

Demographic performance of a large herbivore: effects of winter nutrition and weather

NATHAN J. JACKSON ^{1,†} KELLEY M. STEWART ¹ MICHAEL J. WISDOM,²
DARREN A. CLARK ³ AND MARY M. ROWLAND ²

¹Department of Natural Resources and Environmental Science, University of Nevada, Reno, Nevada 89557 USA

²United States Forest Service Pacific Northwest Research Station, La Grande, Oregon 97850 USA

³Oregon Department of Fish and Wildlife, La Grande, Oregon 97850 USA

Citation: Jackson, N. J., K. M. Stewart, M. J. Wisdom, D. A. Clark, and M. M. Rowland. 2021. Demographic performance of a large herbivore: effects of winter nutrition and weather. *Ecosphere* 12(1):e03328. 10.1002/ecs2.3328

Abstract. Variation among demographic rates for a population reflects the allocation of available energy by individuals to competing life-history strategies. Species exhibiting slow-paced life histories often prioritize energy allocation to adult survival over any single reproductive event, therefore maximizing future reproductive potential. Survival of adult female ungulates is generally high with little variability, whereas survival of young is lower and often highly variable. When adult survival is high with low variability, juvenile survival may have a proportionally greater effect on population growth or decline. Weather also may affect population dynamics directly by influencing survival of young or adults, or indirectly through changes in nutritional condition of adult females that influence population growth rates. We experimentally manipulated forage availability during winter, by supplementing native forage with high-energy pelleted feed ad libitum, to a subset of a population of mule deer (*Odocoileus hemionus*) to understand the effects of winter nutrition on survival of adult females and their young born the subsequent summer. We evaluated the effects of winter nutrition, individual-based parameters, and environmental covariates on survival of adult female mule deer from 2013 to 2018, and neonatal mule deer from 2014 to 2016. We documented a 26% decrease in annual survival of adult female mule deer in 2017 in response to increased snowpack during the preceding winter. Neonates born to females that receive enhanced nutrition during winter preceding parturition had higher survival to weaning (0.49, SE = 0.12), compared to neonates born to females that did not receive enhanced nutrition (0.29, SE = 0.07). We observed no effect of enhanced winter nutrition on survival of adult females. Our results suggested winter nutrition of maternal females may influence juvenile survival and demonstrates the importance of forage quality available to adult females during mid-pregnancy. Although we were unable to detect an effect of winter forage on survival of adults, direct effects of deep winter snow resulted in lower survival of adult females. Low survival of adult females in our study population is indicative of a declining population.

Key words: adult survival; demographic; drought; juvenile survival; nutrition; *Odocoileus hemionus*; Palmer drought severity index; snow; temperate; winter severity.

Received 27 November 2019; revised 12 July 2020; accepted 27 July 2020. Corresponding Editor: James W. Cain III.

Copyright: © 2021 The Authors. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† **E-mail:** nathanjackson@nevada.unr.edu

INTRODUCTION

Population performance is driven by allocation of available energy by individuals to competing life-history strategies. Long-lived species often

prioritize energy allocation to adult survival over any single reproductive event, therefore maximizing future reproductive potential (Williams 1966, Stearns 1992, Gaillard et al. 2000, Gaillard and Yoccoz 2003, Hadley et al. 2007, Bårdsen

et al. 2008, Morano et al. 2013). A commonly observed trade-off in large mammals is the allocation of energy between current and future reproduction (Stearns 1992, Tavecchia et al. 2005, Bårdsen et al. 2010). That strategy manifests itself in risk-sensitive reproduction, whereby reproductive investment is contingent upon the current nutritional condition of maternal females, and availability of high-quality forage during the spring and summer (Festa-Bianchet and Jorgenson 1998, Monteith et al. 2013). Long life span and large body size in large mammals, combined with seasonal and annual variation in availability of nutritional resources, contribute to the need for such strategies. Further, those strategies allow reproductive effort to vary annually, which allows accumulation of energy stores in poor environmental conditions to invest in future reproductive events (Bårdsen et al. 2011).

Factors influencing survival, reproduction, and population performance in ungulates are complex, interacting, and often are difficult to untangle. Survival of adult female ungulates tends to be high with low variability for most populations, but small changes in adult survival can cause disproportionately large changes in population growth (Gaillard et al. 2000, Hurley et al. 2011, Monteith et al. 2014). Juvenile survival is prone to high annual variation, which frequently affects population growth even though much larger, per-unit changes are needed to alter population growth in contrast to small changes in survival of adults (Gaillard et al. 2000). Nevertheless, survival and recruitment of young is often most indicative of the population growth rate of long-lived mammals (Gaillard et al. 1998).

Large, herbivorous mammals occur in diverse ecosystems ranging from tropical rainforests to arctic tundra (Nowak 1999). Environmental stochasticity leads to fluctuating availability of resources across seasons and years and can directly influence population performance. Consequently, evaluation of the relative importance of seasonal ranges has long been a topic of inquiry regarding performance of ungulate populations in highly variable environments (Mautz 1978, Moen 1978, Cook et al. 2004, Stewart et al. 2005, Couturier et al. 2009, Bårdsen and Tveraa 2012, Monteith et al. 2013, 2014, Shallow et al. 2015). Summer nutrition has been demonstrated to be a critical determining factor influencing

population dynamics of ungulates. Quality of summer range available to ungulates directly influences the replenishment and recovery of body reserves lost over winter (Mautz 1978, Bårdsen and Tveraa 2012), provides energetic currency for females provisioning offspring, and aids acquisition of somatic reserves for the following winter (Moen 1978, Monteith et al. 2013, 2014). Several studies have demonstrated the importance of summer nutrition on reproductive success and population performance of ungulates (Cook et al. 2004, Stewart et al. 2005, Couturier et al. 2009, Monteith et al. 2013, Shallow et al. 2015). Shallow et al. (2015) documented the positive effects of high-quality summer habitat on maternal body condition, reproduction, and neonatal survival in mule deer (*Odocoileus hemionus*) populations in southeast Idaho. Tollefson et al. (2010, 2011) demonstrated the importance of high-quality summer nutrition and documented associated positive effects on mule deer reproduction and recruitment of young by manipulating digestible energy content (forage quality) and intake (forage quantity).

Winter range also plays a crucial role in ungulate population demographics. In temperate and arctic regions, considerable emphasis has been placed on evaluating the effects of winter range on population productivity (Bergman et al. 2015). Winter conditions can be taxing on somatic reserves because individuals are often faced with limited nutrient uptake during energetically demanding conditions (Bender et al. 2007, Bårdsen et al. 2008, 2010). Furthermore, unpredictable climatic conditions that occur in temperate regions can magnify the variable effects of summer and winter conditions on ungulate population performance. Bishop et al. (2009) documented increased overwinter survival of adult and juvenile mule deer, as well as small increases in neonate survival to weaning, resulting from enhanced nutrition during winter. Therefore, quality of forage on seasonal range has the potential to carry over across seasons to help or hinder nutritional condition, reproductive success, and population performance (Monteith et al. 2013).

We assessed the influence of winter nutrition on survival of adult female and neonatal mule deer in a variable environment. We experimentally increased available forage during winter for

a subset of the population to test hypotheses relative to effects of winter nutrition on survival and nutritional condition of adult females, and survival of young born the subsequent summer to weaning. This experimental approach allowed us to measure responses of mule deer relative to contrasting nutritional planes during winter. Our objectives were to (1) evaluate the influence of nutrition during winter on survival of adult female and neonatal mule deer, and (2) identify and evaluate the influence of physical attributes of individuals, environmental, and climatic variables on survival of adult female and neonatal mule deer in a variable climate. We hypothesized that survival of adult females would be negatively influenced by winter snowpack. In addition, we hypothesized that adult females and their offspring that received enhanced winter nutrition would have higher survival than individuals that did not.

MATERIALS AND METHODS

Study area

We conducted our study from 2013 to 2018 on the Starkey Experimental Forest and Range (hereafter: Starkey) managed by the U.S. Forest Service in northeastern Oregon. Starkey (45°12' N, 118°3' W) is positioned in the central portion of the Blue Mountains, a mountain range spanning from south-central Oregon into southeastern Washington (Fig. 1). The Starkey Project was initiated in 1987 following the installation of a 2.4-m fence along the perimeter of 10,125 ha of public land within Starkey (Rowland et al. 1997). The enclosure, designed to prevent immigration and emigration of large herbivores, encompasses a mosaic of forests and grasslands representative of the vegetation communities available in the greater Blue Mountain ecosystem. Topography in Starkey was characterized by gradually sloped uplands separated by drainages with slopes up to 49° and elevations ranging from 1120 to 1500 m. We focused our experiment on the Main Study area and winter feedground of Starkey which encompassed 8673 ha (Fig. 1). The winter feedground is a separate pasture enclosed with the same 2.4-m fence. A subset of the mule deer population voluntarily enters the winter feedground each year through one-way gates where they spend the winter.

Seasons were defined in accordance with a climograph delineated by Stewart et al. (2002), in which months were grouped based on similar ranges of mean temperature and precipitation. Spring was defined as April to June and was characterized by moderate temperatures ($9.1^{\circ} \pm 3.2^{\circ}\text{C}$, SD) and high precipitation (62.1 ± 4.27 mm, SD). Summer was defined as July to September and was characterized by higher temperatures ($16.0^{\circ} \pm 1.8^{\circ}\text{C}$, SD) and low precipitation (22.2 ± 6.2 mm, SD). Autumn was defined as the month of October and was characterized by moderate temperatures (7.3°C) and precipitation (39.5 mm). Winter was defined as November to March, and was characterized by low temperatures ($-0.7^{\circ} \pm 2.2^{\circ}\text{C}$, SD) and high precipitation (60.5 ± 12.7 mm, SD), typically in the form of snow. During the first two years of the study (2014 and 2015), Starkey experienced below average (2–5% below the 17-yr average) winter precipitation, whereas precipitation and snowpack in winter 2015/2016 and 2017/2018 more closely resembled 17-yr average conditions. In winter 2016/2017, Starkey experienced well-above average (25% increase compared to the 17-yr average) amounts of precipitation and snowpack (Fig. 2). In mild winters, precipitation fell mostly as rain rather than snow.

