, Eberhardt et al. 2003). Furthermore, many processes, such as predation or weather, can mimic density dependence by acting on vital rates in the same progression as expected by density often through density-climate interactions (Saether 1997, Clutton–Brock and Coulson 2002, Hebblewhite 2005, Hurley et al. 2011).

Nutritional limitation by conspecifics is hypothesized to be the primary mechanism governing density dependence in ungulates (McCullough 1979). Density-dependent effects (e.g., reduced survival or fecundity leading to decreased population growth) are expected as populations approach or exceed nutritional carrying capacity, especially in non-linear density dependence that manifests only at high density (Stewart et al. 2005). In large mammals, density dependence is expected to first act in parallel to the responses of vital rates to environmental variation, affecting first juveniles, then reproduction, and finally adult female survival (Fowler 1981, Eberhardt 2002, Gaillard & Yoccoz 2003). Ungulates conform quite well across species to this predicted sequence (Bonenfant et al. 2009). Ungulate populations near carrying capacity are thus expected to exert negative impacts through herbivory on plants (Mysterud 2006), and through competition withother species.

Population dynamics are also limited by factors unrelated to population density, and, the interaction of density-dependent and independent factors(Bonenfant et al. 2009). Understanding the relationship between density-dependent (i.e., regulatory) and density-independent (i.e., limiting, *sensu* Sinclair 1989) drivers of population dynamics remains an important challenge of population ecology. Environmental stochasticity in resource availability and climate can affect population dynamics a multitude of different ways (Saether 1997). A single species can exhibit density-dependent responses in one population and not another, as evident in elk (*Cervus elaphus*) and caribou/reindeer (*Rangifer* spp.) in relation to latitude (Post 2005, Ahrestani et al. 2013). Thus, despite the general evidence for density-dependence in large mammal populations, the strength of density dependent and independent factors vary across populations.

Interactions of weather, forage quality, and predation may prevent manifestation of density-dependence on this predicted sequence of changes in vital rates if densities are kept low by density-independent factors. This is especially true for non-linear density dependence (convex) where a critical threshold may need to be reached before density dependent changes to vital rates are evident. For instance, density dependence was weak at high latitudes or under predation, suggesting weather and predation limited densities below where density-dependence would be important in these low productivity environments (Wilmers et al. 2006, Wang et al. 2009). Similarly, roe deer (*Capreolus capreolus*) density was lower at higher latitude, low productivity environments in Europe, and experienced stronger top-down effects of predation in these same environments (Melis et al. 2009). Larger bodied ungulates are also generally less vulnerable to predation, and thus experience stronger effects of density-dependence (Sinclair and Pech 1996, Sinclair et al. 2003). However, avoidance of predation may cause smaller bodied ungulates to select resources inconsistent with nutritional carrying capacity alone, leading to a lower density than predicted by nutritional carrying capacity. Population growth rate becomes difficult to predict if the functional relationships between survival and habitat quality (forage and predation risk) changes with density. Therefore, rigorous statistical approaches are often required to test between competing hypotheses about regulating or limiting factors.

Unfortunately, identifying mechanisms of density-dependence in population dynamics has been statistically challenging. Most researchers have focused on testing for density dependence using time-series of population counts (Taper and Gogan 2002, Turchin 2003), but criticisms of non-independence between axes (Elkington 2000)has caused researchers to develop statistical approaches to address this limitation (Dennis and Taper 1994, Sibly and Smith 1998). Models have been developed to test for linear, non-linear, and higher-order forms of density-dependence that represent different competing hypotheses of the mechanisms of density-dependence (Elkington 2000, Bjornstad and Grenfell 2001). These more complex models often, unfortunately, exceed the resolution of the data to distinguish between because of the quality of count data, as well as the limiting effect of time-series length on detecting density dependence (De Valpine and Hastings 2002, Brook and Bradshaw 2006). More recently, researchers have started to appreciate that these pattern-based approaches based on count data have limited value at exposing the underlying mechanisms of density-dependence (Saether et al. 2007, Abadi et al. 2012).

An alternative approach is to understand the underlying processes (e.g., changes in vital rates) driving patterns of density-dependence. The development of state-space models (Royle et al. 2007, Kery and Schaub 2012) offer a promising solution to some of these statistical and conceptual challenges (Abadi et al. 2012). The ability to integrate the biology and sampling variance while estimating vital rates simultaneously allows us to share information across data types and quality, providing more realistic demographic estimates, including for time-series missing data (Royle et al. 2007, Kery and Schaub 2012). Most studies have applied such state-space models to estimating the strength of density dependence and density independence only with time-series of counts, though, limiting their ability to identify the vital rate mechanisms driving population changes (Ahrestani et al. 2013, Koons et al. 2015, Lee et al. 2015). Developing state-space models using vital rates would be especially useful to identify the most density-dependent vital rate. This approach has been used successfully by combining both information about counts and vital rates (survival, fecundity) for Red-backed shrikes (*Lanius collurio*) to estimate the strength of density dependence in an integrated population model (Abadi et al. 2012). In ungulates, time-series counts have been combined with climatic effects to estimate both density dependence and density independence (Koons et al. 2015, Lee et al. 2015). But, to date, there have been only a few studies that combined counts, vital rate data, and climate data to estimate both density-dependence and density-dependent forces in an integrated population modeling framework for ungulates (Johnson et al. 2010).

Understanding the relative contribution of density-dependent and density-independent drivers of ungulate population dynamics, as well as their possible interaction, is important because of their ecological and economic importance (Gordon et al. 2004). In particular, for mule deer, the evidence for density-dependence seems contradictory (Peek et al. 2002, Bergman et al. 2015). For example, in one study, Peek et al. (2002) showed that both density dependence and climatic variation explained their dynamics, but climatic factors dwarfed the effect of density. White and Bartmann (1998) showed that overwinter survival of fawns interacted strongly with density at extreme densities. However, the bulk of the literature paints only a weak picture of density dependence in both time-series counts, and vital rates (reviewed by Bergman et al. 2015). The relatively weak support for density-dependence in mule deer is especially puzzling given the strong experimental field evidence for it in their close relative, the white-tailed deer (*Odocoileus virginianus*; McCullough 1979, Patterson and Power 2002). A plausible explanation is that across the semi-arid west, mule deer may be a species for which the relative interplay between density-independent and dependent factors is in favor of density-independent climatic variation.

In this study, our objectives were to test for the relative strength of density-dependent and density-independent forces in driving mule deer population dynamics across six population units in Idaho, USA. We developed an integrated population model (IPM, *sensu* Abadi et al. 2012) and incorporate density dependent effects on each of our measured vital rates and weather effects on the most variable vital rate, winter fawn survival. We hypothesize that mule deer populations are limited by frequent weather-caused die-offs, limiting our ability to detect density-dependence. We expect density effects first in recruitment to 6 months of age, then overwinter juvenile survival, and lastly adult survival and thus predict negative density dependence will be strongest in either recruitment or winter fawn survival (Hurley et al. 2011; Bergman et al. 2015). We predict that density dependence should be strongest on recruitment (fawn:adult female ratio in December) due to the interaction of predation and density especially at high density (Chapter 4). Alternatively, density-dependence should be strongest on winter fawn survival (6 months to 12 months old) because of competition on winter range (Bartmann et al. 1992, White and Bartmann 1998). For weather related limitations on vital rates, we hypothesized that the patterns observed with density related reduction and weather reduction will be similar. If this is true, we predict that the addition of an important weather variable to an IPM containing a density dependent term will reduce the density dependent effect. We predict populations that experience the mildest climate will show the strongest effect of density. We predict that populations least likely to show density dependence should be those areas of contiguous good quality habitat that show a strong effect of weather related reductions in fawn survival.

STUDY AREA

Our study area covered a wide climate, predation and habitat gradient of mule deer range in Idaho and is fully described in (Hurley et al. 2016, Chapter 3). We monitored population size, age and sex composition, survival of fawns and adult females, and harvest in six Population Management Units (PMU) across central and southern Idaho. In Idaho, Game Management Units (GMUs) are nested within Population Management Units (PMUs) that are grouped together to represent ecological (interbreeding) populations, which form the basis for management. Through a hierarchical cluster analysis we identified three main habitat types (called ecotypes hereafter) based on the dominant overstory canopy species on summer range; coniferous forests, shrub-steppe, and aspen woodlands and assigned each PMU to a ecotype (Chapter 3). Elevation and topographic gradients within PMUs affect snow depths and temperature in winter, and precipitation and growing season length in the summer, with elevation increasing from the southwest to the northeast. Areas used by mule deer in the winter in conifer ecotypes (Boise River, Central Mountains, and Weiser-McCall) ranged in elevation from 1001 to 1928m, but most were <1450m. Winter precipitation (winter severity) varied widely (from 10 to 371mm) in coniferous GMUs. Coniferous ecotype summer ranges are dominated by conifer species interspersed with cool season grasslands, sagebrush, and understory of forest shrubs. Shrub-steppe PMUs (South Hills) were semi-desert and ranged from 1545 to 2105m, with winter precipitation from 24 to 105 mm. Summer range within shrub-steppe ecotypes was dominated by mesic shrubs (e.g., bitterbrush (*Purshia tridentata*), sagebrush (*Artemsia* spp.), rabbitbrush (*Chrysothamnus* spp.), etc). Aspen ecotype PMUs (Bannock and Caribou) were located in the east and south with winter use areas ranging from 1582 to 2011m, and winter precipitation ranging from 25 to 146 mm. In summer, productive mesic aspen (*Populus tremuloides*) woodlands were interspersed with mesic shrubs.

