To the University of Wyoming:

The members of the Committee approve the thesis of Brendan Oates presented on 11/18/2016.

Dr. Matthew J. Kauffman, Co-chairperson

Dr. Jacob R. Goheen, Co-chairperson

Dr. Shannon E. Albeke

Dr. Kevin L. Monteith

APPROVED:

Dr. Donal C. Skinner: Department Chair, Zoology and Physiology.

Dr. Paula M. Lutz, College Dean

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Predation and resource limitation typically interact to influence survival and fecundity of animals, yet the demographic mechanisms through which this occurs is unclear. We tested theoretical predictions of top-down and bottom-up forcing on ungulate demography through the lens of demographic rates, quantifying the influence of resource limitation and predation on population growth rates (λ) of two moose (*Alces alces*) populations exposed to starkly different densities of large carnivores. We analyzed a time series of vital rates (pregnancy, parturition, neonatal, overwinter juvenile, and adult survival) and potentially influential covariates at the scale of the seasonal home range from 102 individuals in a population experiencing high densities of wolves (*Canis lupus*) and grizzly (brown) bears (*Ursus arctos*), and from 84 individuals in an adjacent population exposed to markedly lower predator density. We conducted Life-Stage Simulation Analyses (LSAs), which indicated that variation in adult survival was responsible for most of the variability in λ for both populations. We then extended the LSA to estimate the vital rates as a function of top-down and bottom-up covariates, predicting their influence on λ. In the population with high predator density, drought on summer range and relative wolf density during winter reduced overwinter adult survival, moderately and strongly influencing λ, respectively. Fire positively influenced overwinter adult survival, yet reduced neonatal survival, resulting in a negligible effect on λ. In the population with low predator density, pregnancy, parturition, and overwinter adult survival were largely driven by body condition, strongly implicating resource limitation on λ, despite weak environmental signatures. Our findings depart from the classic life-history

characteristics of ungulates, suggesting that vital rate variability and disparate influences from predation and resource limitation may be more contextually dependent than previously appreciated.

Quantifying how animals behave under the risk of predation is fundamental to understanding predator-prey dynamics. The starvation-predation hypothesis predicts that when prey experience resource deficits, they avoid starvation by foraging as much as possible, even when risk of predation is high. As winter progresses, ungulates experience resource deficits due to senescence of forage and increasing snow accumulation, and therefore should temper antipredator responses to avoid starvation. We tested this prediction by assessing antipredator response of moose (*Alces alces*) to wolf (*Canis lupus*) presence during winter in the Greater Yellowstone Ecosystem of North America. Using simultaneously-collected GPS locations of collared moose and wolves, we identified interactions (minimum distance at which a moose came to a wolf) at three distance categories (0-500m, 500m-1km, 1-1.5km). We assessed the antipredator response of moose by measuring speed, displacement, and habitat use 24 hours before and after interactions with wolves at each distance category. Additionally, we assessed how the progression of winter influenced movement rates and habitat use of moose before versus after interactions with wolves. Moose did not alter their movement rates or habitat use after encountering wolves at any distance category when time was ignored; however, when day-of-year was incorporated, we found that movement rates gradually diminished as winter progressed. Moose did not avoid their preferred foraging habitat (riparian areas) following encounters with wolves and, in early winter, more strongly selected riparian areas after wolf encounters. Our work demonstrates that antipredator

response of moose to wolves is ephemeral as winter progresses, and supports theoretical predictions that prey experiencing resource deficits exhibit muted antipredator behavior. Our findings integrate antipredator responses with a long history of work on starvation-predation tradeoffs, suggesting that nutritional condition of prey may buffer against run-away risk effects in food webs featuring large mammals.

EFFECTS OF PREDATORS AND RESOURCE LIMITATION ON DEMOGRAPHY AND BEHAVIOR OF MOOSE IN THE GREATER YELLOWSTONE ECOSYSTEM

By

Brendan A. Oates

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DEDICATION

To my parents, for fostering my fascination with the natural world at a young age, and for their unwavering support throughout my academic career and personal endeavors. To my late and beloved dog, Mina, for her steadfast commitment to our exploration of the outdoors, for her uncanny ability to make me laugh, and most importantly, for keeping me honest. To my friends near and far, for their inspiration, adventures, creativity, and humor.

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CHAPTER ONE

DEMOGRAPHIC RATES INTERACT WITH RESOURCE LIMITATION AND PREDATION TO LIMIT POPULATION GROWTH OF A LARGE HERBIVORE

ABSTRACT

Predation and resource limitation typically interact to influence survival and fecundity of animals, yet the demographic mechanisms through which this occurs is unclear. We tested theoretical predictions of top-down and bottom-up forcing on ungulate demography through the lens of demographic rates, quantifying the influence of resource limitation and predation on population growth rates (λ) of two moose (*Alces alces*) populations exposed to starkly different densities of large carnivores. We analyzed a time series of vital rates (pregnancy, parturition, neonatal, overwinter juvenile, and adult survival) and potentially influential covariates at the scale of the seasonal home range from 102 individuals in a population experiencing high densities of wolves (*Canis lupus*) and grizzly (brown) bears (*Ursus arctos*), and from 84 individuals in an adjacent population exposed to markedly lower predator density. We conducted Life-Stage Simulation Analyses (LSAs), which indicated that variation in adult survival was responsible for most of the variability in λ for both populations. We then extended the LSA to estimate the vital rates as a function of top-down and bottom-up covariates, predicting their influence on λ. In the population with high predator density, drought on summer range and relative wolf density during winter reduced overwinter adult survival, moderately and strongly influencing λ, respectively. Fire positively influenced overwinter adult survival, yet reduced neonatal survival, resulting in a negligible effect on λ. In the population with low predator density, pregnancy, parturition, and overwinter adult survival were largely driven by body condition, strongly implicating resource limitation on λ, despite weak environmental signatures.

Our findings depart from the classic life-history characteristics of ungulates, suggesting that vital rate variability and disparate influences from predation and resource limitation may be more contextually dependent than previously appreciated.

Key words: bottom-up, demography, moose, predation, predator density, resource limitation, top-down, ungulate, vital rates

INTRODUCTION

The relative importance of predation and resource limitation in structuring the dynamics of animal populations has been debated for decades, in part catalyzed by the Green World Hypothesis (GWH; Hairston, Smith & Slobodkin 1960). The GWH states that producers, decomposers and carnivores should be limited through competition, but that herbivores are limited by their predators. More than half a century later, it is now largely recognized that most communities are simultaneously influenced by both top-down (i.e., predation) and bottom-up (i.e., resource limitation) forces (Hunter & Price 1992; Power 1992; Polis & Strong 1996; Ford *et al.* 2014; Owen-Smith 2015). For prey populations, the continuum of top-down and bottom-up forcing implies that trade-offs occur between the acquisition of resources for survival and susceptibility to predation (McNamara 1987), mediated by proximity to carrying capacity (*K*) (Fretwell & Barach 1977; White 1978; Sinclair & Krebs 2002). However, it is still unclear how bottom-up and top-down factors differentially influence the growth of prey populations through multiple demographic pathways. The demographic variability exhibited by ungulates offers a useful predictive framework to assess the influence of predation and resource limitation on animal populations (Gaillard *et al.* 2000; Eberhardt 2002; Bonenfant *et al.* 2009).

The proximity of prey populations to *K* has considerable influence on the relative strength of top-down and bottom-up forces in structuring ungulate demography (Kie, Bowyer &

Stewart 2003). For example, populations near *K* tend to be in poorer nutritional condition as expressed through reduced fecundity and survival (McCullough 1979; Simard *et al.* 2008; Bonenfant *et al.* 2009). However, predator populations can obfuscate these density-dependent feedbacks by killing prey and reducing intraspecific competition (Boyce, Sinclair & White 1999). Consequently, we expect vital rate responses and their influential factors to differ for populations with strong top-down limitation versus those that are bottom-up limited. For example, in prey populations exposed to strong top-down limitation, intraspecific competition should be reduced and nutritional condition should increase (Bowyer *et al.* 2014). In this instance, predation should dampen signals of resource limitation by pushing prey populations well below *K* (Owen-Smith & Mills 2006; Hopcraft, Olff & Sinclair 2010). In contrast, populations without predators should exhibit stronger signals of resource limitation as density increases, due to higher intraspecific competition (Coulson *et al.* 2001; Stewart *et al.* 2005; Monteith *et al.* 2014). Although interactions between resource limitation and predation can obscure their relative influence at the population level, studies on vital rate variability from the individual level can help tease apart their underlying effects (Gaillard *et al.* 2000; Bowyer *et al.* 2013).

The effects of resource limitation on population dynamics in ungulates often occurs through predictable and sequential changes in vital rates: reduced survival of young should be followed by increased age at first reproduction, reduced rates of pregnancy, parturition, and finally, reduced survival of prime-aged adults (i.e., the "Eberhardt Model"; Eberhardt 2002). Typically, adult survival is high and largely invariant for ungulates, and the greater variability in juvenile survival commonly drives population dynamics (Gaillard, Festa-Bianchet & Yoccoz 1998; Gaillard *et al.* 2000; Raithel, Kauffman & Pletscher 2007). Extreme weather, however, can alter the variability of adult survival and its influence on interannual population growth rates (Gaillard & Yoccoz 2003). For example, populations succumbing to resource limitation are likely to be more sensitive to weather, and experience more variable adult survival (Kie, Bowyer & Stewart 2003). Consequently, environmental variability can lead to dramatic changes in lambda (λ) for resource-limited populations (Coulson *et al.* 2001; Boyce *et al.* 2006). The responses of different vital rates to variability in predation and resource limitation offer a powerful lens into the factors that shape ungulate demography.

We sought to quantify how resource limitation and predation differentially influence population dynamics of ungulates through the lens of vital rate variability. The influence of predation on ungulates is commonly studied by manipulating densities of predators or prey and observing demographic responses (Boutin 1992; Serrouya, McLellan & Boutin 2015), however, such experiments are often logistically prohibitive. The Greater Yellowstone Ecosystem (GYE) in western North America exhibits a gradient of predator density and habitat changes from fire, offering a unique opportunity to evaluate top-down and bottom-up influences on ungulates. Fires in 1988 (hereafter "1988 fires") burned over a million acres throughout the region (Schullery 1989), producing a mosaic of burned and unburned patches (Romme *et al.* 2016). The recovery of grizzly (brown) bears (*Ursus arctos*) and gray wolves (*Canis lupus*) to the Jackson study area (hereafter, "Jackson"; Fig. 1) around the turn of the 21st century coincided with the decline of Jackson moose (*Alces alces*; Appendix S1: Fig. S1*a*) and a post-fire landscape frequently exposed to drought (Appendix S1: Fig. S1*b*). Moose in Jackson are suspected to have declined considerably due to predators, but habitat changes from fire and drought have likely altered the influence of predation on their demography (Vartanian 2011; Monteith *et al.* 2015). South of Jackson, moose in the Sublette study area (hereafter, "Sublette") have been exposed to substantially lower densities of predators (Fig. 1) and few fires. The gradients of predator density and habitat changes from fire between Jackson and Sublette offer a means to understand interactive effects of resource limitation and predation.