Data collection

Adult female capture and monitoring.—We captured adult female mule deer during mid-November to mid-February from 2013 to 2018 via baited panel traps and drop-nets (Wisdom et al. 1993). Panel trapping occurred both in Main Study and the winter feedground, whereas drop-netting occurred solely in the winter feedground. Captured individuals were restrained, blindfolded, and hobbled before processing. We fit each adult female with a Global Position System (GPS) radio collar equipped with a mortality sensor. We used Lotek 4400S, IridiumTrackM (Lotek, Newmarket, Ontario, Canada), and Vectronics Vertex (Vectronic Aerospace, Berlin, Germany) GPS radio collars. We assessed body condition and nutritional status via palpation scoring, measurement of body mass (kg), and ultrasound measurements of maximum rump fat (mm), biceps femoris (mm), and latissimus dorsi to calculate IFFB (ingest-free body fat; mm; Stephenson et al. 2002, Cook et al. 2010). For females

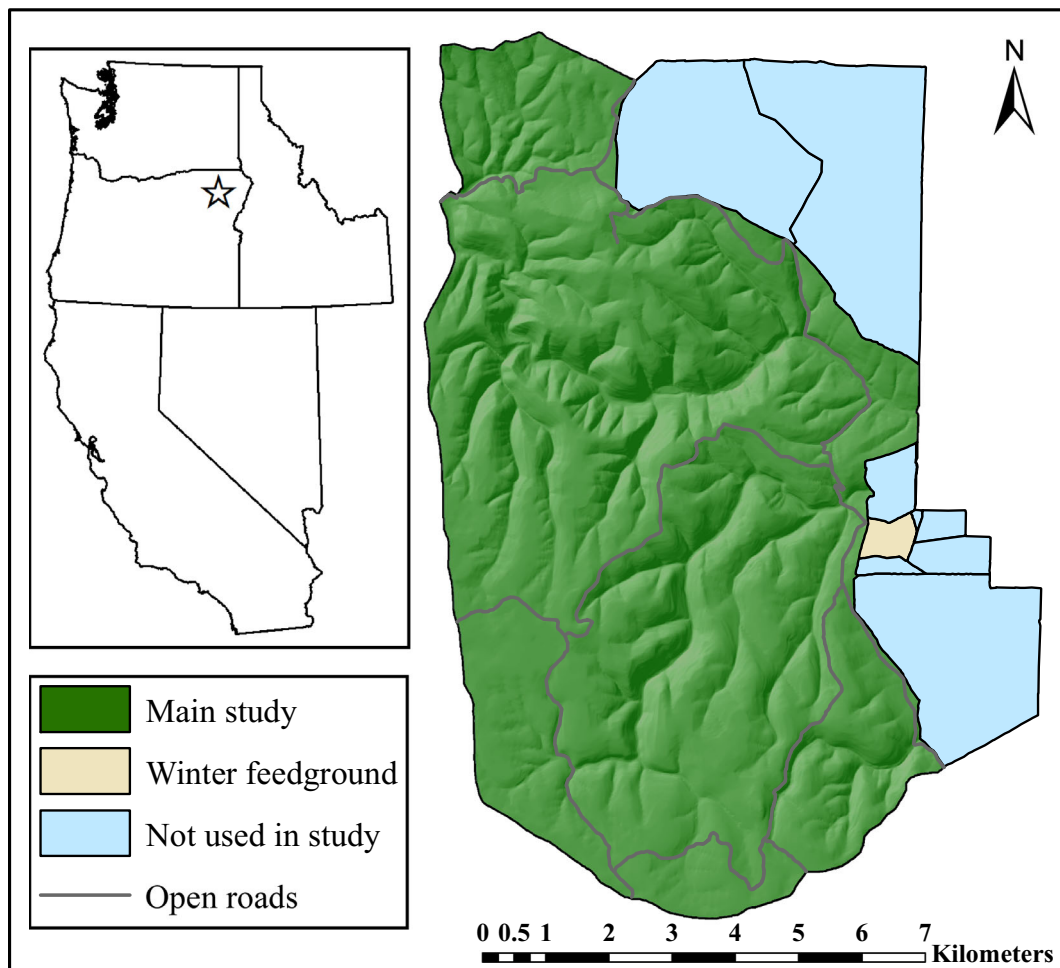


Fig. 1. Map of the Starkey Experimental Forest and Range, Oregon, USA. Main Study is delineated by green hillshade, indicating topography. The tan polygon indicates the winter feedground where a subset of the mule deer population receives supplemental feed during the winter. Areas not used in the study are delineated by blue polygons. Inset map shows the location of the study area (star) relative to Oregon, Nevada, California, Washington, and Idaho, USA.

captured during January or February, we assessed the pregnancy status via ultrasonography. Pregnant females were implanted with a vaginal implant transmitter (VIT; Advanced Telemetry Systems, Isanti, Minnesota, USA; Lotek, Newmarket, Ontario, Canada; Vectronic Aerospace, Berlin, Germany), equipped with temperature and photo sensors to aid in the capture of neonates immediately following parturition (Bishop et al. 2007, 2011). Several individuals were recaptured in multiple years or multiple times per season. Individuals that survived to the next capture season were usually

recaptured, although some individuals did not reenter traps and were not recaptured. Trapping methods limited our ability to recapture all adult females twice each season because animals must enter the traps on their own will to retrieve the bait and trigger the trap. Some individuals were recaptured, but we were unable to resample others because they never entered a trap again that year. Therefore, some individuals were only captured in early or late winter, whereas others were captured in both early and late winter. To estimate early- and late-winter body condition, we designated measurements collected

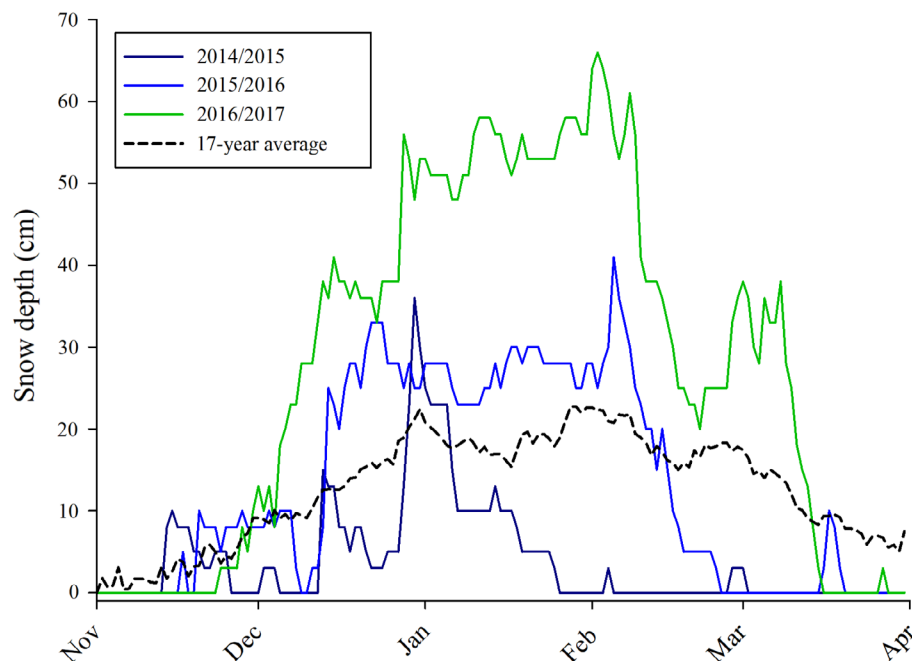


Fig. 2. Daily winter snow depth measurements (2015–2017) acquired from the NRCS-operated SNOTEL weather station (ID- 422) located within Starkey Experimental Forest and Range, Oregon, USA. For simplicity, we display only 3 yr because snow depth in winters 2014 and 2018 closely resembled depths observed in winter 2015.

November–December were considered early winter, whereas measurements collected in January–February were considered late winter. For individuals captured in subsequent years, we collected the entire suite of measurements listed above and fit them with a new GPS collar and VIT if pregnant. We did not extract teeth during capture to evaluate the effects of age on survival of adult females; however, there is evidence suggesting that mortality senescence may occur after 7 yr and decrease survival rates in some ungulate species (Loison et al. 1999).

All mule deer in our study were free-ranging during summer in the Main Study area, with access to similar nutritional resources. Individuals that voluntarily entered the winter feed-ground in December and January were retained until late March, when they were released back into Main Study. Approximately one-third (5–8) of the individual mule deer captured annually spent the winter in the winter feed-ground, where they had access to a daily high-energy supplement in the form of pelleted feed (CHS, Sioux

Falls, South Dakota, USA) developed to meet the nutritional requirements of cervids. We distributed feed *ad libitum* from early January to late March ensuring that all animals on the winter grounds had daily access to enough supplemental feed to meet or exceed nutritional requirements. Each winter we counted the number of mule deer on the feedground, which allowed us to calculate the amount of daily feed required to support the overwintering population. This experiment allowed us to evaluate survival of adult female mule deer and their offspring under varied levels of winter nutrition. Proximity to the feedgrounds appeared to be the primary factor determining whether animals entered the feedground or not. Animals with summer home ranges in the southern portion of the Main Study area tended to enter the feed-ground and returned there each year regardless of nutritional condition.