Because we wanted to associate individual deer to the weather and spatial covariates associated with its seasonal range, we estimated within-GMU level seasonal ranges across all six PMUs (Figure 5-2, Chapter 3). Deer were captured within each PMU in each primary winter range (range 1-6 different winter ranges) in proportion to the distribution of deer and abundance (IDFG unpublished data). Migratory periods were excluded from the seasonal home range estimates; locations between 1 June and 30 September were used for summer ranges and 1 December to 31 March for winter ranges (e.g., Sawyer et al. 2005). We created combined seasonal 95 % kernel density utilization distributions for deer from each winter and summer range by using telemetry locations from all individuals and years for the entire study area (Chapter 3). Climate and habitat information was then summarized within the seasonal home ranges of radiocollared deer for winter and summer, the basis of the spatial covariates.

METHODS

(a) Integrated Population Model Development

We used an integrated population model (IPM) to evaluate the relative strength of density-dependent and density-independent forces on mule deer population dynamics across our six populations. IPMs allow for the incorporation of many different types of population data of varying quality that are integrated into a population model to provide improved rigor in both population estimates and projections (Besbeas et al. 2002, Johnson et al. 2010, Kery and Schaub 2012). Our mule deer data included annual estimates of survival and fecundity from marked individuals, annual harvest data, but only infrequent sightability-adjusted aerial surveys, obviously a key component for evaluating density dependence. To solve the problem of estimating density-dependent effects with only infrequent density estimates, we developed and fit an IPM to six PMUs with varying amounts of empirical data to estimate an annual population density given age-class specific vital rates. We then used this model to test the influence and strength of density on each individual vital rate in the following predicted order from strongest to weakest; fall recruitment, overwinter fawn survival, adult survival. We will first describe the data sources used to parameterize the IPM and then the model structure of the IPM and the methods used to evaluate density dependence and the influence of weather covariate on model fit and the strength of density dependence.

Population estimates

We conducted PMU-wide population surveys using sightability models corrected for visibility bias once every 4-5 years (Unsworth et al. 1994). Surveys were conducted via a Bell 47 helicopter during mid-winter (January - February) for total deer numbers only. We surveyed 100% of subunits (quadrats) that were occupied by deer.

Age and Sex ratio estimates

Early winter fawn:adult female ratios are a measure of age-specific fecundity and fawn survival for the first six months of life. We used helicopter surveys to estimate age and sex composition for each PMU every December (Unsworth et al. 1994). We surveyed a previously defined stratified random sample of medium to high-density subunits. Sampling emphasized obtaining an adequate sample size and representative geographic distribution across each PMU. Adult male:adult female ratios were obtained concurrently with fawn:adult female ratios, however survey design and emphasis was placed on obtaining accurate and precise estimates of fawn:adult female ratios for all PMUs. Adult male:adult female ratios were included in the model when additional survey effort was expended to obtain similar accuracy and precision of fawn ratios To maintain repeatability across PMUs and years, age and sex classification procedure was limited to only three or four primary observers, one of whom would be on every flight along with secondary regional observers. Surveys were conducted between1 December and 31 December, prior to antler shed, with a Bell 47 helicopter.

Survival monitoring

We monitored survival of 1,961 six-month-old male and females and 1,061 adult females (4,776 adult years) within six Population Management Units in southern Idaho, 2001–2013. We varied capture methods as described previously in Hurley et al. (2014; Chapter 2, 3), and deployed 320– 400 gram collars on adults that were permanently affixed, and for female fawns, permanent collars with a temporary pleat or surgical tubing for male fawns that allowed collars to drop off after approximately 8-10 months. All collars had a mortality signal. An Idaho Department of Fish and Game (IDFG) veterinarian or veterinary technician was on site during most captures to assist with sampling and assure animal welfare. Animal capture protocols were approved by the Animal Care and Use Committee, Idaho Department of Fish and Game Wildlife Health Laboratory, Caldwell, Idaho, USA, and University of Montana IACUC (protocol #02-11MHCFC-031811). Deer were monitored with telemetry for mortality from the ground at least once a month between capture (7 December to 15 January) and 1 June. If radio signals could not be detected from the ground within 1 week, animals were located via aircraft. When a mortality signal was detected, cause of death was determined using a standard protocol (Wade and Bowns 1982). Animals that lost radiocollars or with radiocollars that failed were removed (censored) from the analysis at the point of failure.

Harvest estimation

We used harvest data to estimate the ratio of males and females in the IPM. Idaho estimated harvest with a mandatory reporting procedure and a follow up non-response telephone survey (IDFG 2013). The non-response survey accounted for the biased reporting rate based on hunting success and hunter demographics (IDFG 2013). Harvest is specific to antlered vs. antlerless mule deer and number of antler points on male deer.

(b) Integrated Population Model Parameterization

We developed a Bayesian state-space integrated population model (BSS; Besbeas et al. 2002, Kery and Schaub 2012) to both backcast and forecast population density from the combined estimates of vital rates, harvest, and, when available, population abundance. Our estimates of female age class survival, fawn ratios, male:female ratios, harvest data and population estimates have inherent differences in completeness and variance between years. Fortunately, BSS models allow integration of data of varying quality (Kery and Schaub 2012). We used a post-breeding, sex-specific and age-structured matrix model (Caswell 2000) modified from a standard large herbivore model in the timing of inclusion of juveniles as follows (Figure 5-1):

$$\begin{bmatrix} 0 & R & 0 \\ S_j(1-r) & S_{AF} & 0 \\ S_j r & 0 & S_{AM} \end{bmatrix} \begin{bmatrix} N_{jt-1} \\ N_{Ft-1} \\ N_{Mt-1} \end{bmatrix} = \begin{bmatrix} N_{jt} \\ N_{Ft} \\ N_{Mt} \end{bmatrix} \tag{1}$$

where *R* = ratio of fawns to adult females in December, *r* = male fawn sex ratio such that $S_j(1-r)$ = Survival of female fawns from 15 Dec to 31 May, $S_j r$ = Survival of male fawns, S_{AF} = Survival of adult (here defined as older than 1 year old) females from 16 Dec to 15 Dec, and S_{AM} = Survival of adult males from 16 December to 15 December. The model is constructed with a 6-month-post-birth matrix because December is the data collection start or end point for fawn ratios, winter fawn survival, and harvest. An unmeasured life-stage was survival from 12 to 18 months which was included in the S_j estimate as 1 because of the very high expected survival for this 6 month time period (M. Hurley, unpublished data; Hurley et al. 2011). To estimate the total number of deer in the population at 15 December each year, the harvest is subtracted from each age class and then the current number of 6 month-old-fawns (N_y) was added to the estimate (eq. 5, 7, 8). Both information from the individually-based vital rate information and aerial population surveys, and their variances, are combined to provide improved estimates of abundance in all years.

We modeled the number of deer in each age and sex class; 6 to 18 month-old juveniles, adult females, and adult males in years with a Normal approximation of a binomial distribution parameterization as (μ, τ), where $\tau = 1/\hat{\sigma}^2$, and truncated at 0 on the lower bound to prevent MCMC from searching negative values. Six month-old fawns were estimated with:

$$n_{y,t} \sim Norm(N_{AF,t} \times R_t, 1/(N_{AF,t} \times R_t) \times (1 - R_t))) \tag{2}$$

We assumed an even sex ratio of fawns in the ratio estimate on December 15 and modeled the number in the yearling age class, which is dependent on the previous year fawn ratios and winter survival of juveniles, as:

$$n_{j,t} \sim Norm(0.5 \times n_{y,t-1} \times S_{j,t-1}, 1/(0.5 \times n_{y,t-1} \times S_{j,t-1} \times (1 - S_{j,t-1}))) \tag{3}$$

We estimated the number of deer in the adult female class by first estimating the survival of adult females from the previous year as:

$$n_{AF,t} \sim Norm(N_{AF,t-1} \times S_{AF,t-1}, 1/(N_{AF,t-1} \times S_{AF,t-1} \times (1 - S_{AF,t-1}))) \tag{4}$$

We then estimated the total number of adult females in the current year by adding the yearling class (4) and subtracting harvest of both adult and yearling females ($H_{F,t}$):

$$N_{AF,t} = n_{AF,t} + n_{j,t} - H_{F,t} \tag{5}$$

We estimated the number of deer in the adult male class by first estimating the survival of adult males from the previous year as:

$$n_{AM,t} \sim Norm(N_{AM,t-1} \times S_{AM,t-1}, 1/(N_{AM,t-1} \times S_{AM,t-1} \times (1 - S_{AM,t-1}))) \tag{6}$$

Total estimate of adult males is then calculated to include the addition of the yearling class (4) and reductions due to harvest of both adult and yearling males ($H_{M,t}$):

$$N_{AM,t} = n_{AM,t} + n_{j,t} - H_{M,t} \tag{7}$$

The estimate of total population size is then calculated as the summation of young of year, adult females and adult males:

$$N_t = n_{y,t} + N_{AF,t} + N_{AM,t} \tag{8}$$

To account for sampling error in the observed data, we modeled the count and survival using the mean of the data estimated precision as $1/\hat{\sigma}^2$. We used binomial distribution for survival data, and assumed a Normal distribution for the observation model abundance estimates, where abundance estimates were the outcome of a Normal distribution with mean equal to model parameter and the precision parameter was approximated by the estimated standard error from the sightability correction model (Unsworth et al. 1994). This distribution approximation has been shown to be more efficient for fitting count data in a Bayesian IPM than the traditional Poisson distribution (M. Hurley, unpublished data).