The gradient of predator density between Jackson and Sublette moose in the GYE allowed us to test well-established predictions of the influence of resource limitation on ungulate demography. It is expected that where prey experience high predator density, the influence of resource limitation should be weak due to reduced intraspecific competition, whereas in areas of low predator density, competition for food should increase and signals of resource limitation should strengthen (Sinclair & Krebs 2002). In Jackson moose, we predicted high predator density would override environmental signals of resource limitation due to reduced intraspecific competition. In Sublette, where predators were largely absent and female harvest is low, we predicted moose would be more sensitive to environmental signals of resource limitation and density dependence. We estimated the vital rates of individuals from both populations, allowing us to evaluate predictions of vital rate variability and their relative influence on λ (Gaillard, Festa-Bianchet & Yoccoz 1998) in the context of Eberhardt's model (Eberhardt 2002). Specifically, we expected to see (1) reductions in neonatal and overwinter juvenile survival and fecundity if resource limitation was occurring (Eberhardt 2002); and (2) invariant adult survival, relative to other vital rates (Gaillard, Festa-Bianchet & Yoccoz 1998). We then used deterministic matrix models and life-stage simulation analysis (LSA; Wisdom, Mills & Doak 2000) to assess population-level responses to predator density and resource limitation. Our approach quantifies the interplay among top-down and bottom-up factors as they manifest through the life history characteristics of moose in a variable environment.

METHODS

Moose captures—We captured 85 adult (> 2.5 years) female moose in Jackson in January-March from 2005-2007 (n = 48; Becker 2008), and 2008-2009 (n = 37; Vartanian 2011). Moose were fitted with either global positioning system (GPS) radio collars containing store-on-board technology (n = 51) or very high frequency (VHF) radio collars (n = 34) (Appendix S1). An additional 17 moose had been previously fitted with VHF transmitters before our research began (Becker 2008), and were included for our analyses but were never handled during our study. We captured 84 adult female moose in Sublette in mid-February from 2011 to 2014, all of which were fitted with GPS collars (Appendix S1). We estimated body condition of Sublette moose via percent-ingesta-free-body-fat (hereafter "IFBFat") for years 2012-2014. We used ultrasonography with a 5-MHz transducer to determine the maximum depth of subcutaneous rump fat, and palpation to estimate a body condition score. We then used the rump fat measurement and body condition score with a predictive equation modified from Cook *et al.* (2010) to estimate IFBFat for moose. Because assessing prime-aged survival is important for detecting density dependence in ungulates exposed to few predators (Festa-Bianchet, Gaillard & Côté 2003), we collected an incisor for aging either at the capture or mortality site (Appendix S1). For analyses, we omitted all mortalities that occurred within 2 weeks of capture (4 in Sublette and 3 in Jackson). Capture and handling procedures were approved by the University of Wyoming Institutional Animal Care and Use Committee. Study area descriptions are listed in Appendix S1.

Monitoring of Vital Rates

Pregnancy and parturition—BioTracking LLC determined pregnancy status via the presence of Pregnancy-Specific-Protein-B (PSPB; Huang *et al.* 2000) in serum derived from blood samples collected at capture (Appendix S1). We surveyed captured females deemed pregnant from PSPB levels as well as Jackson moose that were not handled during our study, for parturition events between May 31 and June 13, shortly after the period of peak parturition for moose (Schwartz 1998:141-171; Poole, Serrouya & Stuart-Smith 2007). We defined parturition events as the detection of one or more neonates present at mother's heel during surveys completed either on foot or aerially with a Bell-47 helicopter. We calculated pregnancy and parturition rates as the proportion of pregnant and parturient individuals to those not pregnant or parturient, respectively. For parturition rates of Jackson moose, we located unhandled, collared moose during winter and collected fecal samples to test for progestogen levels indicative of pregnancy (Becker 2008). Twinning rates were calculated by dividing the number of females observed with twins by the total number of females with neonates during the June survey.

Neonatal and overwinter juvenile survival—Juvenile ungulates are most vulnerable to mortality during the first six weeks of life (i.e., the neonatal phase), after which mortality typically decreases until winter (Ballard, Whitman & Reed 1991; Adams, Dale & Mech 1995; Barber-Meyer, Mech & White 2008). Thus, we distinguished between survival of neonates (parturition to mid-July) and overwinter survival of juveniles (mid-July to mid-February). Approximately 4-8 weeks after parturition surveys, we relocated adult females from the ground or air to estimate neonatal survival (i.e., neonate present or absent at mother's heel). Females with a neonate at heel in July were relocated from the ground or air the following February or March to estimate overwinter survival of juveniles. We used Kaplan-Meier estimators (Pollock *et al.* 1989) to estimate survival rates of neonates and calves.

Adult survival—We conducted monthly flights with fixed-wing aircraft or ground surveys to monitor survival of VHF-collared moose and to retrieve collars from the field. Annual survival rates were calculated using a Kaplan-Meier estimator, with the biological year starting 1 June and ending 31 May.

Seasonal Ranges of Moose and Covariates

We delineated summer and winter ranges of individual moose (Fig.1). We distinguished migrants from residents and seasonal ranges through visual inspections of Net-Squared Displacement (Appendix S1). We delineated seasonal ranges of GPS-collared moose using 95% isopleth of dynamic Brownian bridge movement models (dBBMMs; Kranstauber *et al.* 2012; Appendix S1). To calculate seasonal ranges for VHF-collared individuals in Jackson, we buffered one winter-capture and summer-survey location annually by the median area of dBBMM seasonal ranges of GPS collared individuals in that year (Appendix S1).

To test each vital rate for the influence of predator density and resource limitation, we extracted a suite of covariates from the seasonal ranges of individual moose annually. For new captures of moose in both study areas (i.e., individuals for which the previous year's summer and winter ranges were not estimated), we used the seasonal range from the current year to represent the seasonal range for the previous year. We believe this is justified because migratory moose in the GYE are faithful to their seasonal ranges (Vartanian 2011). For all environmental covariates, we used the spatially-weighted mean of the raster value extracted from the moose seasonal range (i.e., the 95% isopleth of dBBMM from GPS-collared moose or buffered seasonal location of VHF-collared moose). Twenty-five moose died their first winter after capture, and therefore had no measurable summer range for extracting bottom-up covariates. We felt it was critical to include these moose in covariate analyses of survival, because they constituted a considerable proportion of total mortalities, so we applied the annual mean value of each bottom-up covariate (discussed below) extracted from all other summer home ranges. All modeling and data extraction were done with R version 3.3.1 (R Core Team 2016).

Relative Predator Density—In Jackson, wolves were captured and fitted with either VHF- or GPS-collars by US Fish and Wildlife Service and National Park Service personnel during summer and winter from 2005 to 2010 (Appendix S1). Using locations from both GPS and VHF data, we randomly selected one location per day for a balanced sample size per season and pack (Otis & White 1999), and calculated 90% fixed-kernel density estimates of winter and summer wolf territories annually (Appendix S1). The influence of relative wolf density was tested on neonatal survival, overwinter juvenile survival and adult survival of Jackson moose only, because established wolf packs were scarce in Sublette, and deemed biologically unimportant for moose survival (Fig 1; Appendix S1: Table S1).

We used a preexistent raster (14 km^2 resolution; example in Fig. 1) of relative grizzly bear density (Bjornlie *et al.* 2014) to evaluate the response of neonatal, overwinter juvenile, and adult survival to bears (Appendix S1). We only extracted relative grizzly bear density from summer ranges of Jackson moose for analyses of neonatal (June-July) and overwinter juvenile survival (July-February/March). Adult survival of moose was calculated monthly, therefore we used the winter range of adult moose only for months April and May, because bears hibernate until late spring (Haroldson *et al.* 2002).

Resource Limitation— Length of spring and growing season have been found to influence fecundity and survival in ungulates (Herfindal *et al.* 2006; Hamel, Côté & Festa-Bianchet 2010). As proxies for resource limitation on summer ranges of moose, we used the Normalized Difference Vegetation Index (NDVI) from the MODIS terra satellite (8-day temporal resolution) to calculate the length of spring (start to end of spring-green up of vegetation) and growing season (start of spring-green up until senescence of vegetation) in days (Appendix S1: Table S1). Depending on the vital rate, we used the previous year's NDVI value to account for carry-over effects of covariates and to represent maternal condition (Cook *et al.* 2004). For example, we assessed pregnancy status during February using previous year's value for spring length and length of the growing season (Appendix S1).

We tested the influence of the 1988 fires on all vital rates for Jackson moose by calculating the total percent-overlap of summer ranges with the burned areas using raster data from the Monitoring Trends in Burn Severity Project (Eidenshink *et al.* 2007; Appendix S1). Similar to the NDVI metrics, we used the previous year's value of percent-burned of Jackson summer home range for vital rate analyses to represent carry-over effects on pregnancy, overwinter juvenile survival, and overwinter adult survival.

We estimated drought using mean seasonal values from PRISM (Daly, Neilson & Phillips 1994) raster data of the Palmer Drought Severity Index (PDSI; Palmer 1965; Appendix S1). Drought influences animal populations at large spatial scales, therefore, we averaged PDSI values across all individuals relative to each study area and year from June-August for summer, and March-April for late winter. Warm temperatures during late winter associated with reduced snow cover have been correlated with winter tick (*Dermacentor albipictus*) abundance the subsequent year (Delgiudice 1997), which can decrease body condition of moose through loss of blood and hair (Samuel 2007).

To assess the energetic costs of snow on moose vital rates, we used raster data of Snow Water Equivalence (SWE) from Daymet (Thornton, Running & White 1997), extracted from the winter range of each moose. We calculated the cumulative daily values of SWE annually from January 1 to May 31 for each individual. For adult survival, we allowed SWE to accumulate monthly, whereas all other vital rates were assessed using one seasonal SWE value (Appendix S1).

Endogenous fat reserves are a critical for survival and fecundity of ungulates (Cook *et al.* 2004). For Sublette moose captured from 2012-2014, we measured and tested the influence of IFBFat in addition to the aforementioned environmental covariates on pregnancy, parturition, overwinter juvenile survival and adult survival. Measurements of IFBFat were not available for Jackson moose.

Statistical Analyses

Vital Rate Models—We tested the influence of covariates using generalized linear-mixed models (GLMMs) on probability of pregnancy, parturition, neonatal survival, and overwinter juvenile survival, and used the Andersen-Gill formulation (Andersen & Gill 1982) of Cox proportional hazards models (CPHs; Cox 1972) to model the effects of covariates on adult survival during summer and winter (see Appendix S1 for protocol of vital rate modeling). We used an information-theoretic approach for all analyses of vital rates by performing model selection of all possible combinations of covariates based on second-order Akaike information criteria adjusted for small sample size (AIC_c), ΔAIC_c and Akaike weights (w_i) (Burnham & Anderson 2002). We deemed covariates important if their 85% confidence intervals did not overlap zero within 4 ΔAIC_c of the top model, an appropriate confidence level for identifying a best-approximating model with AIC model selection (Arnold 2010).