We monitored collared individuals using VHF (very high frequency) telemetry and Iridium satellite alerts throughout the year for detection

of mortality signals. We monitored adult females using VHF telemetry on a weekly basis throughout most of the year with few exceptions. Mortality sensors on collars were set to document a mortality event after 8 h of inactivity. We investigated mortality events as soon as possible upon detection in an effort to assess cause-specific mortality. Exact dates of mortality were determined from patterns in GPS location data (i.e., lack of movement).

Neonate capture and monitoring.—We captured neonatal mule deer during May to June from 2014 to 2016. Neonate captures were initiated by signal detection of an expelled VIT. For collared females not implanted with a VIT or with a failed VIT, we used VHF telemetry to obtain visual observations of these individuals every 1–2 d to assess parturition status. Subsequently, we conducted a search for neonates in the location where the female was last observed, and limited search times to 30 min. If neonates were not located within 30 min, we relocated the female the following day to conduct an additional 30-min search. We captured neonates by hand, and blindfolded individuals before data collection and processing. We fitted each neonate with a VHF transmitter with an elastic collar that was designed to expand as they grew and fall off before it impeded growth (Advanced Telemetry Systems, Isanti, Minnesota; Vectronic Aerospace, Berlin, Germany). Neonate collars were programmed to document a mortality event after 10 h of inactivity, to reduce the frequency of false mortality signals. We collected morphometric measurements that included body mass (kg), metatarsus length (cm), and chest girth (cm). We employed several tactics to minimize risks associated with handling-induced abandonment, which included limiting search times and strict handling protocols. Capture and handling of neonates was conducted using nitrile gloves. Capture gear, blindfolds, and technician clothing was cleaned with scent-free detergent between handling events.

We monitored collared neonates daily from birth through the end of July and weekly from August to 120 d post-parturition (weaning). Upon detecting a mortality event from a collared individual, we conducted a field investigation to assess cause-specific mortality when possible. Mortality events were investigated within 1–2 d

of detection from birth to July and within 7 d from August to weaning. All procedures for handling animals were in accordance with guidelines established by the American Society of Mammalogists for capture and handling of wild mammals for research (Sikes 2016), complied with U.S. laws, and were approved by the Institutional Animal Care and Use Committees of the Starkey Project (Protocol 92-F-0004) and the University of Nevada Reno (Protocol #00565).

ANALYSES

Adult female survival

We estimated monthly survival of adult females using the nest survival module in Program MARK (White and Burnham 1999) to account for irregular detection and monitoring intervals during winter, due to limited use of telemetry during that season. We estimated annual survival as the product of monthly survival estimates. Annual survival estimates were calculated from November to October each year to facilitate inclusion of individuals from the time they were captured, assess winter effects each individual year, and assess carryover effects of drought using Palmer Drought Severity Index (PDSI; hereafter: drought index) across seasons (e.g., November 2013–October 2014 is 2014). Standard error and confidence intervals of annual survival were estimated using the delta method (White and Cooch 2017).

When assessing models for survival of adult females, we used a sequential model building process where we assessed temporal effects followed by individual and environmental covariates. We first retained the best-ranked model that accounted for year and season and then we evaluated the relative effects of three individual level covariates on survival: enhanced winter nutrition, litter size, and ingesta-free body fat (IFBF) of females entering winter. We used measurements collected during November and December to estimate IFBF entering winter (Cook et al. 2010). We next considered three environmental covariates separately: mean snowpack (cm), mean drought index carryover, and plant phenology (amplitude; Table 1). Enhanced winter nutrition was included in the models as a categorical covariate, indicating the individual received (treatment) or did not receive (control)

Table 1. Definitions of predictor variables used to evaluate factors influencing survival of 50 adult female mule deer (2013–2018) and 67 neonatal mule deer (2014–2016) from birth to weaning (120 d) at Starkey Experimental Forest and Range, Oregon, USA.

Level	Predictor	Units	Definition
Adults			
Population	Snowpack	cm	Average snowpack depth during the current winter November–March
	PDSI carryover	index	Mean Palmer Drought Severity Index from the previous period. Periods delineated as November–March and April–October
	Amp	%	Maximum increase in canopy photosynthetic activity above the baseline
Individual	Year	category	Parameter allowing response to vary as a function of year
	Enhanced nutrition	category	Supplemental feeding of individual females in the current winter
	IFBF early	%	Estimated percent ingesta-free body fat of individual females measured in November–December
	Litter size	number	Number of neonates born to individual females
Neonates			
Population	Mar snowpack	cm	Average snowpack depth during March preceding birth
	Mar snow water	mm	Water content of snowpack during March preceding birth
	Apr-Jun precip	mm	Mean monthly precipitation April–June preceding birth
	PDSI	index	Mean Palmer Drought Severity Index in May–July
	Amp	%	Maximum increase in canopy photosynthetic activity above the baseline
Individual	Year	category	Parameter allowing response to vary as a function of year
	Age	category	Specified trend of survival dependent on age in days
	Body size	Index	Principle component 1 from PCA of chest girth and metatarsus length at birth
	Julian birth	Julian date	Estimated date of birth via vaginal implant transmitters
	Sex	category	Male or female
Maternal	Woody debris	%	Woody debris hiding cover estimated within 15-m radius of birth site
	Big trees	number	Trees >2 m tall within 15-m radius of birth site
	Cosine aspect	direction	Degree of northerly or southerly orientation of birth site
	IFBF late	%	Estimated percent ingesta-free body fat of the maternal female measured January–February
	Enhanced nutrition	category	Supplemental feeding of maternal female during winter preceding birth

supplemental feed during winter. We evaluated the relative effects on survival associated with the potential costs of lactation based on the number of neonates captured at parturition (litter size). We estimated the nutritional condition of females using methods developed by Cook et al. (2010) for calculating IFBF. We obtained monthly snow depth measurements from an automated snow telemetry (SNOTEL) weather station (ID-422), operated by the Natural Resources Conservation Service (NRCS) and located on Starkey. We calculated mean annual snow depth across 5 months (November to March) each year and included that value as a population level environmental covariate. We obtained monthly

drought index values for the northeast division of Oregon (NCDC NOAA) and calculated mean drought index for November–March (winter) and April–October (non-winter seasons combined) each year. We evaluated carryover effects of the mean drought index from the current period on survival during the subsequent period to assess the influence of past environmental conditions on future survival (i.e., we evaluated the effects of the mean drought index from April to October on survival during the following November–March and the effects of the mean drought index from November to March on survival during the following April–October). We evaluated the effect of plant phenology

(amplitude) on survival of adult females using spatial phenology data obtained from the United States Geological Survey for Starkey from 2014 to 2017 (Meier and Brown 2014). Amplitude is derived from values of the Normalized Difference Vegetation Index (NDVI), which is a measure of plant greenness. Amplitude of NDVI is the maximum increase in canopy photosynthetic activity above the baseline value for that year and is calculated as the difference between the maximum NDVI value and NDVI at the start of the growing season for each pixel in a 250-m grid. We calculated the mean amplitude across the study area and evaluated the effects on survival of adult females.

Neonate survival

We estimated daily survival of neonates from birth to weaning (120 d). We used the nest survival module in Program MARK to account for irregular monitoring and imperfect detection associated with VHF telemetry (White and Burnham 1999). We used a sequential model building process where we first evaluated potential differences between years of the study and retained the best-ranked model. Next, we evaluated age trends on survival comparing daily, weekly, and monthly intervals including combinations of each where appropriate (e.g., a combination of trends may consist of increasing daily survival probability for the first 30 d and monthly thereafter). After identifying the age trend that was best supported by our data, we retained this model and then assessed a suite of individual and population level covariates (Table 1). We established an index of body size using principal component analysis (PCA) that included chest girth and metatarsus length (Dunteman 1989, R 3.4.1, R Core Team). Scores from principal component 1 (PC1) explained 86% of the variation, and because the loadings for each of the two body size variables were similar, PC1 was used as an index of body size. We also evaluated the effect of other individual covariates on neonate survival: (1) maternal body condition during late winter using estimated maternal IFBF in January and February preceding parturition; (2) whether enhanced nutrition was provided to the maternal female during the winter preceding birth; and (3) date of parturition. Previous analyses of birth site selection by mule deer at Starkey suggested

selection for birth sites characterized by south-facing slopes, with high numbers of trees >2 m tall and large numbers of woody debris (Walsh 2016). Based on those findings, we tested for birth site effects (during the initial 7 d following parturition) on survival of neonates because survival during early stages of life is highly dependent on the ability to hide and thermoregulate. We also tested for environmental effects at the population level related to late winter snowpack depth and snow water content. In addition, we evaluated the effects of mean spring precipitation from April to June and mean drought index values during May–July on neonate survival. We also evaluated the influence of the mean amplitude of plant greenness on survival of neonates.

Model selection

We used an information-theoretic approach to rank candidate models used to estimate survival for adult female and neonatal mule deer (Buckland et al. 1997, Anderson et al. 2000). Models with lower Akaike's information criterion adjusted for small sample sizes (AIC_c) values were considered more parsimonious, and all models within $\leq 2 \Delta AIC_c$ of the top model were considered competitive with the best model (Burnham and Anderson 2002). Arnold (2010) provided guidance that use of 85% confidence intervals is most appropriate for model selection using information-theoretic approaches, specifically AIC model selection. Therefore, confidence intervals were set at 85% to more closely align with information-theoretic approaches, in contrast to 95% confidence intervals that are more appropriate to frequentist approaches (Arnold 2010, Thalmann et al. 2015). We followed this guidance and used 85% CIs when presenting our results. We have also provided the parameter estimate and the level of uncertainty for each estimate. The uncertainty, when combined with the parameter estimate itself, should provide guidance on interpretation of the effect. For example, a parameter estimate with a small effect (i.e., small and centered near 0) with a CI that broadly overlaps 0 (e.g., $\hat{\beta} = 0.005$, 85% CI = -0.512 to 0.986) is likely an uninformative or poorly estimated effect (Arnold 2010, Thalmann et al. 2015). A parameter estimate that is strongly negative or positive and has a CI that does not overlap 0 is strongly informative (e.g., $\hat{\beta} = 1.13$,

85% CI = 0.99 to 1.28). Alternatively, a parameter that may have a large estimated effect (e.g., $\hat{\beta} = 0.45$, 85% CI = -0.02 to 0.90), but is uncertain (i.e., 85% CI narrowly overlaps 0) would be moderately informative (Clark et al. 2013). We used this approach when interpreting model coefficients and strength of evidence for an effect for parameters included in our models.