The population estimates were distributed as:

$$C_t \sim Norm(N_t, 1/\hat{\sigma}^2_{C,t}) \tag{9}$$

The observed ratio of the young of year (6-month-old fawns) to females ≥ 18 months old (*yf*)was distributed as:

$$YF_t \sim Norm(R_t \times 100, 1/\hat{\sigma}^2_{YF,t}) \tag{10}$$

The observed ratio of males ≥ 18 months old to females ≥ 18 months old (*mf)* was distributed as:

$$MF_t \sim Norm(mf_t \times 100, 1/\hat{\sigma}^2_{MF,t}) \tag{11}$$

We estimated observed survival using the non-parametric Kaplan-Meier (K-M) estimator (Kaplan and Meier 1958) then used a Normal distribution (μ, τ) truncated between 0 and 1 to model survival. Survival of females ≥ 18 months old from 16 December of the previous year to 15 December of the current was distributed as:

$$S_{AF,t} \sim Norm(S_{AF,t}, 1/\hat{s}^2_{SAF,t}) \tag{12}$$

Juvenile survival from 6 months of age to 1 June was distributed as:

$$S_{j,t} \sim Norm(S_{j,t}, 1/\hat{\sigma}^2_{Sj,t}) \tag{13}$$

Testing for Density Dependence

For IPM's built only on count data, the classic parameterization has been to use the simplest form of linear density dependence characterized on the log scale of abundance using Gompertz models (Ahrestani et al. 2013, Koons et al. 2015). To further decompose the effect of density on population growth, we first estimated linear density-dependence in each of our measured vital rates, recruitment (R), winter fawn survival (S_j), and adult female survival (S_{AF}) while holding the other rates constant. We also investigated whether non-linear forms of density dependence provided a better fit to the data using quadratic models. As a first approximation, we used quadratic models ($X+X^2$) to test for evidence of non-linearity. But because model fit was not improved by non-linear forms of density dependence, and converge was rare, we only report linear density-dependence in subsequent models. We created informative priors for the intercepts with μ equal to the mean of the data and precision equal to the standard deviation of observed means. We estimate the standardized effect size of negative density dependence with a non-informative prior ($\beta_{DD} \sim Norm(0, 0.0001)$) on each vital rate as a function of the standardized number of animals estimated with the IPM in the previous year as:

$$Logit(R_t) = \mu R + \beta_{DD} \times ((N_{t-1} - \mu N) / \sigma_N) \qquad (14)$$

$$Logit(S_{j,t}) = \mu S_j + \beta_{DD} \times ((N_{t-1} - \mu N) / \sigma_N) \qquad (15)$$

$$Logit(S_{AF,t}) = \mu S_{AF} + \beta_{DD} \times ((N_{t-1} - \mu N) / \sigma_N) \qquad (16)$$

For time-varying models of juvenile survival we allowed survival to vary from the μ plus or minus a year effect with effect size set to 0 and τ = 50 which approximated the range of survival observed in Idaho from 2001 to 2013:

$$S_{j,t} \sim Norm(0_j, 50), T(-5, 5) \tag{17}$$

where tau (τ) = the standard deviation of the true effect size across years.

Testing for Density Independence in Climatic Drivers

We tested for effect of weather on the strength of density dependence in recruitment by adding a density dependent linear slope to recruitment and modeling overwinter fawn survival using the remotely-sensed variables from the MODIS (Moderate Resolution Infrared Spectroscopy) satellite developed by Hurley et al. (Chapter 3). We focus on overwinter fawn survival for two reasons. First, theory predicts we will see density-dependence first in juvenile survival. Second, previous studies showed climate effects manifested the strongest on overwinter fawn survival both in general in mule deer, and specifically in our study area (Bishop et al. 2005, Hurley et al. 2011). Following our hypothesis, we predict that fitting the IPM with winter fawn survival modeled with climate covariates will improve fit and decrease the strength of statistical density dependence that would mimic density dependence. From Hurley et al. (Chapter 3) we included climate and forage covariates identified as the best predictors of overwinter survival; principal components of the Functional Analysis for fall (FPC), mean % snow cover in January to March (W%snow), and number of weeks with >90% snow cover in November and December (FWeeks).

Because the MODIS satellite system was launched in 2001, we truncated the data from 2001 to 2013. We estimated the distribution for each of these parameters as:

$$\beta_{FPC}, \beta_{W\%snow}, \beta_{FWeeks} \sim Norm(0, 0.35) \tag{18}$$

where 0.35 is the measure of range of observations for these three standardized parameters. We then produced three candidate models including: summer, early winter, and winter; only summer and early winter; and only winter with the following equations:

$$Logit(S_{j,t}) = \mu S_{j,t} + \beta_{FPC} \times FPC + \beta_{FWeeks} \times FWeeks + \beta_{W\%snow} \times W\%snow \tag{19}$$

$$Logit(S_{j,t}) = \mu S_{j,t} + \beta_{FPC} \times FPC + \beta_{FWeeks} \times FWeeks \tag{20}$$

$$Logit(S_{j,t}) = \mu S_{j,t} + \beta_{FWeeks} \times FWeeks + \beta_{W\%snow} \times W\%snow \tag{21}$$

Bayesian Model Fitting

We used Markov chain Monte Carlo (MCMC) algorithms to fit IPMs and obtain estimates (Besbeas et al. 2002, Abadi et al. 2012, Kery and Schaub 2012). Posterior distributions of model parameters were estimated by running three parallel chains of 500,000 iterations each with a burn-in of 200,000. We retained every 15th sample resulting in 60,000 samples to produce posterior distributions. We assessed model convergence by visually examining trace plots and posterior distributions for each parameter and assessed convergence with the Rhat statistic (Gelman et al. 2014). We estimated marginal distributions for the posterior likelihoods of model parameters with JAGS 3.4.0 (Plummer 2003), through the R2jags package in R 3.12 (Su et al. 2015). We specified non-informative prior distributions for all parameters estimated in each model, truncated at 0 on the lower distribution tail of population size estimates and truncated between 0 and 1 for survival estimates. We initialized population size of each age class using the mean total counts and the proportion animals in each age class determined by ratio estimates. We used a normal distribution with a vague precision (Brooks et al. 2004). We also used normal priors with mean recruitment or survival data and vague precision (0.0001).

RESULTS

(a) Density dependence on vital rates

We first estimated the influence of density on vital rates by applying density dependent (DD) terms on each of the individual vital rates for all PMUs. Of the simple models we evaluated (one DD term each) density dependence effects on recruitment was the most supported vital rate, followed by juvenile survival through winter, and then adult female survival (Table 5-1). Boise River was the exception where density dependence on juvenile survival was most supported with a lower DIC (Δ DIC = 4.5). Applying density dependence to adult female survival increased the DIC > 40% from the best model in all PMUs suggesting poorer overall IPM fit.

(b) Strength of density dependence on recruitment

We used the most supported model from Table 1, density dependence of recruitment and time varying juvenile survival to compare the strength of density across our environmentally diverse study areas. The strength of density dependence (effect size) declined in this order: South Hills, Boise River, Bannock, Central Mountains, Weiser-McCall, and Caribou (Table 5-2, Figure 5-2). Boise River and

South Hills were both predicted to have the strongest negative density dependence as we observed, β_{DD} = -0.759, SD = 0.692 and β_{DD} = -0.165, SD = 0.81 respectively. Caribou (β_{DD} = 0.085, SD = 0.046) was the only PMUs that displayed no negative density dependence in recruitment (Table 5-2, Figure 5-2, 5-6) as we predicted.

(c) Density or weather

We used the best model from each of 3 model sets; 1) density dependence on recruitment and time varying juvenile survival (density only), 2) time varying recruitment and juvenile survival modeled with weather covariates (weather only), and 3) density dependence on recruitment and juvenile survival modeled with weather covariates (density + weather) to test the effects density and weather across the 6 PMUs. For four of the six PMUs, the most supported model considered a density dependent term on recruitment and time varying winter fawn survival (DDO; Table 5-3). The two exceptions were Boise River and Central Mountains, where the weather effects on juvenile survival with time varying recruitment models were most supported (weather only; Table 5-3). The addition of weather covariates to the density dependent models decreased the magnitude of the effect of density dependence on recruitment in all PMUs with the exception of Caribou, where the effect changed from slightly positive to a highly variable negative effect(β_{DD} = 0.085, SD = 0.046 vs. β_{DD} = -0.389, SD = 0.493; Table 5-3). The resulting weather plus density models fit the data poorly in contrast to the density only models as displayed in Figures 5-3 and 5-4. In general, we found density of the previous year depressed recruitment in the following year, thereby limiting population growth in most populations in Idaho.

(d) Effects of Weather

We found variation between PMUs in density-independent weather effects, and the strength or each weather covariate on population growth (Table 5-3, Figure 5-5). For the late summer forage quality (FPCA) measure, we found a strong negative effect on mule deer abundance in Boise River, and a weak effect on the Central Mountains and Weiser-McCall PMUs. In Bannock, Caribou, and South Hills, late summer forage conditions increased mule deer abundance (Table 5-3, Figure 5-6). Similarly, the number of fall weeks covered by snow had no consistent effects on Bannock, Caribou, Central Mountains, but negative effects on abundance in Boise, South Hills and Weiser-McCall (Figure 5-5). Finally, winter snow cover from January to March had strong negative effects only on the Boise PMU where density-dependence was also strong. In all other units, even when winter severity was included as a covariate in some models, the effect was weak with posterior estimates overlapping zero (Figure 5-5).

Contrary to our predictions, we did not observe a clear pattern of weather effects in relation to effect size of density dependence in recruitment. There was no clear negative relationship between the strength of density-dependence and the strength of density-independence within a PMU for any of the climatic covariates considered here (Figure 5-5). In fact, if anything, there was some evidence for interactive effects of density and climate insomuch that the units that experienced the strongest signs of density dependence (Boise, South Hills) also experienced the strongest climatic effects (Figure 5-2, 5-6).

DISCUSSION

Our first prediction, that mule deer populations are primarily weather limited and thus will not experience density dependent reductions in vital rate was only partially supported. Weather effects were more important than density in 2 of our 6 populations, the remaining showed some evidence that density was more important. We observed the strongest density dependent effect in recruitment, followed by winter fawn survival and finally adult survival constant with our predictions. The pattern of density dependence within these vital rates were consistent with those predicted and documented for a variety of ungulate species (Eberhardt 2002, Gaillard and Yoccoz 2003). We observed a reduction in the strength of density parameter when weather covariates were added but at the same time a significant overall reduction in model fit, clouding the interpretation of this prediction. The effect of density-dependence was not replaced with weather effects as we predicted. It was unclear whether this change in parameter strength was a biological effect or reduction in model fit, it could also be due to the interaction of density and weather effects. Lastly, density dependent effects decreased with increasing environmental severity, as we predicted.