Life-Stage Simulation Analysis— To determine which vital rates were driving population growth, we conducted LSA (Wisdom & Mills 1997; Wisdom, Mills & Doak 2000) separately for Jackson and Sublette moose (Appendix S1). A LSA simulates population growth through matrix population models by randomly drawing estimates of vital rates (e.g., pregnancy, parturition, neonatal survival, overwinter juvenile survival, and adult survival) derived from beta distributions that are based off the mean and variance from field estimates of demographic data. *Covariate LSA*— While traditional LSA evaluates the relative influence of vital rates on λ, it does not assess the sources of variability. We sought to extend the LSA framework to include the variation in top-down and bottom-up covariates transferred through the vital rates to generate variability in λ. To do this, we simulated 10,000 unique values within the observed range of each covariate, then randomly sampled those values independently, similar to an all-possible-combinations framework. We then used the vital rate models (GLMMs and CPHs) to estimate fecundity and survival as a function of simulated covariate values over 10,000 iterations to populate the matrix models. We derived 10,000 estimates of λ, allowing us to infer the overall influence of each covariate on λ through their effect on vital rates, while also accounting for the importance of the vital rate in explaining the proportion of variation (r^2) in λ (Appendix S1).

RESULTS

In Jackson, the study area with high predator density, summer drought reduced overwinter adult survival and pregnancy (Fig. 2*b*, *e*; Table 1), and relative wolf density had a negative influence on overwinter adult and juvenile survival (Fig. 2*c*, *f*; Table 1). The 1988 fires in Jackson reduced neonatal survival, but positively influenced overwinter adult survival (Fig. 2*a*, *d*; Table 1). Although relative grizzly bear density was not supported as a top covariate during model selection, an ad-hoc analysis of Jackson neonatal survival revealed a negative influence of grizzly bear density in a univariate model (β = -0.53; 95% CI: -1.33, -0.01; Appendix S2: Fig. S2).

In Sublette, where predators were scarce, IFBFat strongly improved overwinter adult survival, pregnancy and parturition (Fig. 3*a*, *b*, *d*; Table 1), but was negatively related to neonatal survival (-1.06; 85% CI: -1.88, -0.36). Drought from the previous summer also negatively influenced rates of parturition (Fig. 3*c*). When IFBFat was omitted from analyses of Sublette vital rates, summer drought and shorter spring length $_{t-1}$ reduced parturition and overwinter survival of adults, respectively (Appendix S3: Table S12, Fig. S3). Cox-Proportional Hazards models of adult survival during summer did not converge due to limited mortalities in Jackson ($n = 2$) and Sublette ($n = 4$).

Although population growth of ungulates is typically driven by high variation in juvenile survival, our LSAs revealed that variation in adult survival was a strong driver of interannual changes in λ for both populations (Jackson $r^2 = 0.79$, Sublette $r^2 = 0.70$; Fig. 4*a, f*). Variation in neonatal survival, overwinter juvenile survival, parturition, and pregnancy contributed comparatively little to population growth (Fig. 4*b-f*). Elasticity values for fecundity, juvenile, and adult survival were 0.12, 0.12, and 0.64 for Jackson and 0.12, 0.12, 0.63 for Sublette, respectively. The Jackson population was estimated to be declining annually at a rate of three percent ($\lambda = 0.970$), largely due to reduced adult survival, in addition to decreased rates of pregnancy and neonatal survival, although overwinter juvenile survival was comparatively higher (Table 2). In contrast, Sublette was estimated to be increasing at a rate of 2.7% ($\lambda = 1.027$), as neonatal survival remained stable and high whereas overwinter juvenile survival was stable, but slightly reduced (Table 2). Twinning rates were low for both populations (Table 2). In Sublette, prime-aged (2.5-8 years) moose accounted for 63% (SE ± 0.10; $n = 15$) of total adult mortalities ($n = 24$), and 84% of individuals were ≤ 8 years ($\bar{x} = 6$; range: 2.5-15 years). Model selection results for vital rates from both populations are shown in appendices S2-S4.

The covariate LSA for Jackson showed that relative wolf density during winter explained 59% of the variation in λ, influencing population growth through overwinter adult and juvenile survival (Fig. 5*c*). Summer drought in Jackson explained 28% of the variation from its combined, negative influences on overwinter adult survival and pregnancy (Fig. 5*b*). The 1988 fires explained only 3% of the variation, as the positive influence on winter adult survival was washed out by the negative influence on neonatal survival (Fig. 5*a*). The covariate LSA for Sublette with environmental covariates only (IFBFat omitted from analyses) showed spring length $_{t-1}$ to explain 45% (Fig. 6*b*) and summer drought $_{t-1}$ to explain 9% of the variation in λ, respectively. When IFBFat was added to the simulation, it explained 87% of variation in λ through its combined influence on overwinter adult survival, parturition and pregnancy (Fig. 6*a*), whereas drought explained only 1% of the variation through its influence on parturition.

DISCUSSION

Our work reveals how moose populations can be interactively influenced by resource limitation and predation through their disparate influences on vital rates. In Jackson moose, we detected signatures from bottom-up factors (drought, fire) in combination with top-down factors (relative wolf and grizzly bear densities). This result was in contrast to the theoretical prediction that signatures of resource limitation would be relatively undetectable for Jackson moose that have declined sharply while coexisting with high densities of wolves and grizzly bears. In Sublette, where predators were largely absent, the substantial variation in λ explained by IFBFat as opposed to environmental covariates clearly illustrated that this population was resource limited and experiencing density dependence, aligning with theoretical predictions. Despite the typical vulnerability of juveniles and robustness of adults to environmental variation (Gaillard & Yoccoz 2003), we found that nutritional condition of adults strongly predicted their own survival, yet had no predictive power for overwinter juvenile survival. Further, LSA results from both populations depart from typical expectations for the life-history characteristics of ungulates where variation in juvenile survival typically drives population dynamics (Gaillard, Festa-Bianchet & Yoccoz 1998; Gaillard *et al.* 2000). In our study, annual changes in population growth rates were driven most strongly by variation in adult survival regardless of predator density, while juvenile survival explained substantially less variation (i.e., neonatal and overwinter juvenile survival combined: Jackson $r^2 = 0.15$; Sublette $r^2 = 13$). Integrating the hierarchical effects of covariates on vital rates at the population level together with LSAs revealed how high variability in adult survival, rare in ungulate demography, can be strongly linked resource limitation alone or in conjunction with predation. Findings herein serve as a reminder that detecting environmental signatures of resource limitation and predation are contextually dependent, and that the relative influence of each factor can be obscured or magnified depending on the strength of density dependence in a population.

The detection of both resource limitation and predation limiting population growth in Jackson, an area of high predator density, reveals the interactive nature of top-down and bottom-up forces on ungulate demography. Wolves suppressed overwinter survival of juvenile and adult moose, similar to other studies at northern latitudes (Gasaway *et al.* 1992; Hayes & Harestad 2000; Boertje *et al.* 2009). Moose in Jackson may have experienced high levels of winter predation during a rapid numerical increase of wolves from 2004 to 2009 and a corresponding decrease in the availability of elk, which are primary prey for wolves in the GYE (Smith *et al.* 2004; Metz *et al.* 2012) (Appendix S5; Fig. S4). As the ratio of moose to elk increased considerably and simultaneously with a rapidly growing wolf population, wolves may have prey switched from elk to moose (Appendix S5). Drought also limited population growth, which likely compounded the effect of wolves on adult survival and contributed to high variability in the vital rate. Warmer temperatures reduce forage quality for ungulates (Langvatn *et al.* 1996;

Hamel *et al.* 2009b), limiting the accretion of somatic reserves for ungulates during the growing season that are necessary for reproduction and overwinter survival (Cook *et al.* 2013). Indeed, Jackson moose experienced reduced rates of pregnancy, which were attributed to drought, as well as low rates of twinning (Table 2), a common symptom of resource limitation in moose (Boertje *et al.* 2007). A sub-sample of adult moose that died during late-winter of 2008 following three consecutive years of drought (Appendix S1: Fig. S1*b*) had a median percent-marrow fat of 29.8% (SD ± 25.6%; $n = 11$), indicative of acute malnutrition (Sand *et al.* 2012). That Jackson adult survival was sensitive to both predation and resource limitation suggests that even when existing among high densities of predators, ungulates can still express signs of bottom-up forcing.

Ungulates that forage in early-seral stage habitats often benefit from disturbance created by fire (Schwartz & Franzmann 1989; Proffitt *et al.* 2016), and forage quality generally peaks for moose between 10 and 26 years after ignition (Nelson, Zavaleta & Chapin 2008) . Our work documents novel, negative effects of a stand-replacing fire in a montane ecosystem on neonatal survival of moose. The lower forage quality in the burned summer home ranges of moose (Vartanian 2011), and the post-fire successional trajectory of vegetation (Romme *et al.* 2016) coupled with nearly 7 consecutive years of drought (2000-2007; Appendix S1: Fig. S1*b*) may have accelerated forage maturation in burned home ranges of Jackson moose, shortening the optimal window of post-fire forage quality. Further, the negative influence of relative grizzly bear density on neonatal survival may be linked to grizzly bear selection of habitat disturbed by fire, not only to forage in successional shrub communities, but also to increase encounters with ungulate prey (Hamer & Herrero 1987; Milakovic *et al.* 2012). These combined factors suggest that both resource limitation and predation contributed to lower neonatal survival of Jackson moose. Interestingly, the loss of a neonates in burned home ranges may have also released reproductive moose from the cost of lactation, allowing them to recover lost somatic reserves and possibly explaining the positive effect of fire on overwinter adult survival (Appendix S5).

In Sublette moose, we revealed signals of density dependence through measures of environmental covariates and IFBFat. As prey populations approach *K* and competition for food increases, animals are subject to poorer nutritional condition, and are consequently more sensitive to severe weather (Aanes, Sæther & Øritsland 2000; Kie, Bowyer & Stewart 2003). Measures of IFBFat and the length of spring $_{t-1}$ were linked to overwinter adult survival, a vital rate that is typically robust to environmental variation (Gaillard & Yoccoz 2003). Rates of pregnancy, parturition, adult survival were also reduced for animals with low IFBFat, consistent with feedback processes of negative density dependence (McCullough 1979; Bonenfant *et al.* 2009). For example, adult females experiencing intraspecific competition for forage resources may undergo reproductive trade-offs (i.e., allocate somatic reserves to body maintenance instead of reproduction) due to substantial maternal investments made for gestation and rearing of young (Clutton-Brock 1984). Although density dependence of ungulates is notoriously difficult to detect, our results support the monitoring of vital rates and nutritional condition at the individual level over multiple years to infer the occurrence of resource limitation (Stewart *et al.* 2005; Monteith *et al.* 2014).

We found measures of nutritional condition to be considerably more important than environmental covariates in predicting rates of reproduction and adult survival of Sublette moose. The variability in IFBFat among Sublette moose explained considerable variation in λ compared with the length of spring $_{t-1}$ ($r^2 = 0.87$ versus $r^2 = 0.45$, respectively; Fig. 6), largely due to the cumulative effect sizes of IFBFat on adult survival, pregnancy, and parturition (Table

1). Our results show that measures of nutritional condition are markedly more effective for evaluating the influence of resource limitation on vital rates for ungulates. Similarly, Stewart *et al.* (2005) noted that environmental signatures of resource limitation can be dampened in populations experiencing density dependence. We recommend that future studies examining the effects of predators on ungulates carefully consider multiple pathways, such environmental factors and endogenous fat reserves potentially contributing to density dependence before declaring its absence.