In studies assessing survival of siblings, the potential for overdispersion of variance must be addressed to avoid violation of the assumption that fates of individuals are independent (Bishop et al. 2008). Following methods outlined by Bishop et al. (2008), we bootstrapped 10,000 replicate datasets, resampling litters from radio-collared females with replacement. We estimated the overdispersion parameter, $\hat{c}$, as the ratio of our bootstrap variance ($[SD(\hat{S})]^2$) to our modeled variance ($[SE(\hat{S})]^2$) and used this value to select models using quasi-AIC_c (QAIC_c; Burnham and Anderson 2002).

RESULTS

Cause-specific mortality

We captured 50 adult female mule deer during mid-November to mid-February from 2013 to 2018. We investigated 27 mortalities of adult females during that time period. We censored two deer from survival analysis because their deaths occurred shortly after handling and may have been capture related. Most of the remaining mortalities ($n = 25$) occurred during winter (Fig. 3A). Predation was the proximate cause of most known-cause mortalities ($n = 10$), although two individuals died from apparent malnutrition during winter (Fig. 3A). We observed two mortalities of adult females in the treatment group during October when survival was expected to be high. One of those mortalities was mountain lion predation and the second was unknown cause of death. The primary source of predation of adult females was coyotes (during winter) and mountain lions (Fig. 3A, B). Many of the mortalities, in which cause was unknown, were suspected predation; however, we lumped all unknown predation events and unknown cause of death events together as unknown. Causes of mortality between the two groups were generally similar (Fig. 3A); however, because there were only 5 mortalities of adult females in the

treatment group, we could not reliably compare the proportion of mortality from different sources. Mortalities of adults in the control group peaked in February and August (Fig. 3B); however, there were only five mortalities in the treatment group; thus, we observed no discernible seasonal peak of mortality (Fig. 3B).

We captured 68 neonatal mule deer during the spring from 2014 to 2016. Forty-six neonates and 22 neonates were born to mothers in the control and treatment (enhanced nutrition) groups, respectively. We observed one abandonment and that individual was censored from the survival analysis. We investigated 43 neonate mortalities (birth to weaning) over the duration of the study. Of these, 32 mortalities belonged to the control group and 11 mortalities from the treatment group. Sources of mortality generally occurred in similar proportions for the treatment and control groups (Fig. 4A); however, no mortalities from bears were recorded for adults or neonates in the treatment group. Predation was the cause of mortality for most neonates ($n = 25$) during our study, and frequency of mortalities was highest during the first 30 d of life (Fig. 4B).

Adult female survival

Our top two competing models included snowpack and drought index carryover covariates (Table 2). Our best-supported model, based on AIC_c, included a strong negative effect of snow depth on survival ($\hat{\beta} = -0.51$, 85% CI: -0.72 to -0.31). Inclusion of drought index carryover as an additive effect with snowpack ranked second in our model selection results. This model did not meet our model selection guidelines, however, because the 85% confidence interval of the drought index carryover narrowly overlapped zero, indicating only moderate support for the effect of that parameter on survival of adult females ($\hat{\beta} = 0.38$, 85% CI: -0.02 to 0.78). Therefore, we selected the best-ranked model that only included an effect of snow depth on survival of adult females.

Mean snow depth across the 5 yr of our study was 14 cm (95% CI: 5.12 to 22.88; Table 3). Winter survival rates (November–March) were lower than the rest of the year, and winter effects were most pronounced in 2017 (Figs. 2 and 5). Annual survival of adult females in that year was

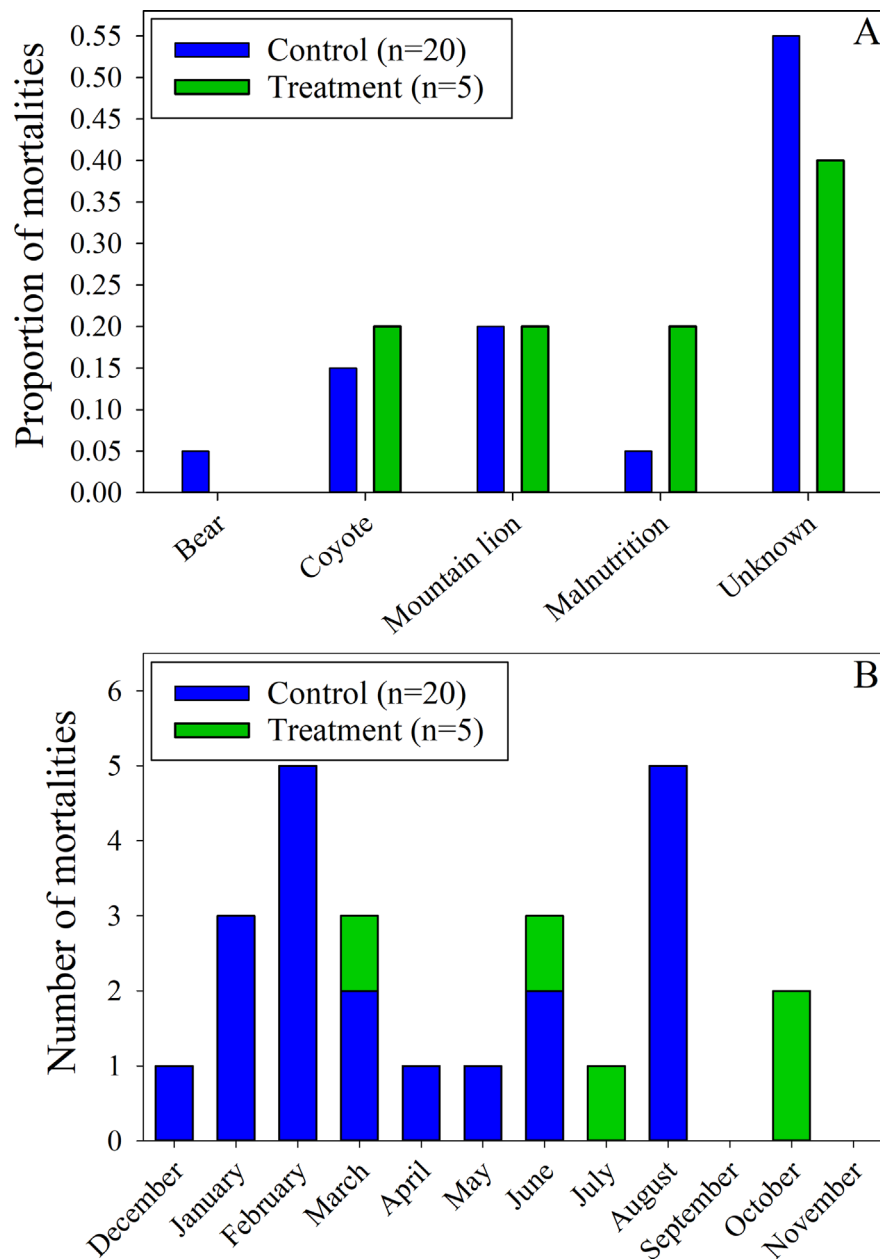


Fig. 3. Cause-specific mortality (A; as proportions of total mortality within each treatment group) and timing of mortality (B) of 25 adult female mule deer that did (treatment) or did not (control) receive supplemental feed during winter at the Starkey Experimental Forest and Range, Oregon, USA, 2013–2018. We observed 20 mortalities of females in the control group and 5 mortalities in the treatment group.

substantially lower than each of the other 4 yr of the study (Table 4; Fig. 6). Overall, mean annual survival of adult female mule deer was 0.76 (SE = 0.04) across all 5 yr of the study.

Neonate survival

We identified minimal evidence for overdispersion in our dataset ($\hat{c} = 1.18$) but used this estimate of $\hat{c}$ to rank models using QAIC_c. Our