Our empirical evidence is similar to Coulson (2000) in that density dependence in ungulates was population specific, especially in the highly variable environmental conditions. In addition to being population-specific, within a population we observed one year experiencing density effects and effects related to weather in the next. The interactive effects of age, weather, and predation can in some cases mimic density effects and combinations of age structure, weather, and density dependence can lead to similar population sizes with very different trajectories (Coulson et al. 2001). Environmental stochasticity in resource availability and climate can affect population dynamics though reduced quality of summer forage, thereby reducing pregnancy and juvenile survival (Cook et al. 2004, Chapter 2). Two studies reported single species exhibiting density dependence in one population and not another based on latitude (Post 2005, Ahrestani et al. 2013). Therefore, predicting ungulate population dynamics may depend on idiosyncratic knowledge of the relative strength of density-dependent and independent drivers on a population specific basis.

The pattern of density dependence within our observed vital rates, recruitment > overwinter survival > adult survival, was consistent with those predicted and documented for a variety of ungulate species (Eberhardt 2002, Gaillard and Yoccoz 2003). This is not unexpected because our recruitment measure, fawn ratio in December, is a measure of pregnancy, fetal rate, and young survival of both primiparous and multiparous mothers. These are the vital rates assumed to be first affected by density in ungulates (Bonenfant et al. 2009). As evidence, we have observed highly variable yearling pregnancy rates in our study area, varying from 12% to 80% although pregnancy is stable for older animals (M. Hurley, Unpublished data). These results have been echoed across temperate ungulate species (Gaillard et al. 2000), and despite the equivocal evidence for density-dependence in vital rates leading to density-dependence in population dynamics of mule deer (Bergman et al. 2015), our study shows that indeed, mule deer populations do respond predictably to increasing density similar to other species.

Another aspect of recruitment, summer neonate fawn survival, may be depressed by density under a predator-mediated density effect discussed in Chapter 4. Effects of density may differ depending if mule deer summer resource selection is best described by an ideal free versus an ideal despotic (territorial) model of habitat selection(McLoughlin et al. 2009). Territoriality during early fawn rearing occurs in many small- to mid-sized ungulates, including mule deer (Mackie et al. 1998). Exclusive space use (territoriality) during fawn rearing may increase recruitment of juveniles by dominant females through exclusive access to high quality forage and low predation risk habitats while displacing subdominant females to lower quality habitat. The described behavior may create a despotic distribution of parturient females across summer range, with an overall reduction of fawn survival as densities increase. In addition to predation risk, the quality of this secondary habitat may be variable with respect to weather conditions, adequate for fawn rearing with high precipitation but nutritionally limited in low precipitation years, as has been observed in roe deer (*Capreolus capreolus*; Pettorelli *et al.* 2005) suggesting density dependence in one year and not the next. Given the strong relationship between winter fawn survival and weather (Hurley et al. 2011, Bishop et al. 2005, Bartmann et al. 1992, Chapter 3) we did not expect overwinter fawn survival to exhibit a strong density effect, consistent with our results. This vital is highly variable (Figure 5-3) and significantly related to weather (Chapter 3), unless latent effect of the resource use described above.

Our results corroborated those of Post (2005) confirming the strength of density dependence decreased as environmental conditions became more severe.

Whereas Post (2005) evaluated the effect of latitude, we observed the same reduction in the strength of negative density dependent strength in our study areas (Caribou, Bannock, and Weiser-McCall) where severe winters or decrease summer forage quality are common, resulting in variable fawn survival and population fluctuation. We did not explicitly test interactions here because of the modeling complexity involved in fitting interactions between density and up to 3 climate covariates, adding another 3-9 parameters to complex IPM models. We recognize this as an important limitation of our study, given the recognized importance of climate-density interactions in ungulate ecology (Portier et al. 1998; Hebblewhite 2005). Regardless, there was only weak evidence for effects of density changing when in the presence of weather covariates in IPM models. Our best models were either density dependent or weather dependent, and spatially distinct. The weather-limited populations were in similar habitats in Central Idaho. We predicted that if populations were truly density independent the addition of weather covariates would decrease the strength of density dependence as we observed. However, the addition of weather covariates to model fawn survival from 6 months to 1 year old to our density dependence models decreased the model fit in all of the PMUs.

We have used an integrated population model to test the effects of density and weather on mule deer populations 6 spatial distinct mule deer populations. The resulting models separated vital rate specific effects of density and weather while simultaneously estimating other vital rates given these effects. These models will vastly improve our understanding of the importance of each vital rate to population dynamics. We conclude that mule deer population dynamics are similar to other ungulates, experiencing the density dependent influences as modified by both summer nutrition and winter energy expenditure.

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TABLES

Table 5-1. Integrated Population Model (IPM) model selection for mule deer (*Odocoileus hemionus*) for 6 Population Management Unit (PMU), Idaho, 2001 – 2013. Shown is the model structure with density dependent (dd) terms added on each vital rate (R- recruitment, jS – juvenile survival, fS – adult female survival, mS – adult male survival) and the prefix denotes dd = density dependence, c = vital rate varies within a given distribution of the global mean for the PMU, and t = vital rate varies within a given distribution for an annual mean. Model diagnostics are the Deviance Information Criteria (DIC), effective number of parameters (pD), Deviance, and parameter estimates for density dependence (DD), and the standard deviation of density dependence (DD SD).

PMU	**Model**	**DD**	**DD SD**	**DIC**	**pD**	**Deviance**
Bannock	ddR_tjS_cfS_cmS	-0.139	0.043	201.2	22.6	178.5
Bannock	tR_ddjS_cfS_cmS	-0.402	0.063	235.4	21.4	214.0
Bannock	cR_ddjS_cfS_cmS	-0.434	0.057	260.7	14.8	245.9
Bannock	ddR_cjS_cfS_cmS	0.067	0.063	282.8	16.2	266.6
Bannock	cR_cjS_ddfS_cmS	0.076	0.059	283.9	11.7	272.1
Boise River	tR_ddjS_cfS_cmS	0.332	0.064	668.1	76.6	591.5
Boise River	ddR_tjS_cfS_cmS	-0.759	0.692	672.6	106.2	566.4
Boise River	cR_cjS_ddfS_cmS	-4.164	0.812	903.7	74.4	829.3
Boise River	cR_ddjS_cfS_cmS	0.284	0.080	1,075.0	105.7	969.2
Boise River	ddR_cjS_cfS_cmS	-0.085	0.032	1,100.7	125.3	975.4
Caribou	ddR_tjS_cfS_cmS	0.085	0.046	209.3	20.6	188.7

Caribou	tR_ddjS_cfS_cmS	-2.304	0.445	298.0	34.9	263.1
Caribou	cR_ddjS_cfS_cmS	-3.514	0.749	465.2	63.3	401.9
Caribou	cR_cjS_ddfS_cmS	1.411	0.233	608.1	44.4	563.6
Caribou	ddR_cjS_cfS_cmS	0.106	0.075	619.2	34.0	585.2
Central Mountains	ddR_tjS_cfS_cmS	-0.076	0.044	232.7	22.2	210.5
Central Mountains	tR_ddjS_cfS_cmS	-0.159	0.058	244.3	22.5	221.8
Central Mountains	ddR_cjS_cfS_cmS	0.086	0.084	309.5	8.8	300.8
Central Mountains	cR_ddjS_cfS_cmS	-0.002	0.081	312.6	9.3	303.3
Central Mountains	cR_cjS_ddfS_cmS	0.225	0.209	313.6	8.8	304.8
South Hills	ddR_tjS_cfS_cmS	-0.165	0.081	76.3	14.4	61.9
South Hills	tR_ddjS_cfS_cmS	-0.585	0.130	89.7	20.7	69.0
South Hills	cR_ddjS_cfS_cmS	-0.393	0.043	107.2	13.1	94.1
South Hills	ddR_cjS_cfS_cmS	-0.353	0.073	137.2	28.2	109.0
South Hills	cR_cjS_ddfS_cmS	0.274	0.098	188.6	61.7	126.8
Weiser McCall	ddR_tjS_cfS_cmS	-0.119	0.050	340.6	58.6	282.0
Weiser McCall	tR_ddjS_cfS_cmS	-0.966	0.099	401.6	60.2	341.4
Weiser McCall	cR_ddjS_cfS_cmS	-1.385	0.067	538.6	85.9	452.8
Weiser McCall	cR_cjS_ddfS_cmS	1.261	0.260	647.1	42.0	605.1
Weiser McCall	ddR_cjS_cfS_cmS	-0.061	0.077	658.7	54.7	604.0

Table 5-2. Integrated Population Model (IPM) model selection for mule deer (*Odocoileus hemionus*) in 6 Population Management Units (PMU), Idaho, years 2001 – 2013. The model structure includes a density dependent term on recruitment, time-varying juvenile survival, constant adult female survival, and constant adult male survival. Parameter estimates for density dependence (DD) and standard deviations (SD) are provided for density dependence (DD). Model fitting diagnostic are Deviance Information Criteria (DIC), effective number of parameters (pD) and Deviance. In this instance ΔDIC describes the relationship to the PMU specific model set to illustrate departure from the best model when another model is used for constancy of model structure for DD covariate comparisons.