Results herein depart from the life-history paradigm proposed by Eberhardt (2002), and deviate from life-history characteristics typical of ungulates (Gaillard *et al.* 2000). Juveniles are typically more sensitive to environmental variation compared with adults and are commonly the first stage class to experience declines as populations approach K (Eberhardt 2002), ultimately driving interannual variability in λ (Gaillard *et al.* 2000). Interestingly, variable adult survival in both populations exposed to starkly different predator densities and asymptotic growth rates explained the majority of variation in λ. Such patterns are considered rare for ungulates, although exceptions have been noted in declining populations exposed to predators, including bighorn sheep (Johnson *et al.* 2010), mountain caribou (*Rangifer tarandus*) (Hebblewhite *et al.* 2007), and tropical ungulates (Owen-Smith & Mason 2005). The decline of the Jackson population was partially attributed to wolf predation, however, variable adult survival in Sublette (low predator density) was also linked to a stable-to-increasing population growth rate. Further, although Sublette moose experienced reduced overwinter juvenile survival (Table 2), it was not predicted by any covariate, whereas adult survival was linked strongly to IFBFat and moderately to the length of spring $_{t-1}$. Thus, adult survival showed greater sensitivity to environmental variation, whereas juvenile survival did not. It is possible that as intraspecific competition for resources increases, the detection of reproductive tradeoffs (lower juvenile survival) relative to environmental variation may be confounded by factors difficult to measure such as experience in rearing young (Hamel *et al.* 2009a), heterogeneity of genotypic quality (van Noordwijk & de Jong 1986) or disease. There are multiple factors that can influence vital rate variability, and as such, their expected patterns (Gaillard *et al.* 2000) may be more contextually dependent than previously appreciated.

Our findings provide three significant contributions to ungulate ecology. First, in a simulation framework using empirical data, we not only detected resource limitation in a population exposed to high densities of large carnivores, but also revealed its link to adult survival, a vital rate that is typically robust to environmental variation. Second, individual measurements of nutritional condition proved to be considerably more informative for detecting density dependence compared with environmental measures, suggesting that seemingly intuitive relationships between environmental measures of resource limitation and vital rates can be distorted in ungulate populations experiencing strong density dependence. Finally, we found unexpected variability in adult survival driving changes in λ, despite two populations with opposing asymptotic growth rates and starkly different predator densities. This suggests that the life-history paradigm and characteristics of ungulates proposed by Eberhardt and Gaillard, respectively, may be more contextually dynamic than originally proposed.

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FIGURES & TABLES

Figure 1. Jackson and Sublette moose exposure to wolf pack territories (90% Kernel Density Estimates) and relative grizzly bear density (top-right panel; black locations are from GPS-collared moose), and examples of seasonal ranges of GPS-collared moose derived from dynamic Brownian bridge movement models (dBBMM) and VHF-collared moose from Jackson (top-left panel) and Sublette (bottom-left panel). Smaller inset maps (center-right) show general location of GYE (tan polygon) and study area (black polygon).

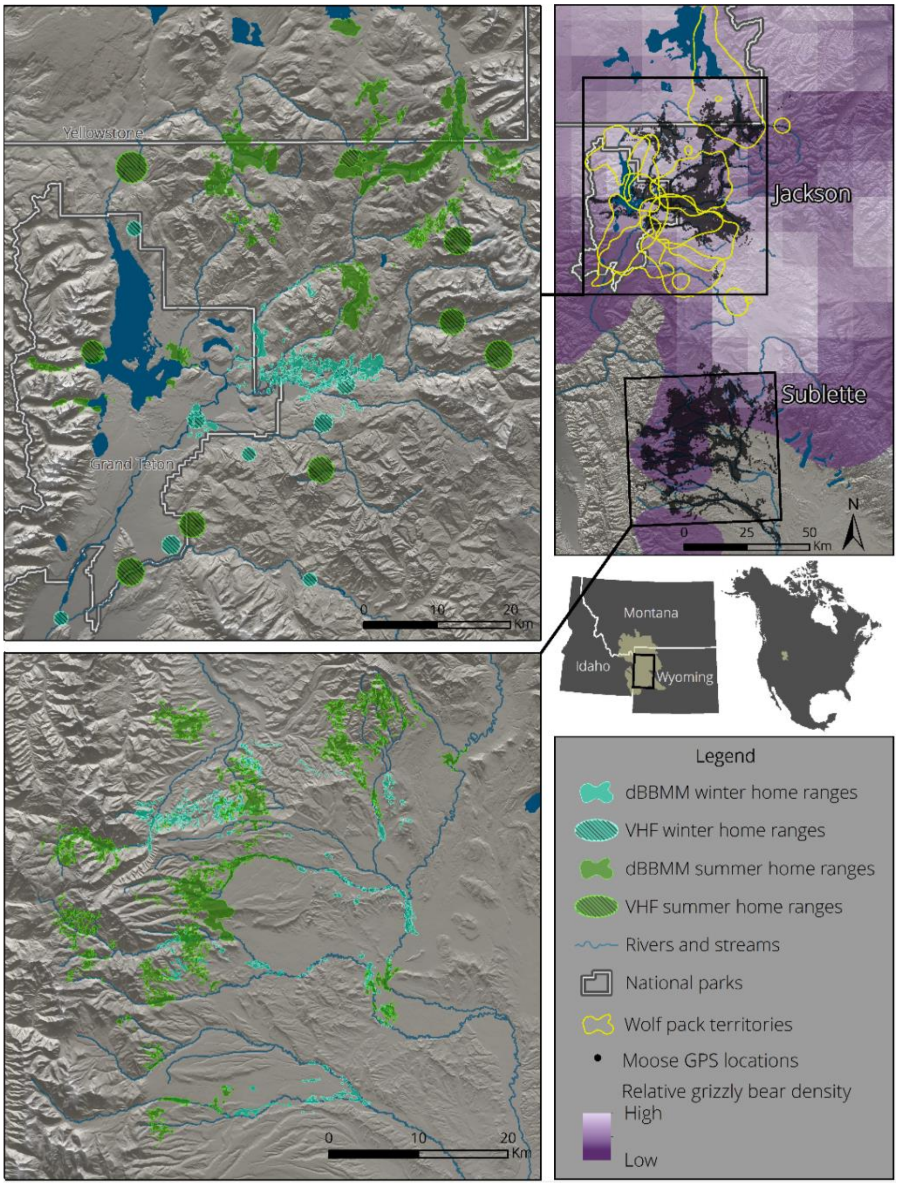


Table 1. Top models derived from AIC$_c$ model selection with coefficient estimates and 85% confidence intervals that did not overlap zero for vital rates relative to each study. Model Fit refers to either the area under the receiver operating characteristic curve from Generalized Linear Mixed-effects Models (GLMMs) or concordance from Cox Proportional Hazards models (CPHs). Negative beta coefficients from CPHs decrease the mortality hazard (positively relate to survival). Top models for Sublette are from analyses that included IFBFat. We did not detect important covariates for overwinter juvenile survival of Sublette moose.

Vital rate	**Model type**	**Study**	**Parameter**	β	**Lower 85% CI**	**Upper 85% CI**	**Model fit**
Pregnancy Status	GLMM logit	Jackson	Mean summer PDSI $_{t-1}$	0.71	0.26	1.51	0.69
		Sublette	IFBFat	1.42	1.07	1.91	0.83
Parturition Status	GLMM logit	Sublette	IFBFat	1.47	1.05	2.39	0.82
			Mean summer PDSI $_{t-1}$	0.83	0.33	1.75	0.82
Neonatal survival	GLMM logit	Jackson	Fire	-0.72	-1.15	-0.34	0.74
Overwinter juvenile survival	GLMM logit	Jackson	Relative wolf density [a]	-0.85	-2.02	-0.28	0.68
Adult Survival	CPH	Jackson	Relative wolf density [b]	0.32	0.13	0.51	0.67
			Fire $_{t-1}$	-0.30	-0.53	-0.08	0.67
			Mean summer PDSI $_{t-1}$	-0.25	-0.47	-0.025	0.67
	CPH	Sublette	IFBFat	-1.07	-1.34	-0.81	0.84

[a] Relative wolf density measured from July to March

[b] Relative wolf density measured during winter from January to May

Table 2. Mean estimates (± SE) and sample sizes by biological year of demographic rates for moose from Jackson (2005-2010) and Sublette (2011-2014). Rates of pregnancy, parturition and twinning are calculated as proportions, and neonatal, overwinter juvenile, and adult survival are Kaplan-Meier estimates based off of the biological year (June 1-May 31).

Study	Year	**Pregnancy**		**Parturition**		**Twinning**		**Neonatal survival**		**Overwinter juvenile survival**		**Adult survival**	
		n	$\bar{x}$ (± SE)	*n*	$\bar{x}$ (± SE)	*n*	$\bar{x}$ (± SE)	*n*	$\bar{x}$ (± SE)	*n*	$\bar{x}$ (± SE)	*n*	$\bar{x}$ (± SE)
Jackson	2005	20	0.90 (0.07)	14	0.79 (0.11)	14	0	13	0.5 (0.13)		na	38	0.84 (0.06)
	2006	20	0.95 (0.05)	19	0.79 (0.10)	16	0.13 (0.09)	17	0.71 (0.11)	6	0.83 (0.15)	41	0.95 (0.03)
	2007	20	0.70 (0.11)	10	0.80 (0.13)	10	0.10 (0.10)	11	0.55 (0.15)	12	0.83 (0.11)	49	0.77 (0.07)
	2008	32	0.75 (0.08)		na	10	0.10 (0.10)	11	0.55 (0.15)	6	0.67 (0.19)	56	0.65 (0.06)
	2009		na		na	19	0.05 (0.05)	18	0.39 (0.12)	6	0.67 (0.19)	39	0.85 (0.06)
	2010		na		na		na		na	7	0.85 (0.13)	31	0.81 (0.07)
	All Years	92	0.81 (0.04)	43	0.79 (0.06)	69	0.07 (0.03)	70	0.54 (0.06)	37	0.78 (0.07)	254	0.79 (0.03)
Sublette	2011	19	0.53 (0.12)	10	0.80 (0.13)	9	0	9	0.71 (0.17)	9	na	23	0.91 (.06)
	2012	47	0.66 (0.07)	28	0.89 (0.06)	26	0.12 (0.06)	28	0.82 (0.07)	9	0.71 (0.17)	50	0.88 (0.05)
	2013	63	0.76 (0.05)	39	0.69 (0.07)	41	0	30	0.93 (0.05)	25	0.72 (0.09)	70	0.79 (0.05)
	2014	40	0.68 (0.08)	30	0.67 (0.09)	27	0.04 (0.04)	22	0.95 (0.04)	22	0.77 (0.09)	53	0.83 (0.06)
	All Years	169	0.69 (0.03)	107	0.75 (0.04)	103	0.04 (0.19)	89	0.89 (0.03)	65	0.74 (0.06)	196	0.84 (0.02)

Figure 2. Predicted probability (± 85% CI) and observed values (bottom-up covariates in blue, and top-down covariates in orange) of overwinter adult female survival (*a*-*c*), neonatal survival (*d*), pregnancy (*e*), and overwinter juvenile survival (*f*) as a function of percentage of burned summer home range (*a*, *d*) mean summer PDSI from the previous year (*b*, *e*; positive values indicate wetter conditions and vertical blue-dotted line is the Palmer Drought Severity Index threshold for drought), and relative wolf density (*c*, *f*) from January-May (overwinter adult survival) and from July-February (overwinter juvenile survival) for Jackson moose in western Wyoming, USA from 2005-2010.