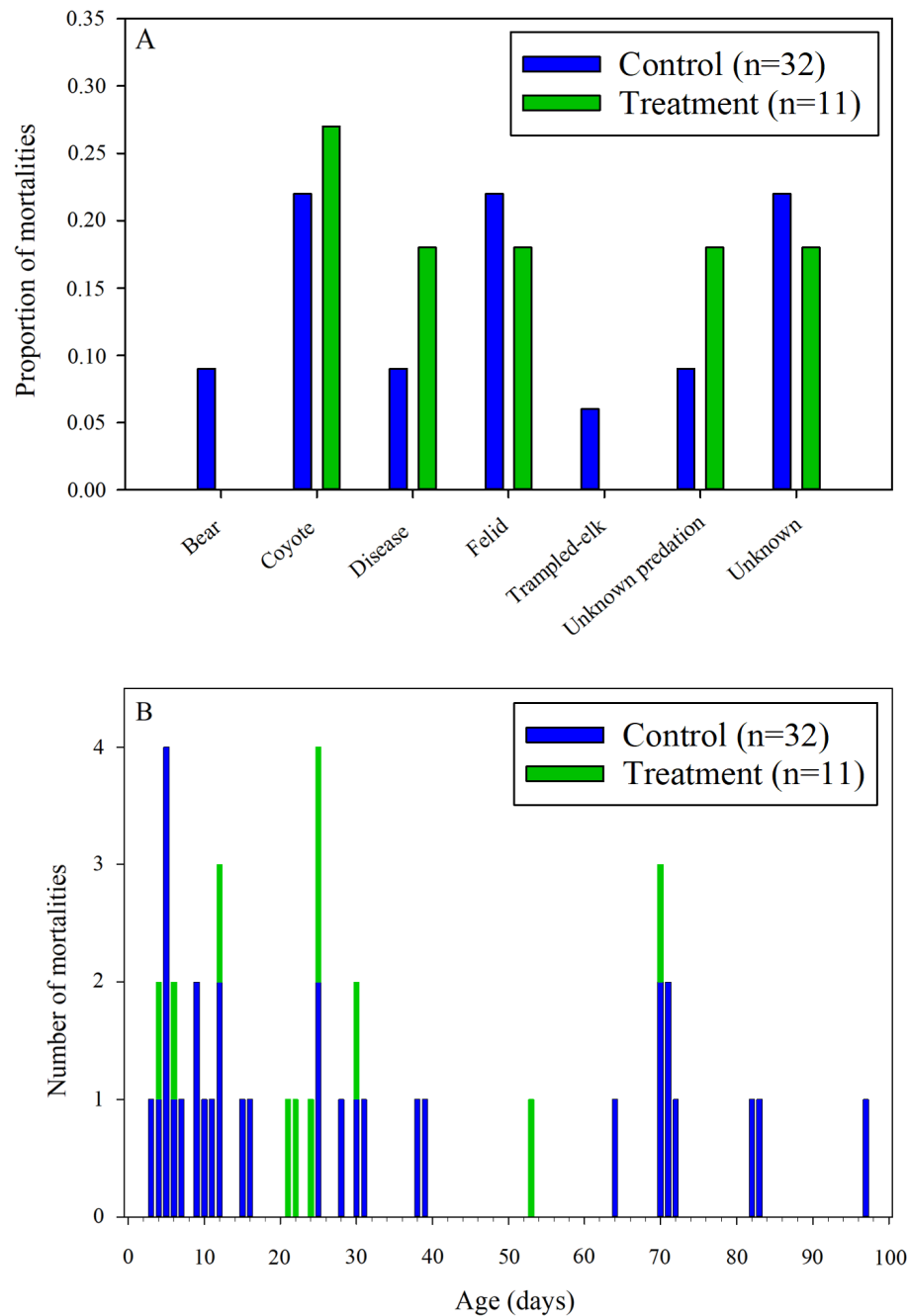


Fig. 4. Cause-specific mortality (A; as proportions of total mortality within each treatment group) and age at time of mortality (B) during the first 120 d of life for 43 neonatal mule deer born to females that did (treatment) or did not (control) receive supplemental feed during the winter preceding birth, on Starkey Experimental Forest and Range, Oregon, USA, 2014–2016. We collared 45 and 22 neonates born to females in the control and treatment groups, respectively. Of these collared individuals, we observed 32 mortalities of neonates in the control group and 11 mortalities in the treatment group.

Table 2. Model selection results from nest survival modeling in Program MARK for survival of 50 adult female mule deer captured on the Starkey Experimental Forest and Range, Oregon, USA, 2013–2018.

Model	AIC _c	ΔAIC _c	AIC _c weights	K	Dev
{S(Snowpack)}	223.82	0.00	0.373	2	219.81
{S(Snowpack + PDSI carryover)}	223.94	0.12	0.35	3	217.92
{S(Snowpack + PDSI carryover + (Snowpack*PDSI carryover))}	225.84	2.02	0.14	4	217.81
{S(PDSI carryover)}	226.17	2.35	0.11	2	222.17
{S(Amp)}	231.01	7.19	0.01	2	227.00
{S(.)}	232.62	8.80	0.00	1	230.62
{S(IFBF early)}	233.54	9.72	0.00	2	229.53
{S(Enhanced nutrition)}	233.90	10.08	0.00	2	229.89
{S(Litter size)}	234.40	10.58	0.00	2	230.39
{S(Year)}	234.71	10.89	0.00	5	224.66

Note: Covariate descriptions are provided in Table 1.

best-supported model included support for daily age trend (survival increases daily with age) and enhanced winter nutrition of the maternal female effects on neonate survival; however, the second-ranked model containing only daily age trend was nearly equally supported by the data, with a model weight only 0.02 less than the best model (Table 5). Daily survival probability increased from birth to weaning (120 d; $\hat{\beta} = 0.02$, 85% CI: 0.01 to 0.03; Fig. 7). Enhanced nutrition of the maternal female had a positive effect on survival of the neonate ($\hat{\beta} = 0.56$, 85% CI: 0.01 to 1.12). Body size and IFBF late were deemed uninformative parameters for predicting neonate survival, because 85% confidence intervals overlapped zero ($\hat{\beta} = 0.14$, 85% CI: -0.09 to 0.38 ; $\hat{\beta} = -0.17$, 85% CI: -0.47 to 0.14 , respectively). We found no support suggesting differences in survival by year for neonates (Table 5; $\Delta\text{QAIC}_c = 17.53$).

We estimated survival of neonates from birth to weaning (120 d) for the population, and separately for each experimental group of maternal females (Table 6). Overall survival to weaning at the population level was 0.35 (SE = 0.09). After accounting for treatment of maternal feeding during winter, we observed neonates born to females in the treatment group had higher survival to

Table 3. Descriptive statistics (mean values with 95% confidence intervals) for continuous variables used in survival analysis of 50 adult female mule deer (2013–2018) and 67 neonatal mule deer (2014–2016) from birth to weaning on the Starkey Experimental Forest and Range, Oregon, USA, 2014–2016.

Level	Predictor	Mean	95% LCI	95% UCI
Adults				
Population	Snowpack (cm)	14.00	5.12	22.88
	PDSI carryover	−1.03	−1.71	−0.35
	Amplitude (%)	29.77	26.20	33.34
Individual	IFBF early (%)	9.05	8.43	9.67
	Litter size	1.46	1.34	1.58
Neonates				
Population	Mar snowpack (cm)	5.99	0.00	12.45
	Mar snow water (mm)	28.49	0.00	66.82
	Apr–Jun precip (mm)	57.38	42.60	72.16
	PDSI	−2.05	−3.24	−0.86
	Amp (%)	29.77	25.65	33.89
Individual	Julian birth	152	151	153
	Woody debris (%)	11.78	8.23	15.33
	Big trees	105.32	74.19	136.45
	Cosine aspect	1.14	0.94	1.34
Maternal	IFBF late (%)	9.38	8.81	9.95

weaning (0.49, SE = 0.12) than those in the control group (0.29, SE = 0.07; Fig. 7, Table 6).

DISCUSSION

We observed strong support for our hypothesis that survival of adult female mule deer would be negatively affected by severe winters as indexed by snow depth. This result was largely influenced by the severe winter of 2016–2017, when winter snowpack was more than twice the depth of any other year in the study and monthly survival of adult females was the lowest observed in our study. Pac et al. (1991) documented similar reductions in survival of adult female mule deer during severe winters. Summaries of demographic studies conducted on mule deer suggest that mortality rates of adult females are generally highest during the winter (Ballard et al. 2001, Forrester and Wittmer 2013). Deep snow is correlated with high energetic expenditures associated with severe winters and

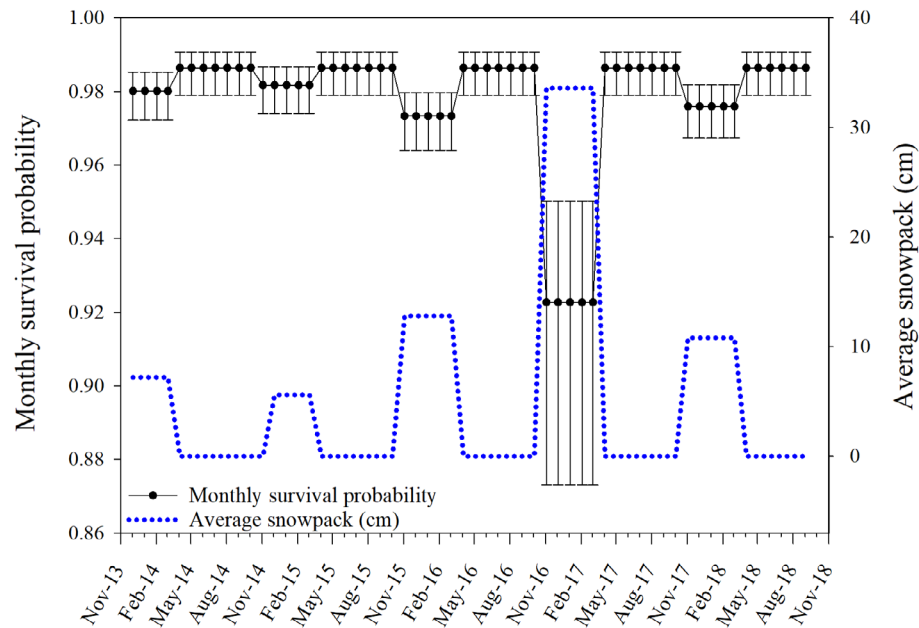


Fig. 5. The effect of winter snowpack (shown in blue) on estimated monthly probability of survival of adult female mule deer (black circles, with 85% confidence intervals) on Starkey Experimental Forest and Range, Oregon, USA, 2013–2018.

Table 4. Annual survival estimates with standard errors for 50 adult female mule deer on the Starkey Experimental Forest and Range, Oregon, USA, 2014–2018.

Year	$\hat{S}$	SE ($\hat{S}$)
2014	0.84	0.04
2015	0.83	0.04
2016	0.80	0.04
2017	0.61	0.08
2018	0.81	0.04

Note: Annual survival estimates were calculated from November to October the following year to facilitate assessment of winter effects each individual year and carryover effects of Palmer Drought Severity Index across seasons (e.g., November 2013–October 2014).

often results in reduced survival of adults and young of the year (Parker et al. 1984, Pac et al. 1991). Forage resources are limited during the winter and snow depth renders available resources less accessible, thus decreasing foraging efficiency (Parker et al. 1984, Wickstrom et al. 1984). Further, deep snow results in increased energetic costs of locomotion and also increases vulnerability of ungulates to predation (Parker et al. 1984).