PMU	**Model**	**DD**	**DD SD**	**ΔDIC**	**DIC**	**Deviance**	**pD**
Boise River	Recruitment DD	-0.759	0.692	4.5	672.6	566.4	106.2
South Hills	Recruitment DD	-0.165	0.081	0.0	76.3	61.9	14.4
Bannock	Recruitment DD	-0.139	0.043	0.0	201.2	178.5	22.6
Weiser McCall	Recruitment DD	-0.119	0.050	0.0	340.6	282.0	58.6
Central Mtns.	Recruitment DD	-0.076	0.044	0.0	232.7	210.5	22.2
Caribou	Recruitment DD	0.085	0.046	0.0	209.3	188.7	20.6

Table 5-3: Model selection results for integrated population models comparing model fit for models with density dependence on recruitment only (DDO), effect of weather and density dependence on recruitment (WDD), and the effect of weather without density dependence (WO). We present the top models for each model type in each PMU to test between factors driving population dynamics; density dependence, weather, or both. For models including weather, we report the covariates in each model. Model fitting diagnostic are the Deviance Information Criterion (DIC), Difference from lowest DIC (ΔDIC), Effective Number of Parameters (pD), Deviance, and validation metrics.

	PMU	Model	Weather Covariates	DD	DD SD	ΔDIC	DIC	deviance	pD
DDO	Bannock	(1)		-0.1394	0.0434	0.0	201.2	178.5	22.6
WO	Bannock	(2)	FPC, FWeeks	NA	NA	24.8	226.0	201.7	24.2
WDD	Bannock	(3)	FPC, FWeeks, Winter	-0.0442	0.0246	57.3	258.5	245.3	13.2
WO	Boise River	(2)	FPC, FWeeks	NA	NA	0.0	602.1	521.2	80.9
DDO	Boise River	(1)		-0.7591	0.6919	70.5	672.6	566.4	106.2
WDD	Boise River	(3)	FPC, FWeeks, Winter	-0.2697	0.0487	284.4	886.5	814.4	72.1
DDO	Caribou	(1)		0.0847	0.0459	0.0	209.3	188.7	20.6
WO	Caribou	(2)	FPC, FWeeks	NA	NA	260.5	469.9	434.0	35.9
WDD	Caribou	(3)	FPC, FWeeks, Winter	-0.3893	0.4931	360.3	569.7	501.6	68.1
WO	Central Mtns.	(2)	FPC, FWeeks	NA	NA	0.0	198.9	178.2	20.6
DDO	Central Mtns.	(1)		-0.0756	0.0444	33.9	232.7	210.5	22.2
WDD	Central Mtns.	(3)	FPC, FWeeks, Winter	0.0589	0.0250	62.2	261.0	249.3	11.8
DDO	South Hills	(1)		-0.1653	0.0809	0.0	76.3	61.9	14.4
WDD	South Hills	(3)	FPC, FWeeks, Winter	0.0014	0.0242	15.0	91.3	80.0	11.3
WO	South Hills	(2)	FPC, FWeeks	NA	NA	16.9	93.2	78.0	15.3

DDO	Weiser McCall	(1)		-0.1191	0.0498	0.0	340.6	282.0	58.6
WO	Weiser McCall	(2)	FPC, FWeeks	NA	NA	72.1	412.7	359.8	52.9
WDD	Weiser McCall	(3)	FPC, FWeeks, Winter	-0.0376	0.0198	271.1	611.7	553.6	58.1

Model Structure:
1. Density dependence on recruitment and time varying juvenile survival.
2. Time varying recruitment and juvenile survival modeled with weather covariates.
3. Density dependence on recruitment and juvenile survival modeled with weather covariates.

FIGURES

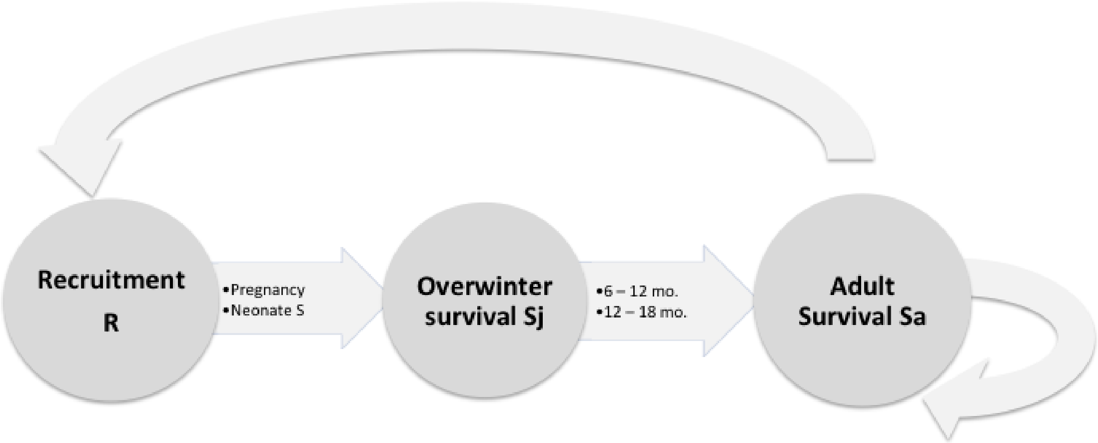

Figure 5-1. Basic age-structured life-cycle for the post-breeding birth pulse matrix model used as the basis for the Integrated Population Model (IPM) for mule deer (*Odocoileus hemionus*) in Idaho. Here, we start the recruitment of individuals as 6 month olds as estimated from fawn to adult female ratio counts in December, estimate survival through winter and summer, and recruit into the adult population at age 18 months. Only adults reproduce as the age of first reproduction is 2 in mule deer.

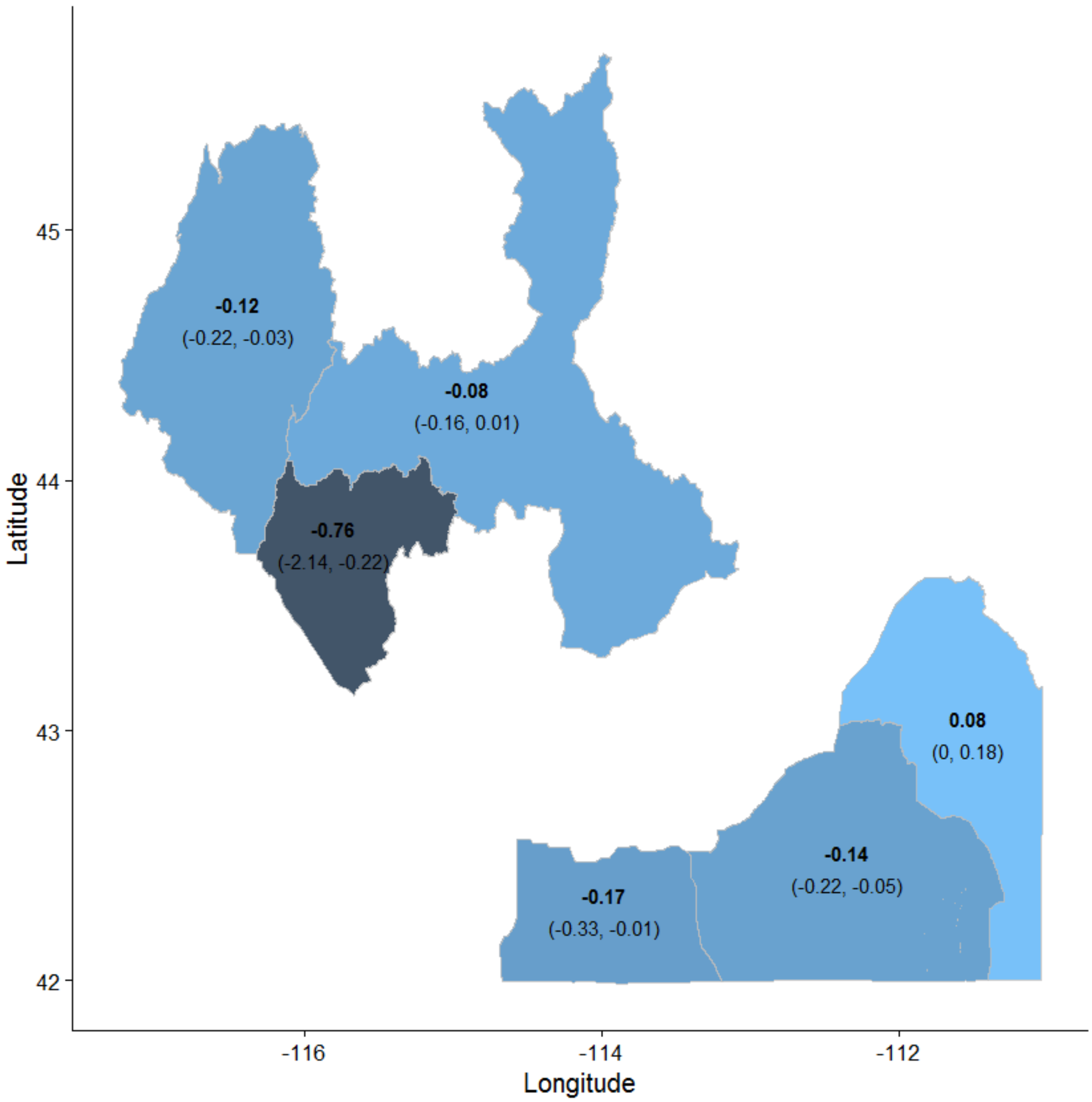

Figure 5-2. Spatial map of the strength of density-dependent population growth rate for Mule deer (*Odocoileus hemionus*) populations estimated with an integrated population model in Idaho, 2001-2013.