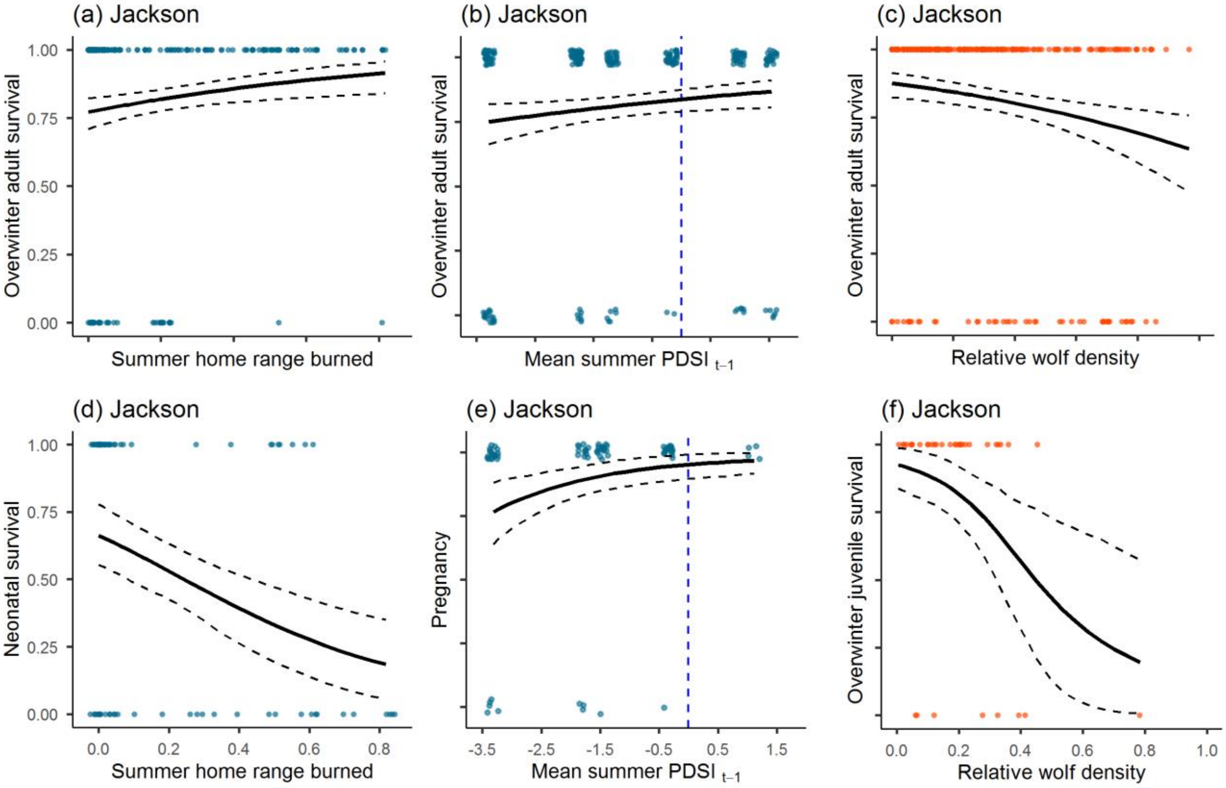


Figure 3. Predicted probability (± 85% CI) and observed of (*a*) pregnancy, (*b*) parturition, and (*d*) overwinter adult survival as a function of IFBFat (%), and (*c*) mean summer PDSI $_{t-1}$ (positive values were wetter conditions and vertical blue-dotted line is the Palmer Drought Severity Index threshold for drought) for Sublette moose in western Wyoming, USA from 2012-2014.

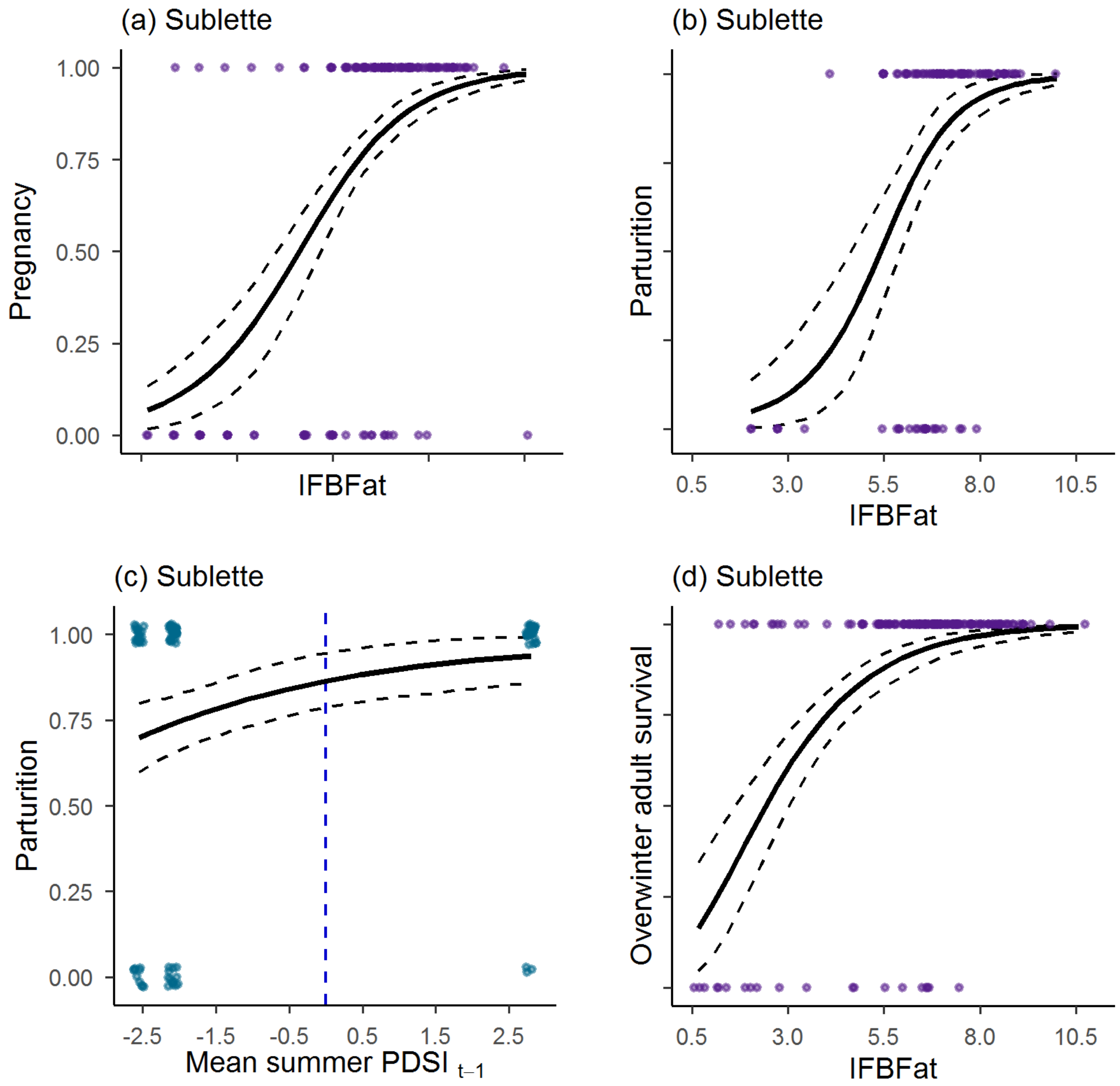


Figure 4. Results from Life-Stage-Simulation analysis for both Sublette (blue) and Jackson (yellow) showing the variation in lambda explained by (a) adult survival (Jackson $r^2 = 0.79$; Sublette $r^2 = 0.70$), (b) overwinter juvenile survival (Jackson $r^2 = 0.07$; Sublette $r^2 = 0.08$), (c) neonatal survival (Jackson $r^2 = 0.08$; Sublette $r^2 = 0.06$), (d) pregnancy status (Jackson $r^2 = 0.02$; Sublette $r^2 = 0.08$), (e) parturition status (Jackson $r^2 = 0.02$; Sublette $r^2 = 0.07$), and (f) summary of proportion of variation in λ explained by each vital rate (see Table 2 for estimates).

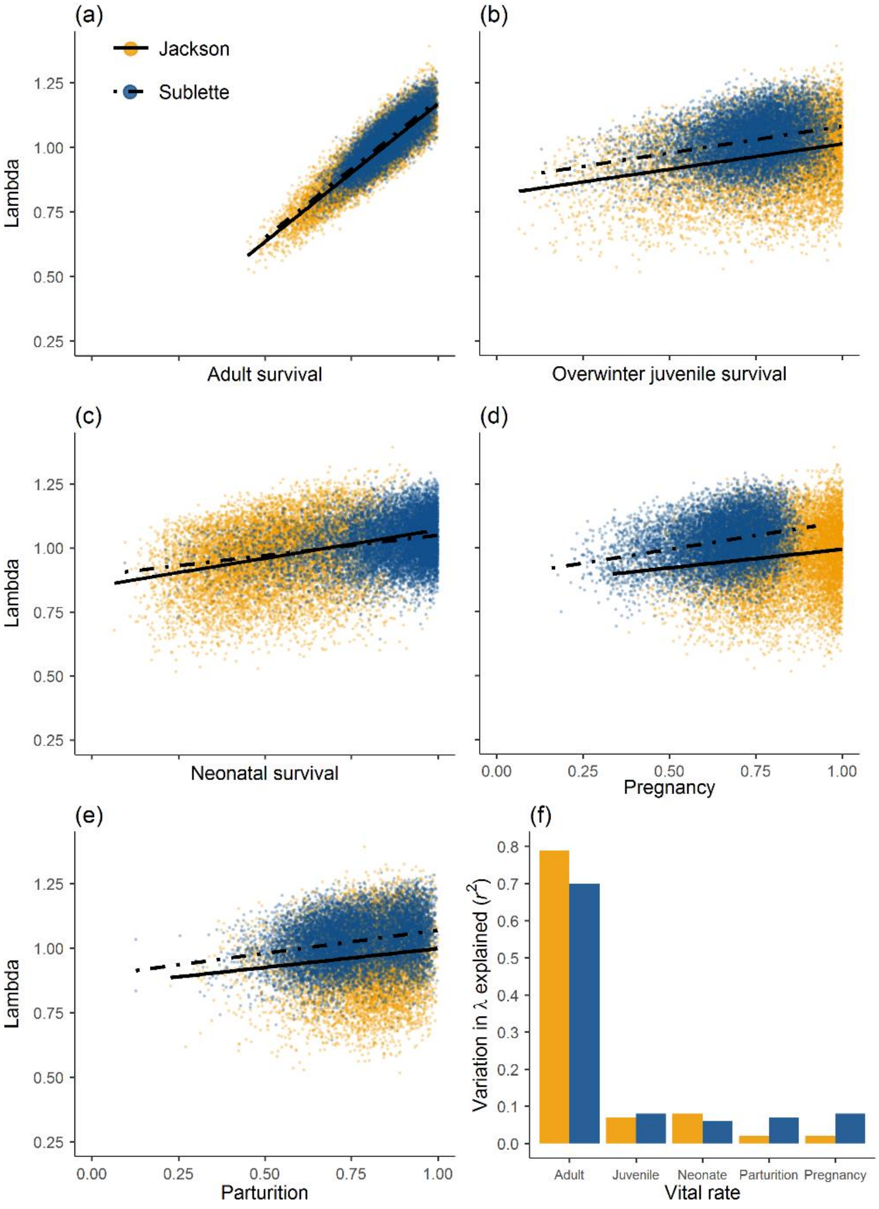


Figure 5. The variation in λ (fitted with smoothing loess) explained by the cumulative effects of (*a*) fire on adult and neonatal survival, (*b*) summer drought on overwinter adult survival and pregnancy, and (*c*) relative wolf density on overwinter adult and juvenile survival for Jackson moose in western Wyoming, USA from 2005-2010.