We are uncertain whether the very low survival of adult mule deer in 2017 may also be explained, in part, by the drought conditions and associated reduction in forage quality and abundance during previous years before the substantially higher snowpack at Starkey in winter 2016/2017. The drought index did not enter our best model; however, Merems et al. (2020) documented that the nutritional quality of forage during summers of 2016 and 2017 at Starkey was insufficient to meet the energetic requirements of lactation for mule deer. Body condition scores of mule deer documented by that study were lower than those required for positive population growth (Monteith et al. 2014, Merems et al. 2020). The Pacific Northwest, specifically north-eastern Oregon, experienced severe drought conditions from 2013 to 2016 with mountain snowpack at near record lows (Dello and Dalton 2015). Although plant phenology was not included in any of our best-ranked models for adult or neonate survival, those drought conditions likely reduced the quality and quantity of summer forage, causing females to enter winter 2016–2017 in low nutritional condition resulting

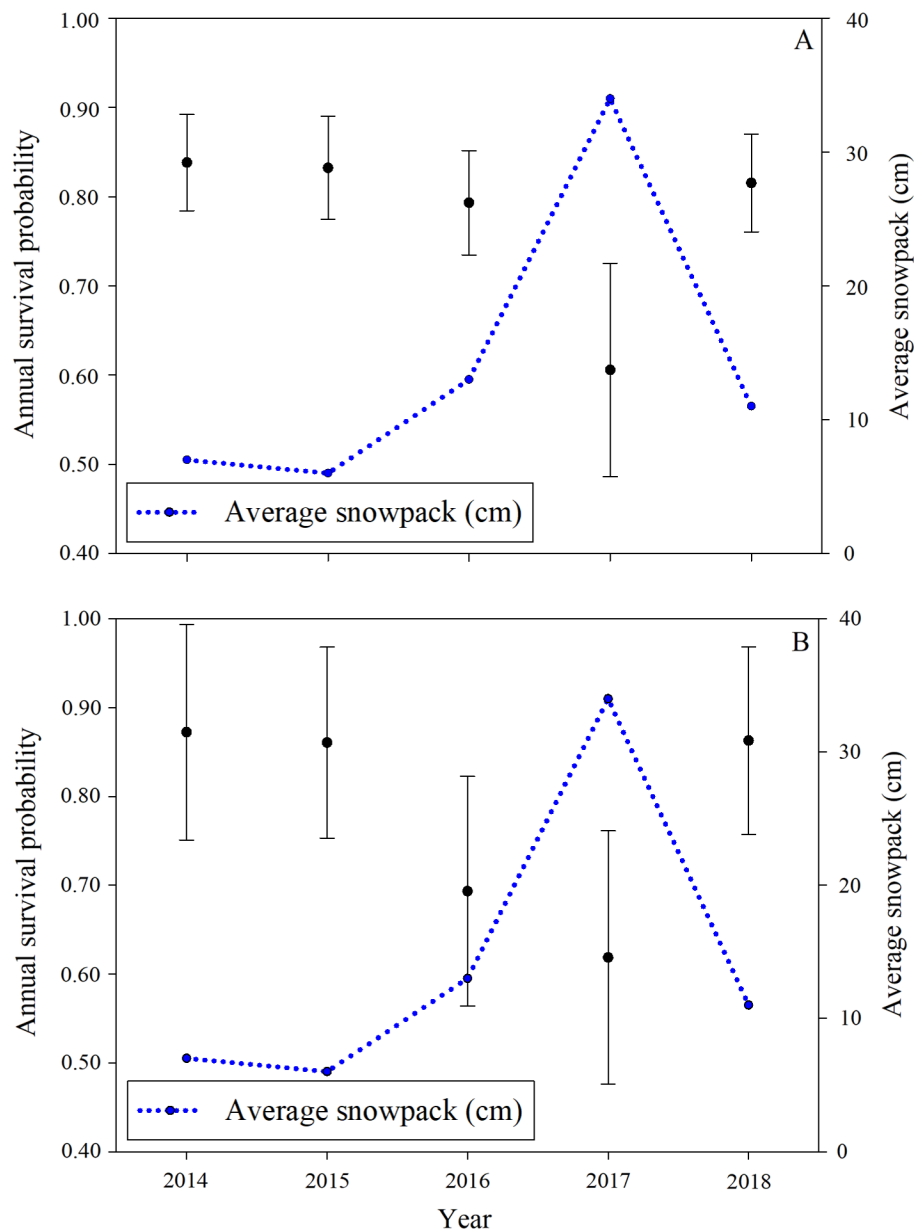


Fig. 6. Variation in annual survival of adult females explained by our best-supported model (A; the effect of winter snowpack), compared to variation explained by the year-only model (B). Estimated annual survival (with 85% confidence intervals; shown in black) of 50 adult female mule deer on the Starkey Experimental Forest and Range, Oregon, USA, 2013–2018. Average winter snowpack is indicated by the blue dotted line.

in high mortality that winter. Adult female captures occurred over a span of three months (November–February) and not all individuals were captured during both early and late winter. This breadth of time for captures, likely limited

our ability to precisely estimate differences in body condition of individuals, and tease apart the relative influence of nutritional condition versus snow depth on adult survival in our study. Further, if all females were in poor condition

Table 5. Model selection results from nest survival modeling in Program MARK for survival of 67 neonatal mule deer captured on the Starkey Experimental Forest and Range, Oregon, USA, 2014–2016.

Model	QAIC _c	ΔQAIC _c	QAIC _c weights	K	QDev
{S(Age-daily + Enhanced nutrition)}	377.71	0.00	0.13	3	371.70
{S(Age-daily)}	377.99	0.28	0.11	2	373.99
{S(Age-daily + Enhanced nutrition + Body size)}	378.27	0.56	0.10	4	370.26
{S(Age-daily + Body size)}	379.23	1.52	0.06	3	373.23
{S(Age-daily + IFBF late)}	379.44	1.73	0.05	3	373.43
{S(Age-daily + Mar snowpack)}	379.71	2.00	0.05	3	373.71
{S(Age-daily + PDSI)}	379.72	2.01	0.05	3	373.72
{S(Age-daily + Apr-Jun precip)}	379.74	2.03	0.05	3	373.73
{S(Age-daily + Amp)}	379.76	2.05	0.05	3	373.75
{S(Age-daily + Mar snow water)}	379.77	2.06	0.05	3	373.76
{S(Age-daily + Woody debris)}	379.86	2.15	0.04	3	373.85
{S(Age-daily + Cosine aspect)}	379.95	2.24	0.04	3	373.94
{S(Age-daily + Julian birth)}	379.97	2.26	0.04	3	373.96
{S(Age-daily + Sex)}	379.99	2.28	0.04	3	373.98
{S(Age-daily + Big trees)}	379.99	2.28	0.04	3	373.99
{S(.)}	391.73	14.02	0.00	1	389.73
{S(Year)}	395.24	17.53	0.00	3	389.23

Notes: We adjusted model results based on modest overdispersion ($\hat{c} = 1.18$) and selected models based on QAIC_c. Covariate descriptions are provided in Table 1.

with low variance between individuals, it would have been difficult to detect an effect of body condition.

Except in the case of events such as extreme winter severity, excessive harvest, and disease outbreaks, adult survival of slow-paced species has been shown to have minimal annual variation in long-term studies (Gaillard et al. 2000). When fluctuations in adult survival occur, however, they are likely to have a disproportionate effect on population growth rates compared with other life-history characteristics (Pac et al. 1991, Gaillard and Yoccoz 2003, Hurley et al. 2011, Monteith et al. 2013). Therefore, lower survival of adults with variable recruitment of young detrimentally contributes to already low intrinsic rates of increase (Stubbs 1977, Pianka 1983). Our estimate of annual survival of adult females in 2017 was among the lowest documented for mule deer populations (Bleich and Taylor 1998, Robinson et al. 2002, Bishop et al. 2005, Bender et al. 2007). Moreover, our estimate of mean annual survival of adult females across all 5 yr of the study (0.76, SE = 0.04) is substantially lower than the weighted mean (0.84, 95% CI: 0.76–0.94) calculated from 21 studies, spanning 30 yr of research across mule deer geographic range (Forrester and Wittmer 2013). Low survival rates of

adult females like those observed during our study are indicative of a declining population (Gaillard et al. 2000, Robinson et al. 2002, Hurley et al. 2011, Monteith et al. 2014).