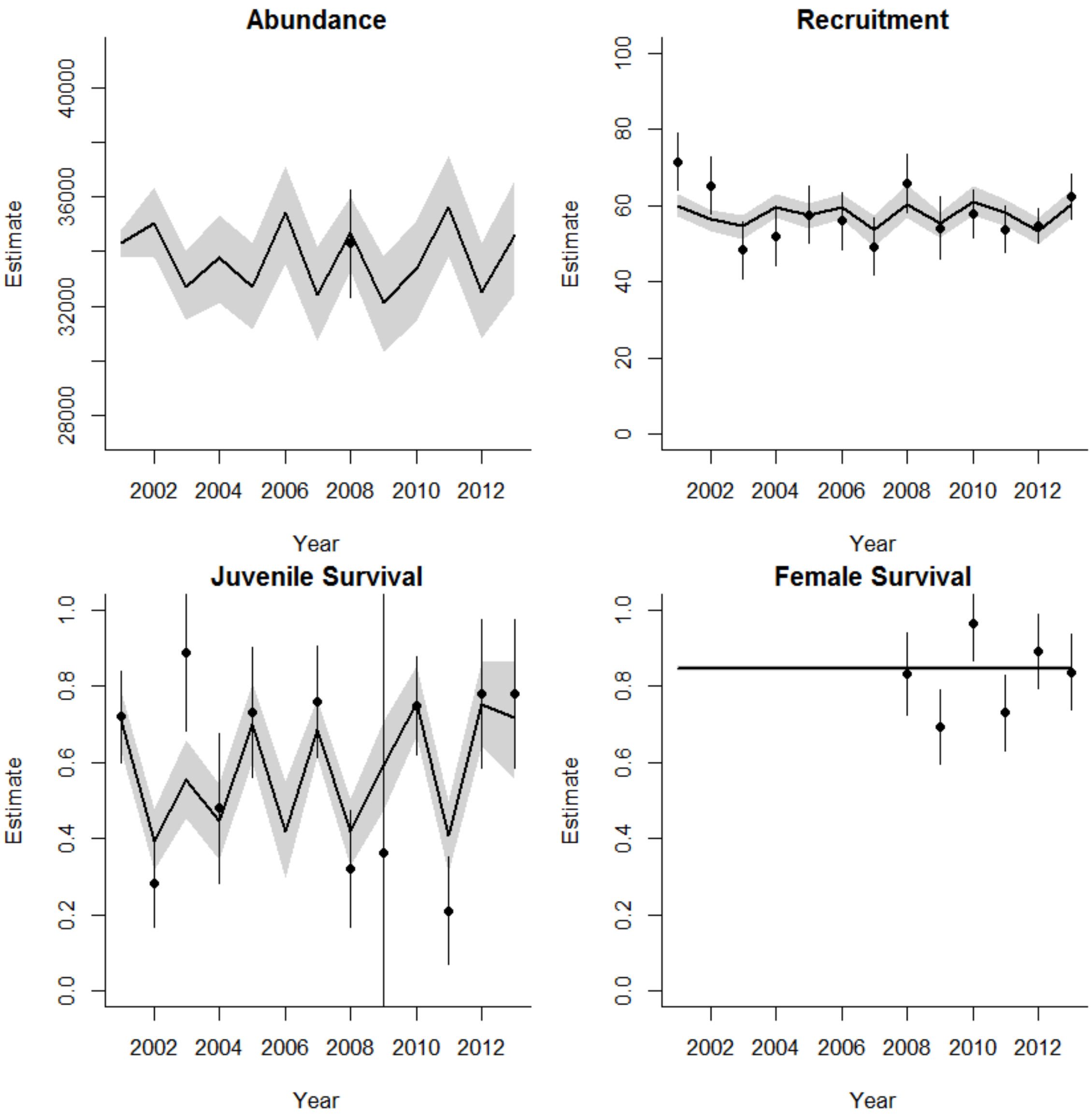

Figure 5-3. Integrated population model (IPM) projections for Mule deer (*Odocoileus hemionus*) in the Bannock population management unit (PMU), Idaho, 2001-2013, showing **time varying juvenile survival**, constant female survival, and population abundance estimates consistent with a density-dependent effect on recruitment only. Lines indicate posterior mean estimate with 95% credible interval (grey shading). Points are field data with 95% confidence interval.

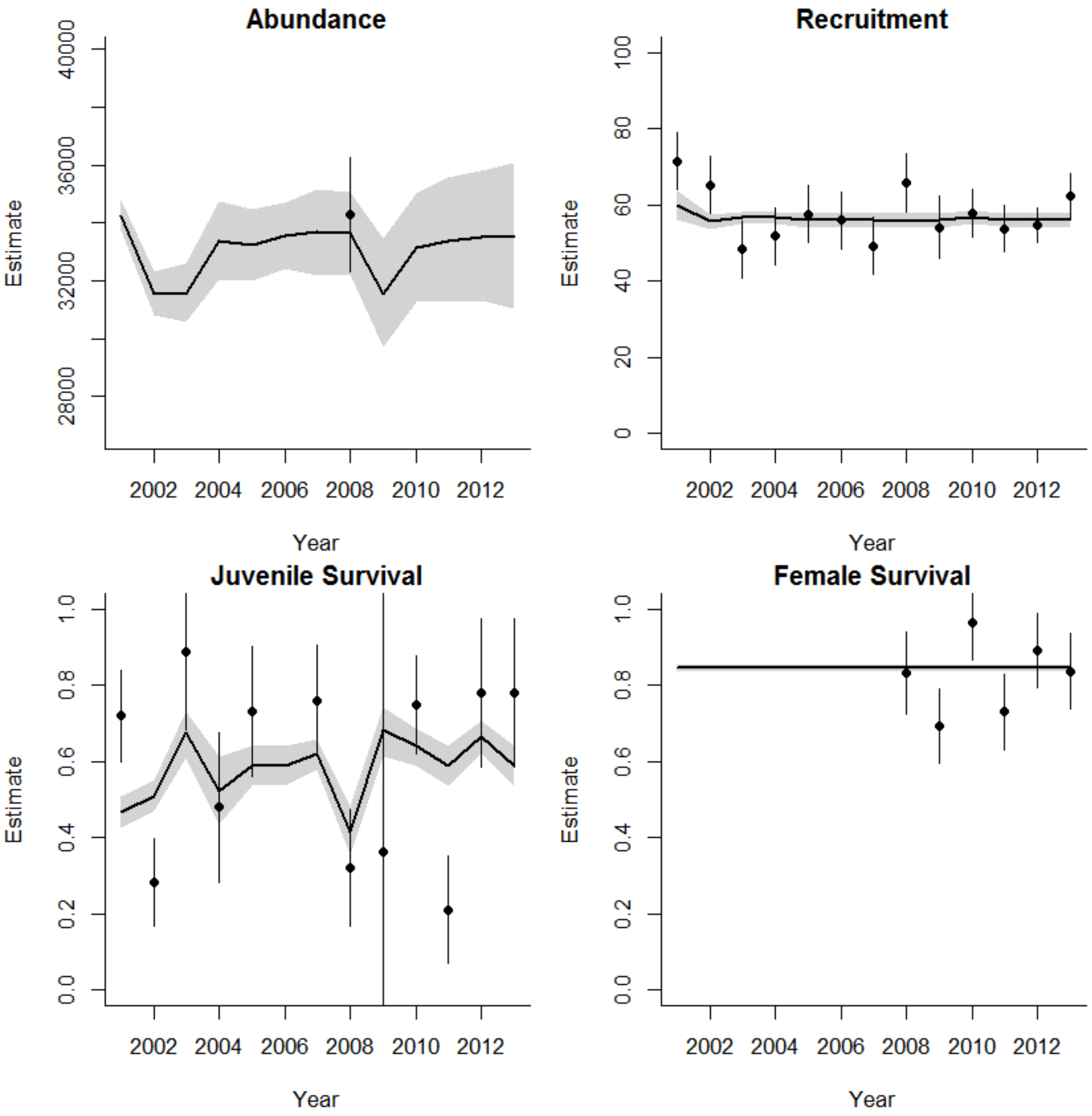

Figure 5-4. Integrated population model (IPM) projections for mule deer (*Odocoileus hemionus*) in the Bannock population management unit (PMU), Idaho, 2001 - 2013, **weather modeled juvenile survival**, constant female survival, and population abundance estimates consistent with a density-dependent effect on recruitment. Lines indicate posterior mean estimate with 95% credible interval (grey shading). Points are field data with 95% confidence interval.