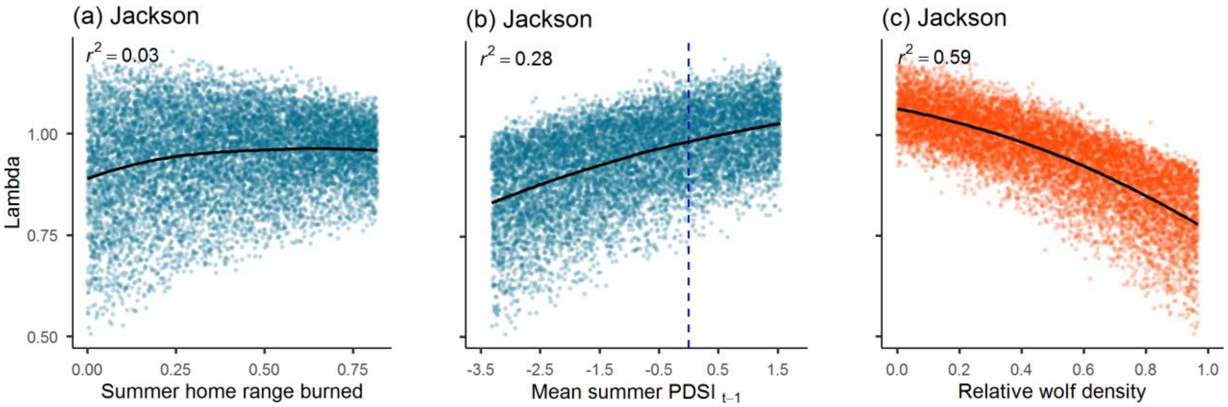
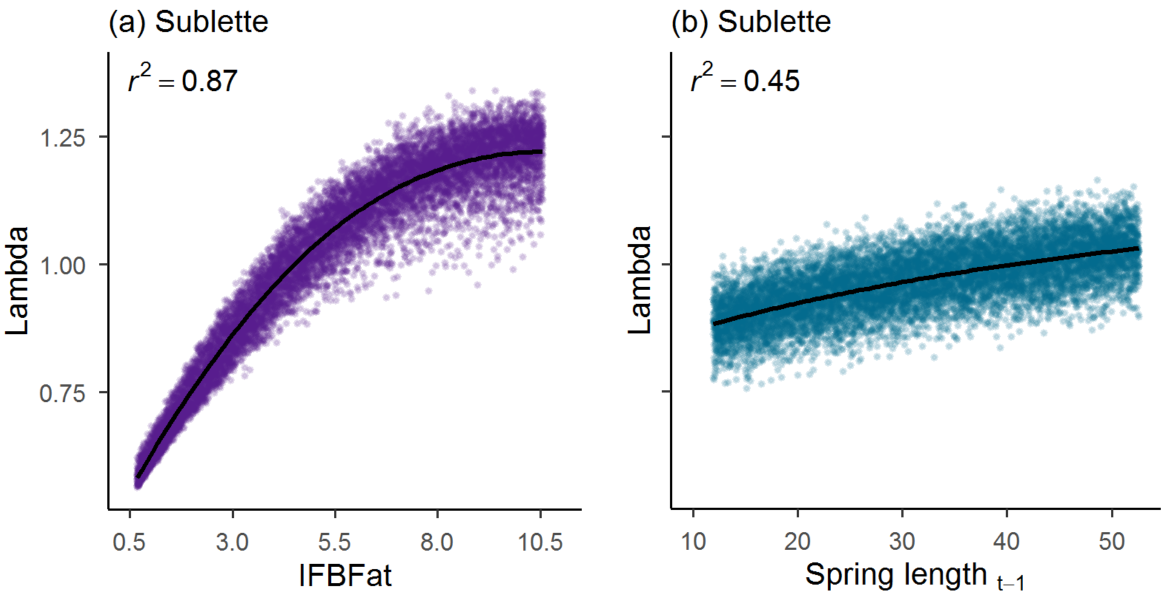


Figure 6. The variation in λ (fitted with smoothing loess) explained by the cumulative effects of (*a*) IFBFat (%) on pregnancy, parturition, and overwinter adult survival for Sublette moose from 2012-2014, and (*b*) spring length $_{t-1}$ (days) where IFBFat was omitted from analyses on overwinter adult survival for Sublette moose in western Wyoming, USA from 2011-2014.



APPENDIX S1. Methods

Study Areas

In Jackson, we monitored 102 moose from February 2005-May 2010, encompassing approximately 6,500 km^2 of mostly public lands in the Greater Yellowstone Ecosystem (GYE), including portions of Grand Teton National Park, Yellowstone National Park, and the Bridger-Teton National Forest (43.5202˚N, -110.2206˚W). During winter, Jackson moose occupied low to mid elevations (1866-2150 m) mainly consisting of riparian areas with willow (*Salix* spp.) interspersed with cottonwood (*Populus* spp.), and aspen (*Populus tremuloides*). Homogenous and mixed-forests of subalpine fir (*Abies lasiocarpa*), lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), and Douglas fir (*Pseudotsuga menziesii*) also occurred throughout. Winter ranges of moose also spanned the relatively flat floodplains of the Buffalo Fork and Snake Rivers, dominated by willow intermixed with cottonwoods. The Jackson population occupied mostly public lands (Bridger Teton National Forest), and was approximately 90% migratory, with migrants moving to higher elevation (mean 2470 m) habitats containing stands of willow, subalpine fir, lodgepole pine, and Douglas fir interspersed with stands of aspen, limber pine (*Pinus flexilis*) and whitebark pine (*Pinus albicaulis*). Herbaceous communities were common in areas burned by the 1988 fires. The Jackson climate is characterized by short, dry summers and long, cold winters with relatively deep snow (mean annual snowfall 339.09 cm SE ± 17.41; from 1911 to 2016 at the Moran 5WNW station).

Approximately 100 kilometers south of Jackson, we monitored 84 moose in Sublette from February 2011-August 2014 in the Upper Green River basin and eastern foothills of the Wyoming Range (42.8653˚N, -110.0708˚W; Fig. 1 in main text). The climate and habitat characteristics of Sublette were similar to Jackson. Land ownership was 60% private and 40%

public lands. The Sublette population was partially (approximately 50%) migratory, with migrants typically moving to higher elevations during summer, comparable to summer ranges in Jackson. Residents resided in willow communities, aspen forests, or mixed-conifer and aspen forest throughout the year.

Both study areas were host to four species of large carnivores and seven wild ungulates (Buskirk 2016), although abundances of large carnivores differed substantially between Jackson and Sublette. Large carnivores included gray wolves, grizzly bears, cougars (*Puma concolor*), and American black bears (*U. americanus*). Elk (*Cervus canadensis*) were the most numerous ungulate in both study areas, and other species included mule deer (*Odocoileus hemionus*), bison (*Bison bison*; Jackson only), and pronghorn (*Antilocapra americana*). White-tailed deer (*O. virginianus*), bighorn sheep (*Ovis canadensis*), and mountain goats (*Oreamnos americanus)* also existed at lower densities.

Capture Methods

Jackson—Jackson moose were immobilized using a combination of darting and net-gunning techniques from the ground or helicopter (for details, see Becker 2008; Vartanian 2011). GPS collars with store-on-board technology (TGW-3700, Telonics, Inc., Mesa, Arizona, USA; n = 51) had various schedules of fix intervals. For years 2005-2007, locations were recorded every hour from 15 November to 15 June and once every 5 hours from 16 June to 14 November. During 2008-2010, GPS collars recorded locations every 3 hours from 16 December to 29 April, and hourly from 31 May to 14 November. Fix intervals of GPS collars from 2008-2010 were lengthened during Fall and Spring migration periods, recording a location every 12 hours from 15 November to 15 December, and 30 April to 30 May. To maintain adequate sample size of individuals for analyses, we captured thirty-four additional moose and fitted them with VHF radio collars (M2710, Advanced Telemetry Systems, Isanti, Minnesota, USA) to replace individuals lost to mortality from 2006-2008. We confirmed stage class of moose (yearling versus adult) by inspecting tooth eruption and incisor-tooth eruption and wear during capture (sensu Hindelang & Peterson 1994), and collected 20 ml blood samples from each female by jugular venipuncture to test for pregnancy status. For 11 females that died in winter 2008, we estimated percent-marrow fat. Marrow from femur, metatarsal, or humerus bone was weighed and dried at 70 °C for 14 days, then weighed again. Fat content was calculated as the ratio of dry to wet mass (Neiland 1970).

Sublette—Sublette moose (*n* = 84) were captured by helicopter net-gunning (Native Range Capture Services, Inc.) without immobilization agents. Moose were blindfolded, hobbled, and restrained in a sternal-recumbent position on their left side. Eighty-one moose were fitted with GPS store-on-board collars (TGW-3700 and -4700, Telonics, Inc., Mesa, Arizona, USA), and 10 were fitted with GPS satellite-uplink collars (various D-cell models, North Star Science and Technology, LLC, King George, Virginia). Telonics collars recorded hourly locations year-round, and North Star collars recorded locations every 3-5 hours, depending on the model. Both Telonics and North Star collars were programmed to release from the animal approximately 2 years after deployment. For 13 moose in 2013 with expiring GPS-collars, we deployed VHF-collars (M2230B, Advanced Telemetry Systems, Isanti, Minnesota) to continue demographic monitoring. GPS-collars were redeployed in subsequent captures if battery life was sufficient. During captures for years 2013-2014, we removed the right-incisiform canine for aging (sensu Swift *et al.* 2002). For study animals that died before 2013, we collected the I-1 incisor from the mortality site. All aging was done via cementum annuli by Matson's Laboratory, Milltown, Montana, USA. Similar to Jackson moose, we collected 20 ml of blood from each female by jugular venipuncture to test for pregnancy.

Vital Rate Monitoring

Pregnancy—Blood samples collected at capture were sent to BioTracking LLC to quantify serum for Pregnancy-Specific-Protein B (PSPB). We used a PSPB cut-off value of ≥ 2.5 ng/ml to identify pregnant females with viable fetuses for each sample (Josh Branen, BioTracking LLC, personal communication). For example, abortions or reabsorptions were identified by PSPB levels between 2.5 and 0.1 ng/ml. PSPB levels between 0 and 0.1 ng/ml were considered not pregnant and attributed to error in the assay). We omitted yearlings (< 2 & ≥ 1 years) from pregnancy analyses because their fecundity rate is usually lower or more variable compared with adults (Gaillard *et al.* 2000; Bonenfant *et al.* 2009).