Our results supported our hypothesis that neonate survival would be increased by enhanced maternal nutrition during winter and highlight the importance of access to high-quality forage during winter for pregnant females. Bishop et al. (2009) conducted a similar experiment to evaluate the effects of winter nutrition on population demographics of mule deer in southwestern Colorado. They reported that supplemental feeding increased overwinter survival of juveniles and annual survival of adult females. They reported only marginal differences in survival of neonates between the treatment and control group. Conversely, we were unable to detect an effect of enhanced nutrition on survival of adult females, and we were unable to estimate overwinter survival of juvenile mule deer because we lacked sufficient sample size of collared juveniles entering winter. The inability to detect an effect of enhanced nutrition on survival of adult females is likely linked to small sample size in the treatment group. Nevertheless, we found support for a treatment effect on survival of neonatal mule deer to weaning by manipulating the nutritional

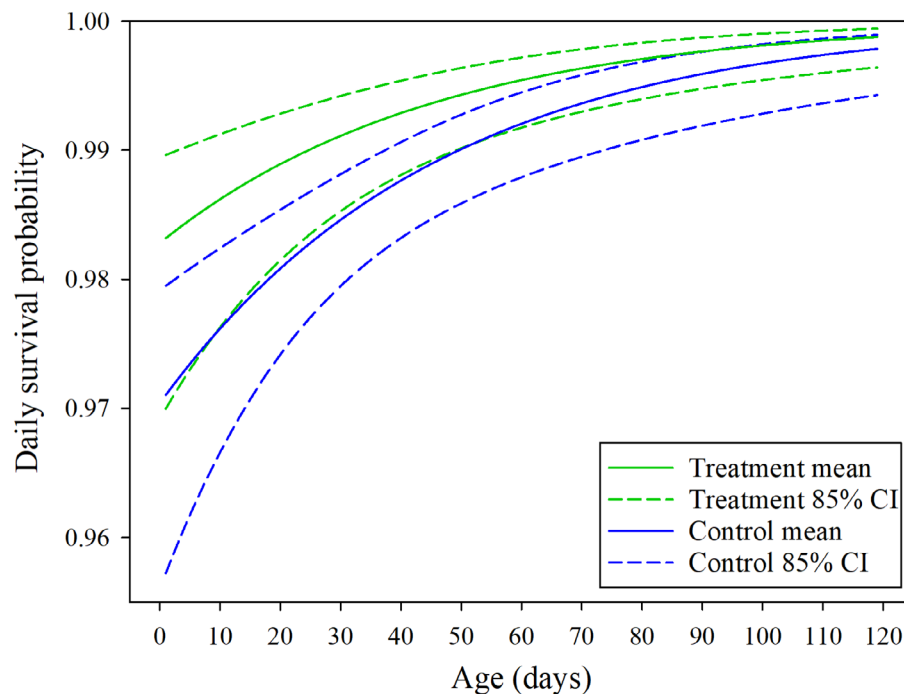


Fig. 7. The effect of enhanced winter nutrition of maternal females on daily survival probability for 67 neonatal mule deer captured on Starkey Experimental Forest and Range, Oregon, USA, 2014–2016. Treatment corresponds to neonates ($n = 22$) born to females that received enhanced winter nutrition the preceding winter. Control corresponds to neonates ($n = 45$) born to females that did not receive enhanced winter nutrition. We back-transformed beta estimates from our best-ranked model to estimate the effect of maternal nutrition on daily survival probability from birth to weaning (120 d) for neonates born to females that received enhanced winter nutrition (treatment) versus those that did not receive enhanced winter nutrition (control) with associated 85% confidence intervals (shown with dashed lines of respective color). Confidence intervals were adjusted for overdispersion ($\hat{c} = 1.18$).

Table 6. Survival estimates from birth to weaning (120 d) with standard errors for 67 neonatal mule deer on the Starkey Experimental Forest and Range, Oregon, USA, 2014–2016.

Period	Experimental group	$\hat{S}$	SE ($\hat{S}$)	n	Mortalities
120 d	Treatment	0.49	0.12	22	11
	Control	0.29	0.07	45	32
	Population	0.35	0.09	67	43

Note: Estimates are provided for neonates born to females that did (Treatment) or did not receive (Control) enhanced winter nutrition and for all neonates regardless of group (Population).

quality of forage available to adult females the preceding winter. Bishop et al. (2009) detected a substantial decrease in survival of fetuses in utero in the control group, which limited the

ability to detect an effect of enhanced nutrition when evaluating neonate survival alone. Our results suggest that enhanced winter nutrition provided adult females that were less fit to successfully rear offspring with capital to invest in reproduction despite the limitations imposed by harsh winters.

Heffelfinger et al. (2018) demonstrated the importance of high-quality forage during mid-pregnancy (January–April) for mule deer occupying an arid environment. The timing of late-winter and early-spring precipitation facilitated rapid green-up in that system during crucial periods of fetal development (Marshall et al. 2005, Heffelfinger et al. 2018). Our findings also indicate the importance of nutritional resources during mid-pregnancy in the Pacific Northwest. Further, access to high-quality nutritional

resources for maternal females was the strongest predictor of neonate survival. Maternal IFBF of adults entering winter did not explain much variation in neonate survival in our study, perhaps being overridden by the effect of winter nutrition. Monteith et al. (2014) identified a positive relationship between maternal IFBF in mid-March and survival of neonatal mule deer. Maternal body condition was not supported in our models as a direct effect on neonatal survival, which was likely a result of limitations associated with measurements of nutritional condition across the three-month capture season. Nevertheless, the detection of the effect of enhanced maternal nutrition during winter is indicative of the influence of contrasting winter nutrition among maternal females on juvenile survival to weaning. Further, based on the findings of Merems et al. (2020) most adult females may have entered winter in poor nutritional condition during 2016 and 2017. Enhanced winter nutrition may have offset the costs of poor summer nutrition and helped them produce neonates with a higher probability of survival.

Evaluation of factors influencing survival of adult females and neonates in our study demonstrates the importance of winter nutrition for maternal females for enhancing survival of neonates, but we were unable to detect differences in adult survival relative to winter nutrition. Nevertheless, winter severity, indexed by snow depth, reduced survival of adult females observed during this study. Under conditions of resource limitation, vital rates of large herbivores are expected to respond first with decreased survival of young then decreased survival of adult females (Gaillard et al. 1998, 2000, Monteith et al. 2014). Winter nutrition was unable to overcome the negative effects of winter severity to prevent winter mortalities of adult females. Nevertheless, those females that entered winter with less risk survived and winter nutrition increased the probability that they produced offspring that survived to weaning.

ACKNOWLEDGMENTS

Funding for this study was provided by Federal Aid to Wildlife Restoration Grants ORF14AF00857, ORF15AF00853, ORF16AF00635, ORF17AF00576, ORF18AF00679, and ORF19AF00513, the Oregon

Department of Fish and Wildlife, the U. S. Forest Service, Pacific Northwest Research Station, University of Nevada, Reno, and the Oregon Hunters Association—Union/Wallowa County chapter. We would like to thank K. Shoemaker and J. Sedinger for their assistance with statistical analyses and modeling. We would like to thank the Starkey field staff of the United States Forest Service (B. Dick, R. Kennedy, and D. Rae) for their continuous support in the field and ensuring that this project was logistically possible. Additionally, we would like to thank Oregon Department of Fish and Wildlife employees (S. Findholt, J. Smith, T. Forrester, P. Perrine, and M. Bianco) for their assistance in monitoring study animals. We would like to thank the graduate student (D. Walsh) and technicians that have worked on this project (B. Regan, T. Allen, J. Magee, J. Gundlach, M. Osterhout, M. Goldman, and S. Ritland) for their assistance with animal capture and data collection.

LITERATURE CITED

- Anderson, D. R., K. P. Burnham, and W. L. Thompson. 2000. Null hypothesis testing: problems, prevalence, and an alternative. *Journal of Wildlife Management* 64:912–923.
- Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. *Journal of Wildlife Management* 74: 1175–1178.
- Ballard, W., D. Lutz, T. Keegan, L. Carpenter, and J. DeVos. 2001. Deer-predator relationships: a review of recent North American studies with emphasis on mule and black-tailed deer. *Wildlife Society Bulletin* 29:99–115.
- Bårdsen, B., P. Fauchald, T. Tveraa, K. Langeland, N. G. Yoccoz, and R. A. Ims. 2008. Experimental evidence of a risk-sensitive reproductive allocation in a long-lived mammal. *Ecology* 89:829–837.
- Bårdsen, B., J. Henden, P. Fauchald, T. Tveraa, and A. Stien. 2011. Plastic reproductive allocation as a buffer against environmental stochasticity – linking life history and population dynamics to climate. *Oikos* 120:245–257.
- Bårdsen, B., and T. Tveraa. 2012. Density-dependence vs. density-independence – linking reproductive allocation to population abundance and vegetation greenness. *Journal of Animal Ecology* 81:364–376.
- Bårdsen, B., T. Tveraa, P. Fauchald, and K. Langeland. 2010. Observational evidence of risk-sensitive reproductive allocation in a long-lived mammal. *Oecologia* 162:627–639.