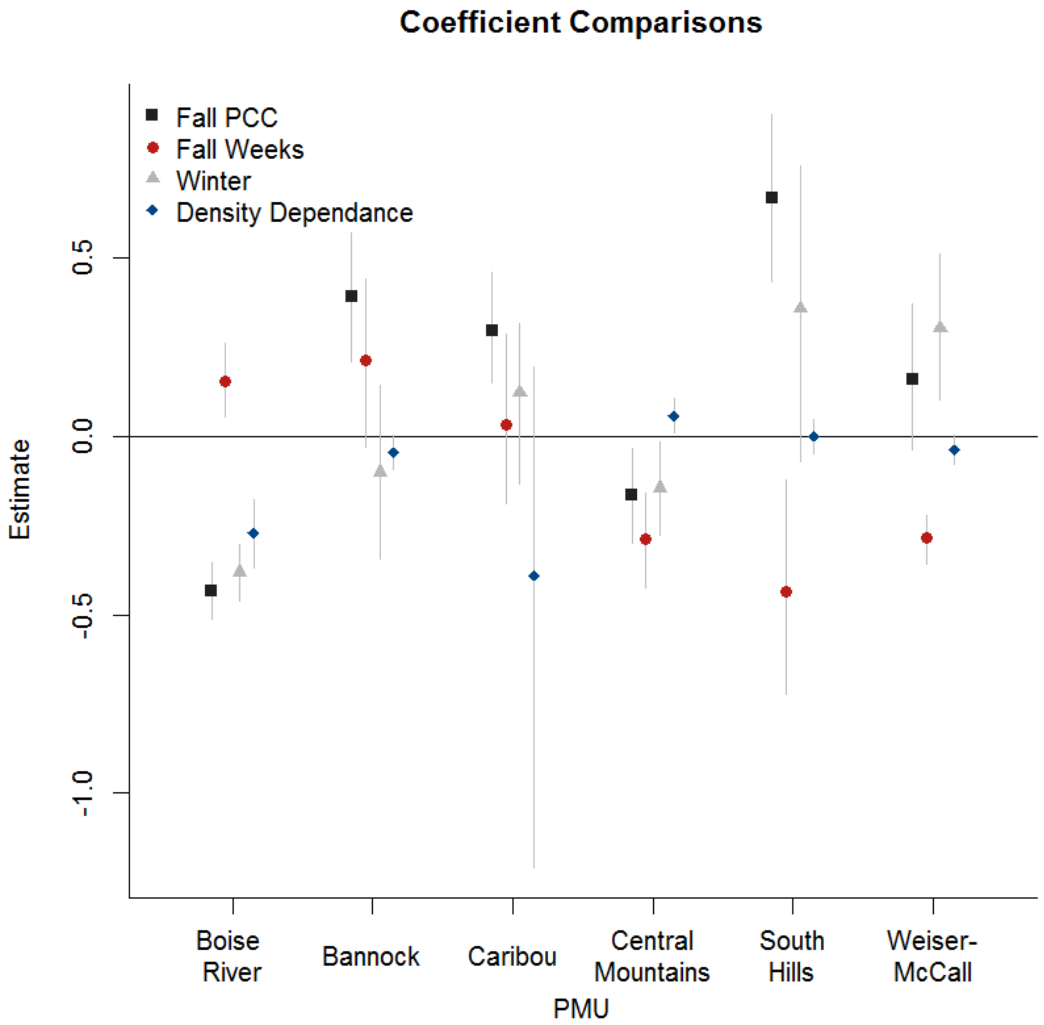

Figure 5-5. Comparisons of parameter estimates for standardized density dependence in vital rates (recruitment) and the best density-independent (weather, forage) covariates on mule deer (*Odocoileus hemionus*) populations in Idaho, 2001 – 2013.

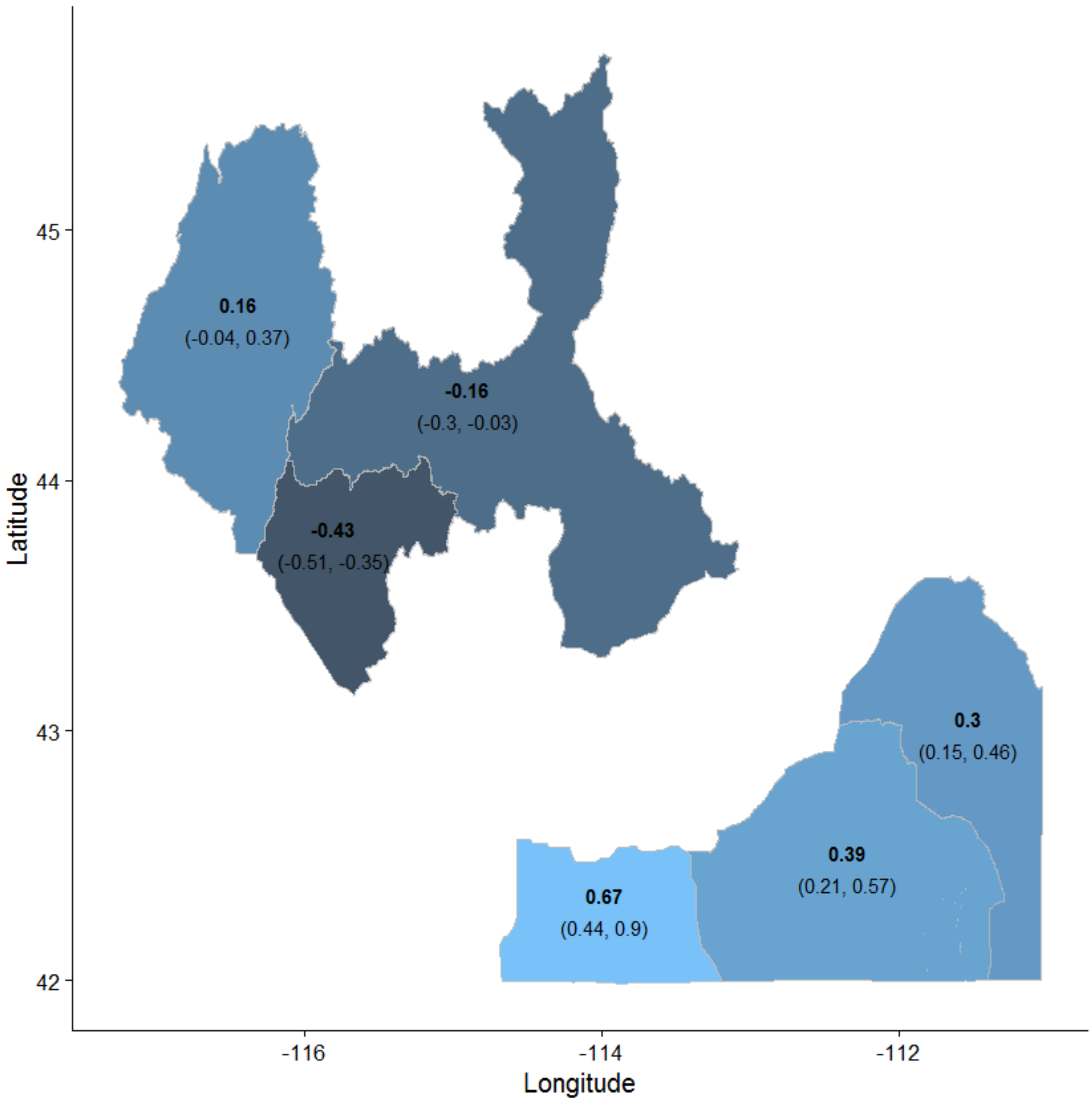

Figure 5-6. Spatial map of the strength of density-independent effects on population growth rate from annual variation in late summer forage quality for mule deer (*Odocoileus hemionus*) populations estimated with an integrated population model in Idaho, 2001-2013.

APPENDIX C. SUPPLEMENTAL MATERIALS

Table 5_S1: Model selection results for integrated population models for mule deer (*Odocoileus hemionus*) with weather covariates. The overall models contain data from all Population Management Units (PMU) and all years. Table A compares the best fitting models with varying covariates. Table B compares only the shorter model with covariates Fall PCC and Fall Weeks for each PMU. The models compare the effects of weather on time varying recruitment and constant juvenile and adult survival with no density dependence. For all models, we report the Deviance Information Criterion (DIC), Difference from lowest DIC (ΔDIC), Effective Number of Parameters (pD), Deviance, and validation metrics.

A.

PMU	**Model**	**Covariates**	**DIC**	**deviance**	**pD**
Bannock	tR_cjS_cfS_cmS_pe_vars.txt	Fall PCC,Fall Weeks	225.9528	201.7095	24.24338
Boise River	tR_cjS_cfS_cmS_pe_vars.txt	Fall PCC,Fall Weeks,Winter	562.5027	491.7094	70.79338
Caribou	tR_cjS_cfS_cmS_pe_vars.txt	Fall PCC,Fall Weeks	469.8585	433.963	35.89542
Central Mtns.	tR_cjS_cfS_cmS_pe_vars.txt	Fall PCC,Fall Weeks	198.8568	178.2267	20.63008
South Hills	tR_cjS_cfS_cmS_pe_vars.txt	Fall PCC,Fall Weeks,Winter	90.2703	74.40333	15.86698
Weiser McCall	tR_cjS_cfS_cmS_pe_vars.txt	Fall PCC,Fall Weeks	412.6944	359.8169	52.87749

Best with just weather (No DD)

B.

PMU	Model	Covariates	Δ DIC	DIC	deviance	pD
Bannock	tR_cjS_cfS_cmS_pe_vars.txt	Fall PCC,Fall Weeks	0	225.9528	201.7095	24.24338
Boise River	tR_cjS_cfS_cmS_pe_vars.txt	Fall PCC,Fall Weeks	39.58291	602.0857	521.2034	80.88227
Caribou	tR_cjS_cfS_cmS_pe_vars.txt	Fall PCC,Fall Weeks	0	469.8585	433.963	35.89542
Central Mtns.	tR_cjS_cfS_cmS_pe_vars.txt	Fall PCC,Fall Weeks	0	198.8568	178.2267	20.63008
South Hills	tR_cjS_cfS_cmS_pe_vars.txt	Fall PCC,Fall Weeks	2.973442	93.24375	77.97827	15.26547
Weiser McCall	tR_cjS_cfS_cmS_pe_vars.txt	Fall PCC,Fall Weeks	0	412.6944	359.8169	52.87749

Shorter model with best overall results with just weather (No DD)

Table 5_S2: Model selection results for overall winter mule deer (*Odocoileus hemionus*) fawn survival with weather density dependence and covariates. The overall models contain data from all Population Management Units (PMU) and all years. The models compare the effects of weather density dependence on recruitment with constant juvenile and adult survival. For all models, we report the Deviance Information Criterion (DIC), Effective Number of Parameters (pD), Deviance, and validation metrics.

PMU	**Model**	**Covariates**	**DD**	**DD SD**	**DIC**	**deviance**	**pD**
Boise River	Weather DD	Fall PCC,Fall Weeks,Winter	-0.270	0.049	886.5	814.4	72.1
South Hills	Weather DD	Fall PCC,Fall Weeks,Winter	0.001	0.024	91.3	80.0	11.3
Caribou	Weather DD	Fall PCC,Fall Weeks	0.048	0.018	544.6	505.2	39.4
Central Mtns.	Weather DD	Fall PCC,Fall Weeks,Winter	0.059	0.025	261.0	249.3	11.8
Bannock	Weather DD	Fall PCC,Fall Weeks	0.128	0.052	251.4	238.9	12.6
Weiser McCall	Weather DD	Fall PCC,Fall Weeks	0.237	0.042	609.8	515.1	94.7

Best overall model for Weather with DD

Table 5_S3: Model selection results for overall winter mule deer (*Odocoileus hemionus*) fawn survival with weather density dependence and covariates. The overall models contain data from all Population Management Units (PMU) and all years. The models compare the effects of weather density dependence on recruitment with constant juvenile and adult survival. These results are based on the full model as compared to Table 5_3 where the “best” models were chosen for each PMU. For all models, we report the Deviance Information Criterion (DIC), Difference from lowest DIC (ΔDIC), Effective Number of Parameters (pD), Deviance, and validation metrics.