Seasonal Ranges of Moose

We delineated summer and winter ranges of individual moose. First, using characteristics of Net-Squared Displacement, we identified individuals as migratory if they exhibited directional movement between distinct, non-overlapping winter and summer ranges. Second, we visually inspected plots of net squared displacement of migratory animals to identify start and end dates of migration. Migratory moose typically left winter ranges from late April to late May and arrived on summer ranges from early to late June, usually returning to winter range around mid- to Late December. If seasonal ranges overlapped between winter and summer, we classified individuals as residents and used the median start and end migration dates from migratory moose relative to year to define the time period of winter and summer ranges. Net-squared-displacement calculations were derived from the GPS-collar locations by calculating the squared distance between the first location identified from capture and every subsequent location along the annual travel path (Bunnefeld *et al.* 2011). After identifying the dates, we delineated seasonal range polygons for moose with GPS collars, using 95% contours derived from dynamic Brownian bridge movement models (dBBMMs; Kranstauber *et al.* 2012). We specified all dBBMMs with a location error of 20 meters, raster cell size of 20 meters, window size of 31 locations and a margin of 11 locations. Fix rates of the GPS collars varied, depending on the year of study and season.

We estimated seasonal home ranges for VHF-collared Jackson moose using helicopter survey locations obtained during summer and winter. Summer locations were collected during neonatal surveys in July, and winter locations were collected either during capture or juvenile surveys in February or March. To verify the accuracy of survey locations relative to a seasonal home range, we confirmed whether the helicopter survey locations of the GPS-collared moose fell within their core (60%) dBBMM seasonal home range. More than 80% of survey locations for GPS-collared moose fell within their core seasonal ranges, so we justified using the survey locations for VHF-collared moose as the center point of their seasonal range. We then circle-buffered the survey locations by the median home range size (range: 8-14 km^2) from 95% dBBMM contours of GPS-collared moose relative to year.

Covariates

Table S1. Descriptions of covariates assessed for their relative influence on probability of pregnancy, parturition (Sublette only), neonatal survival, overwinter juvenile survival (July-February), and overwinter adult survival (January-May) of Jackson (2005-2010) and Sublette (2011-2014) moose in western Wyoming, USA.

Predictor (Data Source)	**Resolution: Spatial (Temporal)**	**Ecological Influence**	**Description**	**Home Range Tested**	**Study Tested**	**Vital Rates Tested**	**Justification**
1988 Fires (MTBS[a])	30 m (1988)	forage quality & digestibility	Percentage of summer home range burned by 1988 Yellowstone fire from previous or current year.	Summer	Jackson only	All	Vartanian (2011)
Spring Length (MODIS, NDVI[b])	250 m (8-day)	forage quality & digestibility	Length of spring in days, from the start to end of spring green-up of vegetation from previous or current year.	Summer	Jackson & Sublette	All	Hamel *et al.* (2009); Pettorelli *et al.* (2007); Hebblewhite, Merrill and McDermid (2008); Monteith *et al.* (2015)
Growing season length (MODIS, NDVI[b])	250 m (8-day)	forage quality & digestibility	Length of the growing season in days, from start of spring green-up to start of fall senescence of vegetation from previous or current year.	Summer	Jackson & Sublette	All	Herfindal *et al.* (2006); Hjeljord and Histøl (1999); Ericsson, Ball and Danell (2002)
Mean Summer Palmer Drought Severity Index (PRISM[c])	4 km (Monthly)	forage quality & digestibility	Mean value of Palmer Drought Severity Index experienced across all summer ranges from June 1st to August 31st from previous or current year.	Summer	Jackson & Sublette	All	Pierce *et al.* (2012); Owen-Smith, Mason and Ogutu (2005)

Mean Late-Winter Palmer Drought Severity Index (PRISM[c])	4 km (Monthly)	tick abundance subsequent winter	Mean value of Palmer Drought Severity Index experienced across all winter home ranges during March and April from previous year.	Winter	Jackson & Sublette	All except pregnancy	Delgiudice (1997); Samuel (2007)
Snow Water Equivalence (DAYMET[d])	1 km (Daily)	winter severity	Cumulative amount of water kg/m2 contained in the snowpack from January 1st to May 31st on winter home ranges from previous or current year.	Winter	Jackson & Sublette	All[i]	Keech *et al.* (2000); Parker, Barboza and Gillingham (2009); Peterson and Allen (1974)
Relative Wolf Density (USFWS[e], NPS[f])	100 m (Seasonal)	predation	Relative density calculated using 90% fixed-Kernel Density Estimates, and multiplying pack size by utilization distribution cell value, then summing all overlapping values.	Summer & Winter	Jackson only	neonatal, overwinter juvenile, & adult survival	Mech and Peterson (2003:131-160)
Relative Grizzly Bear Density (IGBST[g])	14 km (Annual)	predation	Relative measure of bear activity.	Summer & April-May[h]	Jackson only	neonatal, overwinter juvenile, & adult survival	Zager and Beecham (2006); Becker (2008)
Ingesta-Free-Body Fat (nutritional measurements at capture)	Individual (February)	fecundity, survival	Ultrasound measurement of individual body fat levels for a percent-body fat estimate.	None (nutritional measure)	Sublette only	All	Cook *et al.* (2004); Cook *et al.* (2013)

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[a] Monitoring Trends in Burn Severity
[b] Moderate Resolution Imaging Spectroradiometer, Normalized Difference Vegetation Index
[c] Parameter-elevation Regressions on Independent Slopes Model
[d] Daily Surface Weather and Climatological Summaries
[e] US Fish and Wildlife Service
[f] National Park Service
[g] Interagency Grizzly Bear Study Team
[h] April and May were only used to test overwinter survival of adult moose
[i] cumulative monthly values from January 1-May 31 were used to test overwinter survival of adult moose

Relative Wolf Density

Data collection and management—Most wolf packs (> 90%) known to exist in the Jackson study area were collared with at least one VHF- or GPS-transmitter. Wolves were captured via helicopter darting during winter and padded foot-hold traps during summer. Packs with a VHF collar were relocated by fixed-wing aircraft as often as logistically possible, often biweekly. Pack size was recorded annually in mid-December to monitor population trends as was required by the Endangered Species Act listing. To estimate seasonal-space use of wolf packs in Jackson, we filtered out data that represented dispersing individuals, and obvious extra-territorial forays. If more than one individual in a pack was fitted with a GPS collar over the same time period, we used data from the wolf that best represented seasonal territory use based on our knowledge of the individual's hierarchy within the pack. We estimated wolf Kernel Density Estimates (KDEs) using 70% of the reference bandwidth value, because it was the best ad hoc approximation of space use (Worton 1989). Territory KDEs were estimated for winter using months January-April and summer using May-December to approximate seasonal range use of collared moose.

Overlap of wolf territories—Eighty percent of packs had ≥ 30 locations per season, which is considered to be a standard for representing animal space use with KDEs (Seaman & Powell 1996). If KDE sample size was < 30 locations, we assessed intra- and interannual seasonal 2-dimensional overlap of territories seasons between years using the *kerneloverlaphr* function from the adehabitatHR package (Calenge 2006) in R. In these cases, we first assessed 2-dimensional overlap of the pack's seasonal territory between two successive years (e.g., territorial overlap of summer of 2005 with summer 2006). If overlap was ≥ 75%, telemetry data were combined between the two years for the season (Rich *et al.* 2012). If seasonal overlap within a year was > 75%, both the winter and summer territories were combined to represent an annual territory for that year with > 30 locations. If sample size of an annual territory was < 30 locations, we assessed 2-dimensional overlap between two successive years and combined telemetry data if overlap was ≥ 75%.

Density calculation— After KDEs for each pack were created relative to year and season, we calculated seasonal wolf density using the number of wolves counted in the pack each December. Next, we multiplied the pack counts from December to every cell in the Utilization Distribution (100 m resolution) of the pack, and summed utilization distributions from all packs, resulting in one relative wolf density raster per season, per year. For example, for a pack's density estimate in its summer (May-December) territory, we used the December count for that year to represent the adults and pups that survived through the summer and their food needs. For the pack's subsequent winter territory (January-April), we used the same December count, because it accounted for those pups that survived into the winter season. For the pack's following summer territory, we used the next December count. We justified using this protocol because although there were other wolf counts available outside of December, they were not consistent among all the packs in the study area. Overwinter juvenile moose survival was monitored from July to February or March, therefore, the resulting wolf density estimate for each moose was a product of the weighted-average over time. For example, we proportionately assigned seasonal wolf density estimates to moose summer ranges for July-December (6 months; 66% exposure), and to moose winter ranges from January-March (3 months; 33% exposure). We extended the relative wolf density estimate for overwinter juvenile survival to March instead constricting it to February, because 49% of winter calves (n = 18) were observed for survival status in March, and wolf predation on moose calves is most common during winter (Mech et al. 2015).

Vital Rate Tests— For neonatal survival (i.e., early June-mid July), each mother with a neonate observed in June was assigned a relative wolf density estimate from her summer range. For overwinter juvenile survival (mid-July-February/March), each mother with a neonate in July received a temporally-weighted average for relative wolf density between summer and winter home ranges. Adult survival was assessed at monthly intervals, therefore, we applied the relative wolf density estimate from the moose summer home range to monthly intervals of June-December for, and an estimate from moose winter range to monthly intervals of January-May.

Relative Grizzly Bear Density

Grizzly bears are predators of neonatal, and to a lesser extent, juvenile and adult moose (Zager & Beecham 2006). We used a raster of grizzly bear density (14-km^2 resolution) developed by the Inter-Agency Grizzly Bear Study Team (Bjornlie *et al.* 2014) to estimate exposure of Jackson moose to grizzly bears (e.g., Fig. 1 in main text). We extracted relative grizzly bear density from summer home ranges of each Jackson moose for analyses of neonatal and overwinter juvenile survival. Grizzly bear predation of Jackson adult moose was documented from 2005-2007 (Becker 2008), therefore, we tested grizzly bear density on adult survival from summer home ranges for months June-December and winter home ranges for April-May. We did not test relative grizzly bear density experienced by Sublette moose, because density was considered to be very low to non-existent (e.g., Fig. 1 in main text), and thus biologically unimportant.

Data were unavailable for cougars and black bears, however, cougar predation of moose in the southern GYE constituted a small percentage ($\bar{x}$ = 5%) of their prey selection at the time of our study (Bartnick *et al.* 2013), and consumption of ungulates by black bears is substantially less than consumption by grizzly bears (Fortin *et al.* 2013; Costello *et al.* 2016). Given these circumstances, we believe that our data for relative densities of wolves and grizzly bears sufficiently estimates moose exposure to important predators.

1988 Fires

Using a preexisting raster from the Monitoring Trends in Burn Severity Project (Table S1), we defined areas burned by the 1988 fires with delta Normalized Burn Ratio values ≥ 100 (Key & Benson 2006), including all severity classes, from mild to severe.

NDVI Metrics

We calculated NDVI for the entire study area from 2004 to 2014 using the MOD09Q1 data product from the MODIS terra satellite and followed the same NDVI-processing protocol outlined in Merkle *et al.* (2016). We extracted the length of spring and growing season in days from each summer range using the spatially-weighted mean of all cells overlapping the 95% dBBMM isopleth of the home range. The length of spring encompasses a crucial period that directly influences forage availability at its most digestible state for temperate ungulates, as well as subsequent survival (Pettorelli *et al.* 2007; Hebblewhite, Merrill & McDermid 2008; Hamel *et al.* 2009). The length of the growing season is a measure of forage availability over summer, allowing for rapid development of body tissue and fat reserves (Hjeljord & Histøl 1999; Ericsson, Ball & Danell 2002), and higher body mass (Herfindal *et al.* 2006). We defined the length of spring as the number of days from the start to end of vegetation green-up (defined as first- and second-second derivatives of an NDVI curve), and the length of the growing season from the start of vegetation green-up until the start of fall senescence (defined as the third-second derivative) of vegetation. In summary, length of spring usually included the months of May and June, whereas the length of the growing season usually included months May to September. To test responses of vital rates to NDVI metrics, we used either the value from current year, in addition to or in place of the previous year's value, depending on the vital rate. For example, pregnancy status was measured in February, so we used the previous year's value. For neonatal survival (June-July), we tested the current year's length of spring, and tested the previous year's value of growing season length (calculated at the end of summer). We used the previous year's value of spring and growing length to test the response of overwinter juvenile survival (June-February).