- Bender, L. C., L. A. Lomas, and J. Browning. 2007. Condition, survival, and cause-specific mortality of adult female mule deer in north-central New Mexico. *Journal of Wildlife Management* 71:1118–1124.
- Bergman, E. J., P. F. Doherty, G. C. White, and A. A. Holland. 2015. Density dependence in mule deer: a review of evidence. *Wildlife Biology* 21:18–30.
- Bishop, C. J., C. R. Jr Anderson, D. P. Walsh, E. J. Bergman, P. Kuechle, and J. Roth. 2011. Effectiveness of a redesigned vaginal implant transmitter in mule deer. *Journal of Wildlife Management* 75:1797.
- Bishop, C. J., D. J. Freddy, G. C. White, T. R. Stephenson, L. L. Wolfe, and B. E. Watkins. 2007. Using vaginal implant transmitters to aid in capture of mule deer neonates. *Journal of Wildlife Management* 71:945–954.
- Bishop, C. J., J. W. Unsworth, and E. O. Garton. 2005. Mule deer survival among adjacent populations in southwest Idaho. *Journal of Wildlife Management* 69:311–321.
- Bishop, C. J., G. C. White, D. J. Freddy, B. E. Watkins, and T. R. Stephenson. 2009. Effect of enhanced nutrition on mule deer population rate of change. *Wildlife Monographs* 172:1–28.
- Bishop, C. J., G. C. White, and P. M. Lukacs. 2008. Evaluating dependence among mule deer siblings in fetal and neonatal survival analyses. *Journal of Wildlife Management* 72:1085–1093.
- Bleich, V. C., and T. J. Taylor. 1998. Survivorship and cause-specific mortality in five populations of mule deer. *Great Basin Naturalist* 58:265–272.
- Buckland, S. T., K. P. Burnham, and N. H. Augustin. 1997. Model selection: an integral part of inference. *Biometrics* 53:603–618.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information theoretic approach. Second edition. Springer Verlag, New York, New York, USA.
- Clark, D. A., R. G. Anthony, and L. S. Andrews. 2013. Relationship between wildfire, salvage logging, and occupancy of nesting territories by northern spotted owls. *Journal of Wildlife Management* 77:672–688.
- Cook, J. G., B. K. Johnson, R. C. Cook, R. A. Riggs, T. Delcurto, L. D. Bryant, and L. L. Irwin. 2004. Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. *Wildlife Monographs* 155:1–61.
- Cook, R. C., J. G. Cook, T. R. Stephenson, W. L. Myers, S. M. McCorquodale, D. J. Vales, L. L. Irwin, P. B. Hall, R. D. Spencer, S. L. Murphie, K. A. Schoenecker, and P. J. Miller. 2010. Revisions of rump fat and body scoring indices for deer, elk, and moose. *Journal of Wildlife Management* 74:880–896.
- Couturier, S., S. D. Côté, J. Huot, and R. D. Otto. 2009. Body-condition dynamics in a northern ungulate gaining fat in winter. *Canadian Journal of Zoology* 87:367–378.
- Dello, K., and M. Dalton. 2015. Drought in the Pacific Northwest. Spring 2015 Meeting of the Fire and Aviation Leadership Team. <https://www.fs.fed.us/r6/fire/falt/2015-spring/blmdroughtfinal2.pdf>
- Dunteman, G. H. 1989. Principal components analysis. Sage Publishing, Thousand Oaks, California, USA.
- Festa-Bianchet, M., and J. T. Jorgenson. 1998. Selfish mothers: reproductive expenditure and resource availability in bighorn ewes. *Behavioral Ecology* 9:144–150.
- Forrester, T. D., and H. U. Wittmer. 2013. A review of the population dynamics of mule deer and black-tailed deer *Odocoileus hemionus* in North America. *Mammal Review* 43:292–308.
- Gaillard, J. M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends in Ecology and Evolution* 13:58–63.
- Gaillard, J. M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toigo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics* 31:367–393.
- Gaillard, J. M., and N. G. Yoccoz. 2003. Temporal variation in survival of mammals: a case of environmental canalization? *Ecology* 84:3294–3306.
- Hadley, G. L., J. J. Rotella, and R. A. Garrott. 2007. Evaluation of reproductive costs for weddell seals in Erebus bay, Antarctica. *Journal of Animal Ecology* 76:448–458.
- Heffelfinger, L. J., K. M. Stewart, A. P. Bush, J. S. Sedinger, N. W. Darby, and V. C. Bleich. 2018. Timing of precipitation in an arid environment: effects on population performance of a large herbivore. *Ecology and Evolution* 8:3354–3366.
- Hurley, M. A., J. W. Unsworth, P. Zager, M. Hebblewhite, E. O. Garton, D. M. Montgomery, J. R. Skalski, and C. L. Maycock. 2011. Demographic response of mule deer to experimental reduction of coyotes and mountain lions in southeastern Idaho. *Wildlife Monographs* 178:1–33.
- Loison, A., M. Festa-Bianchet, J. Gaillard, J. Jorgenson, and J. Jullien. 1999. Age-specific survival in five populations of ungulates: evidence of senescence. *Ecology* 80:2539–2554.
- Marshall, J. P., P. R. Krausman, and V. C. Bleich. 2005. Rainfall, temperature, and forage dynamics affect nutritional quality of desert mule deer forage. *Rangeland Ecology and Management* 58:360–365.

- Mautz, W. W. 1978. Sledding on a bushy hillside: the fat cycle in deer. *Wildlife Society Bulletin* 6:88–90.
- Meier, G. A., and J. F. Brown. 2014. Remote sensing of land surface phenology. <https://pubs.usgs.gov/fs/2014/3052/pdf/fs2014-3052.pdf>
- Merems, J. L., L. A. Shipley, T. Levi, J. Ruprecht, D. A. Clark, M. J. Wisdom, N. J. Jackson, K. M. Stewart, and R. A. Long. 2020. Nutritional-landscape models link habitat use to condition of mule deer (*Odocoileus hemionus*). *Frontiers in Ecology and Evolution*. <https://doi.org/10.3389/fevo.2020.00098>.
- Moen, A. N. 1978. Seasonal changes in heart rates, activity, metabolism, and forage intake of white-tailed deer. *Journal of Wildlife Management* 42:715–738.
- Monteith, K. L., V. C. Bleich, T. R. Stephenson, B. M. Pierce, M. M. Conner, J. G. Kie, and R. T. Bowyer. 2014. Life-history characteristics of mule deer: effects of nutrition in a variable environment. *Wildlife Monographs* 186:1–62.
- Monteith, K. L., T. R. Stephenson, V. C. Bleich, M. M. Conner, B. M. Pierce, and R. T. Bowyer. 2013. Risk-sensitive allocation in seasonal dynamics of fat and protein reserves in a long-lived mammal. *Journal of Animal Ecology* 82:377–388.
- Morano, S., K. M. Stewart, J. S. Sedinger, C. A. Nicolai, and M. Vavra. 2013. Life-history strategies of North American elk: trade-offs associated with reproduction and survival. *Journal of Mammalogy* 94:162–172.
- NCDC NOAA [National Climatic Data Center, National Oceanic and Atmospheric Administration]. <https://www7.ncdc.noaa.gov/CDO/CDODivisionalSelect.jsp>
- Nowak, R. M. 1999. Walker's mammals of the world. Volume 2, Sixth edition. Johns Hopkins University Press, Baltimore, Maryland, USA.
- Pac, D. F., R. J. Mackie, and H. E. Jorgensen. 1991. Mule deer population organization, behavior and dynamics in a Northern Rocky Mountain environment. Montana Department of Fish, Wildlife and Parks. <https://doi.org/10.5962/bhl.title.55646>
- Parker, K., C. Robbins, and T. Hanley. 1984. Energy expenditures for locomotion by mule deer and elk. *Journal of Wildlife Management* 48:474–488.
- Pianka, E. R. 1983. *Evolutionary ecology*. Third edition. Harper and Row, New York, New York, USA.
- Robinson, H. S., R. B. Wielgus, and J. C. Gwilliam. 2002. Cougar predation and population growth of sympatric mule deer and white-tailed deer. *Canadian Journal of Zoology* 80:556–568.
- Rowland, M. M., L. D. Bryant, B. K. Johnson, J. H. Noyes, M. J. Wisdom, and J. W. Thomas. 1997. The Starkey project: history, facilities, and data collection methods for ungulate research. USDA Forest Service General Technical Report PNW-GTR 396:1–62.
- Shallow, J. R. T., M. A. Hurley, K. L. Monteith, and R. T. Bowyer. 2015. Cascading effects of habitat on maternal condition and life-history characteristics of neonatal mule deer. *Journal of Mammalogy* 96:194–205.
- Sikes, R. S., and the Animal Care and Use Committee of the American Society of Mammalogists. 2016. 2016 guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *Journal of Mammalogy* 97:663–688.
- Stearns, S. C. 1992. *The evolution of life histories*. Oxford University Press, Oxford, UK.
- Stephenson, T. R., V. C. Bleich, B. M. Pierce, and G. P. Mulcahy. 2002. Validation of mule deer body composition using in vivo and post-mortem indices of nutritional condition. *Wildlife Society Bulletin* 30:557–564.
- Stewart, K. M., R. T. Bowyer, B. L. Dick, B. K. Johnson, and J. G. Kie. 2005. Density-dependent effects on physical condition and reproduction in North American elk: an experimental test. *Oecologia* 143:85–93.
- Stewart, K. M., R. T. Bowyer, J. G. Kie, N. J. Cimon, and B. K. Johnson. 2002. Temporospatial distributions of elk, mule deer, and cattle: resource partitioning and competitive displacement. *Journal of Mammalogy* 83:229–244.
- Stubbs, M. 1977. Density dependence in the life-cycles of animals and its importance in K- and R-strategies. *Journal of Animal Ecology* 46:677–688.
- Tavecchia, G., T. Coulson, B. J. T. Morgan, J. M. Pemberton, J. C. Pilkington, F. M. D. Gulland, and T. H. Clutton-Brock. 2005. Predictors of reproductive cost in female Soay sheep. *Journal of Animal Ecology* 74:201–213.
- Thalmann, J., R. T. Bowyer, K. Aho, F. Weckerly, and D. McCullough. 2015. Antler and body size in black-tailed deer: an analysis of cohort effects. *Advances in Ecology* 2015:1–11.
- Tollefson, T. N., L. A. Shipley, W. L. Myers, and N. Dasgupta. 2011. Forage quality's influence on mule deer fawns. *Journal of Wildlife Management* 75:919–928.
- Tollefson, T. N., L. A. Shipley, W. L. Myers, D. H. Keisler, and N. Dasgupta. 2010. Influence of summer and autumn nutrition on body condition and reproduction in lactating mule deer. *Journal of Wildlife Management* 74:974–986.
- Walsh, D. R. 2016. Birth site selection and neonate survival of mule deer in the Blue Mountains of Oregon. Thesis. University of Nevada, Reno, Nevada, USA.

- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46supplement 1: S120–S139.
- White, G. C., and E. G. Cooch. 2017. Population abundance estimation with heterogeneous encounter probabilities using numerical integration. *Journal of Wildlife Management* 81:322–336.
- Wickstrom, M., C. Robbins, T. Hanley, D. Spalinger, and S. Parish. 1984. Food intake and foraging energetics of elk and mule deer. *Journal of Wildlife Management* 48:1285–1301.
- Williams, G. C. 1966. Natural selection, the costs of reproduction, and a refinement of lack's principle. *American Naturalist* 100:687–690.
- Wisdom, M. J., J. G. Cook, M. M. Rowland, and J. H. Noyes. 1993. Protocols for care and handling of deer and elk at the Starkey Experimental Forest and Range. USDA Forest Service General Technical Report PNW-GTR 311:1–49.