PMU	**Model**	**Covs**	**DD**	**DD SD**	**ΔDIC**	**DIC**	**deviance**	**pD**
Caribou	Weather DD	Fall PCC,Fall Weeks,Winter	-0.389	0.493	25.1	569.7	501.6	68.1
Boise River	Weather DD	Fall PCC,Fall Weeks,Winter	-0.270	0.049	0.0	886.5	814.4	72.1
Bannock	Weather DD	Fall PCC,Fall Weeks,Winter	-0.044	0.025	7.1	258.5	245.3	13.2
Weiser McCall	Weather DD	Fall PCC,Fall Weeks,Winter	-0.038	0.020	1.9	611.7	553.6	58.1
South Hills	Weather DD	Fall PCC,Fall Weeks,Winter	0.001	0.024	0.0	91.3	80.0	11.3
Central Mts.	Weather DD	Fall PCC,Fall Weeks,Winter	0.059	0.025	0.0	261.0	249.3	11.8

Full model for Weather with DD, seemed to work the best for a majority of the PMUs’.

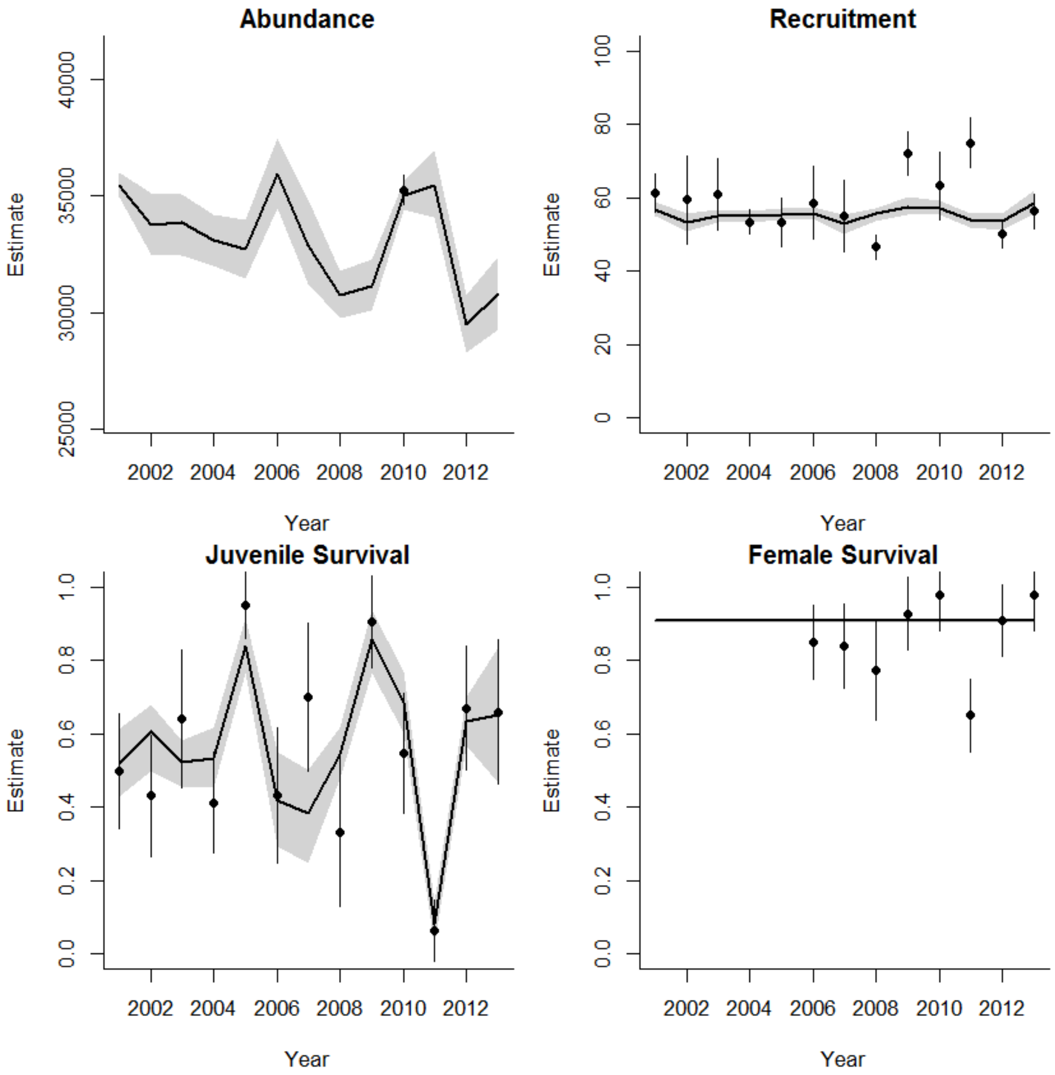

Figure 5-S1. Integrated population model (IPM) projections for mule deer (*Odocoileus hemionus*) in the Weiser-McCall population management unit (PMU), Idaho, 2001-2013, showing time varying juvenile survival, constant female survival, and population abundance estimates consistent with a density-dependent effect on recruitment only. Lines indicate posterior mean estimate with 95% credible interval (grey shading). Points are field data with 95% confidence interval.

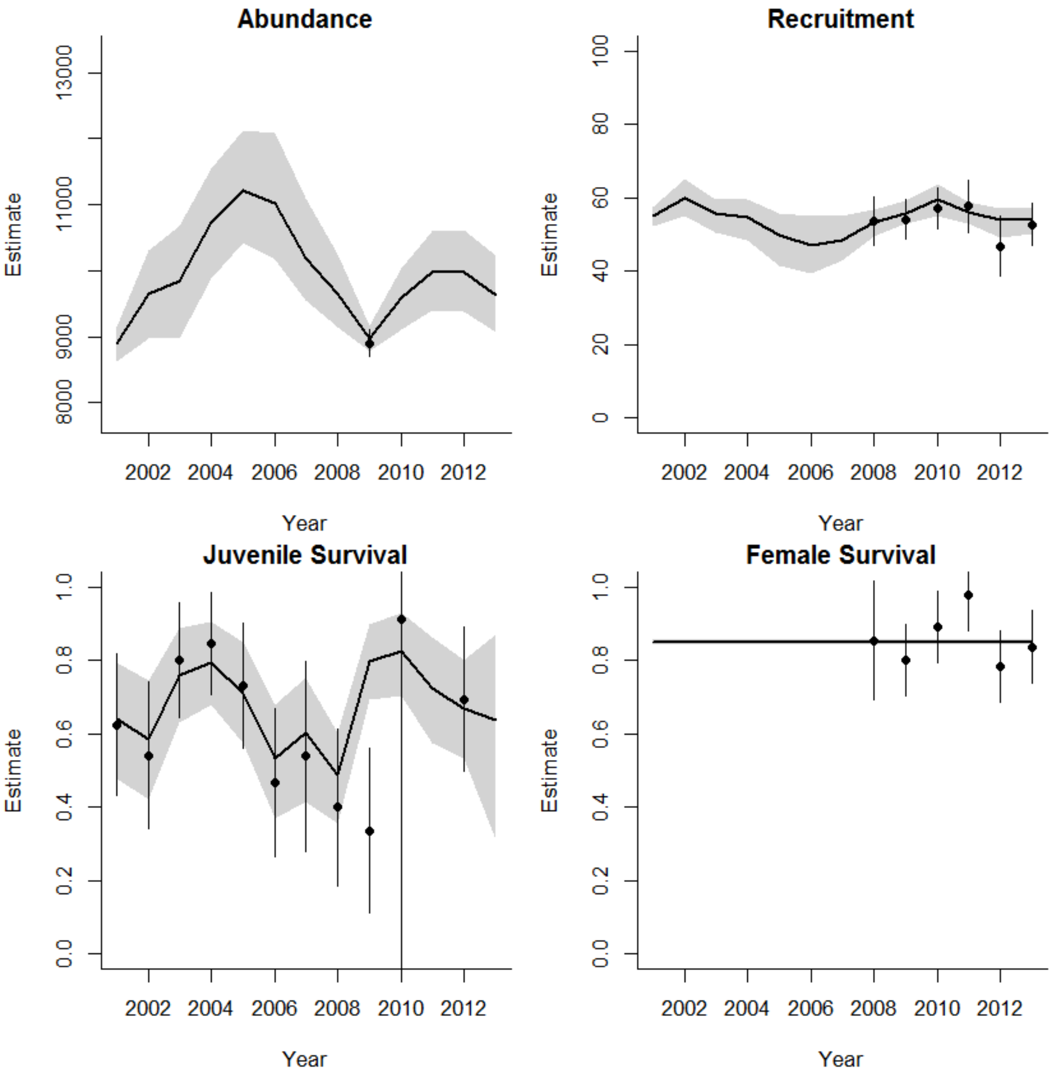

Figure 5-S2. Integrated population model (IPM) projections for mule deer (*Odocoileus hemionus*) in the South Hills population management unit (PMU), Idaho, 2001-2013, showing time varying juvenile survival, constant female survival, and population abundance estimates consistent with a density-dependent effect on recruitment only. Lines indicate posterior mean estimate with 95% credible interval (grey shading). Points are field data with 95% confidence interval.