Drought Metrics

We estimated drought using 4-km^2 resolution raster from PRISM (Daly, Neilson & Phillips 1994) of the Palmer Drought Severity Index. The mean PDSI across summer home ranges of all moose per year was calculated at the end of summer, therefore, we applied the previous year's value of PDSI to test the influence of drought conditions on pregnancy, parturition, neonatal survival, and overwinter adult survival. We used the current year's value of PDSI for testing overwinter juvenile survival. We tested late-winter drought on the survival of calves and adults, but not on pregnancy, because mating season for moose generally occurs in the early stages of tick loading and it would be unlikely that an effect would be detected.

Winter Severity

To relate the energetic costs of snow on moose vital rates, we used raster data of Snow Water Equivalence (SWE) from Daymet (Thornton, Running & White 1997). Although moose are well adapted to deep snow (Coady 1974), harsh winters reduce mobility and increase energetic demands, negatively influencing overwinter survival of juveniles (Peterson 1977; Keech *et al.* 2011) and adults (Peterson & Allen 1974). Additionally, the nutritional costs of moving through snow on maternal condition while calves are in utero could produce less viable neonates (Schwartz 1998:141-171). We calculated the cumulative values of daily SWE from moose winter ranges annually from January 1 to May 31 to test the response of parturition, neonatal survival (SWE experienced while in utero), and overwinter juvenile survival (in utero and first winter as a juvenile). We calculated cumulative values of monthly SWE from January-May to test the influence of winter severity on adult survival.

Cost of Lactation

A growing body of evidence has linked the cost of lactation to condition and survival of ungulates (Testa & Adams 1998; Keech *et al.* 2000; Monteith *et al.* 2014; Ruprecht *et al.* 2016). In a separate set of univariate models, we tested the effect of raising a neonate to July on each vital rate using Generalized Linear Mixed-Models (GLMMs) with year of observation as a random intercept. We deemed relationships important if their 95% confidence intervals did not overlap zero.

Statistical Analyses

For probability of pregnancy, parturition, neonatal survival, and overwinter juvenile survival, we fit binomial GLMMs with the logit link function and year of observation as a random intercept to account for interannual variation in covariates. To assess monthly adult survival, the Andersen-Gill formulation (Andersen & Gill 1982) of Cox proportional hazards models (CPHs; Cox 1972). We used an information-theoretic approach for all analyses of vital rates by conducting model selection of all possible combinations of covariates based on second-order Akaike information criteria adjusted for small sample size (AIC_c), ΔAIC_c and Akaike weights (w_i) (Burnham & Anderson 2002). If Pearson correlation coefficients between each pair of covariates were > |0.5|, we assessed univariate models between each pair and selected the covariate with the minimum AIC to use for model selection. Consequently, all variables that entered AIC_c model selection had Pearson correlation coefficients < |0.5|. To improve convergence of the GLMMs and CPHs, we scaled all covariate values so their mean was zero and their standard deviation was one. For all analyses, we omitted mortalities attributed to anthropogenic causes (i.e., harvest, poaching, and vehicle collisions $n = 6$) and within 2 weeks of capture ($n = 7$). For all vital rate models except overwinter juvenile survival of Jackson moose, we required a minimum of 10 events (i.e., failures, mortalities) per covariate (hereafter, "EPC") that entered a model (Babyak 2004). There were only eight events recorded for overwinter juvenile survival of Jackson moose and seven events recorded for neonatal survival of Sublette moose, therefore, we followed Vittinghoff and McCulloch (2007) and allowed only one covariate to enter each model during AIC_c model selection of those vital rate models. We deemed covariates important if their 85% confidence intervals did not overlap zero within 4 ΔAIC_c of the top model, an appropriate confidence level for identifying a best-approximating model with AIC model selection (Arnold 2010). Model fit was assessed using area under the receiver operating characteristic curve (AUC; Hanley & McNeil 1982). We did not test covariates on the probability of parturition for Jackson moose, because moose that were captured during February were less likely to give birth the year they were handled compared with moose that were not handled ($P < 0.05$; Vartanian 2011).

In Sublette, we conducted AIC_c model selection on bottom-up covariates (omitting IFBFat) for all years (2011-2014) to maximize sample sizes per vital rate and improve detection of environmental influences. We then subsetted years 2012-2014 for which we had IFBFat measurements, and conducted AIC_c model selection with both IFBFat and environmental covariates.

In modeling monthly survival of adults, we assessed winter (January-May) and summer (June-December) separately, because we expected environmental covariates to affect moose survival differently with regard to season (Gaillard *et al.* 2000). We used the Andersen-Gill formulation of CPHs with each month representing a time interval (i.e., the counting process; Therneau & Grambsch 2000), allowing for left-staggered entry and right-censoring of adults (e.g., if the VHF transmitter failed, collar dropped from the individual, or the moose emigrated from study area). Coefficient estimates from CPHs specify the mortality hazard, where positive values increase mortality hazard (i.e., negatively relate to survival). Adults were allowed to contribute to the risk sample every year they were monitored, therefore, we used a robust "sandwich" estimator to account for correlated observations within individuals (Therneau & Grambsch 2000). We chose a recurrent time-scale for seasonal CPHs based off of the biological year (i.e., June 1-May 31), because adult mortality occurred largely during late winter (i.e., a strong seasonal hazard; Fieberg & DelGiudice 2009). We allowed monthly SWE values to cumulatively increase over winter (e.g., a time-varying covariate; Therneau & Grambsch 2000). An interaction of SWE × relative wolf density was tested during model selection, because temperate ungulates can be more vulnerable to predation as snowfall increases (Post *et al.* 1999; Smith *et al.* 2004; Hebblewhite 2005). Model fit of CPHs were assessed using concordance (Harrell 2015), which is analogous to AUC. Diagnostic tests were performed on all CPH models to evaluate the proportional hazards assumption using Schoenfeld residuals (Therneau & Grambsch 2000), but were not reported unless significant violations were detected (i.e., $P < 0.05$).

Life-Stage Simulation Analysis— To assess the influence of interannual variation in vital rates on λ, we followed Morris and Doak (2002), and estimated vital rates separately by biological year, then derived a beta distribution of 10,000 estimates for each vital rate by randomly sampling the mean and variance estimated from each year. To derive the 10,000 estimates of λ from beta distributions for each population separately, we used a 3x3 stage-structured, post-birth, female-based matrix model (Caswell 2001) consisting of the following form:

$$\lambda = \begin{bmatrix} 0 & 0 & (S_a F\, T) \\ S_j & 0 & 0 \\ 0 & S_y & S_a \end{bmatrix}$$

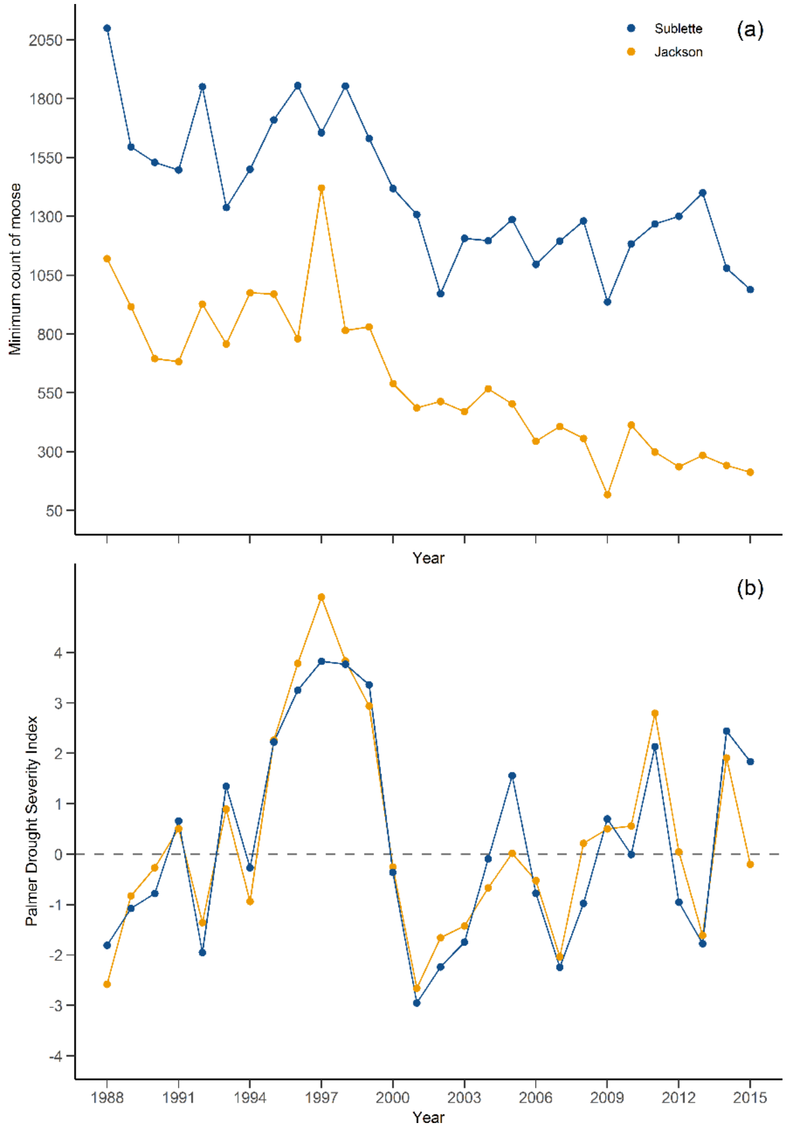
The first stage calculates reproduction rates by multiplying adult survival (S_a) by fecundity (F = pregnancy rate × parturition rate), and probability of twinning T ((1-t) + (2t)). Vartanian (2011) reported a negative effect of capture on parturition rates of Jackson moose. Moose that were captured during February were less likely to give birth the year they were handled compared with moose that were not handled ($P < 0.05$). The handling effect reported by Vartanian (2011) precluded an estimate of parturition calculated as the proportion of pregnant (handled) moose that were observed with a neonate in June, therefore, we estimated a beta distribution of Jackson parturition rates from unhandled moose observed for parturition status from 2005-2007 (details in Becker 2008; Table 2 in main text).

The second stage is juvenile survival (S_j), calculated as the neonatal survival rate × overwinter juvenile survival rate. Our overwinter juvenile surveys were conducted during February and March, therefore, in an attempt to correct for missed late-winter mortality of calves and provide a more realistic estimate of λ, we subtracted an additional 10% from annual estimates of overwinter juvenile survival. Effectively, this additional 10% did not change the variability of the vital in the LSA, and only influenced estimates of λ. The third stage consists of yearling survival (S_y) and adult survival (S_a). We did not measure yearling survival, so we calculated a mean estimate from a range of yearling survival rates for moose reported in Kunkel and Pletscher (1999) and McLaren et al. (2000). On average, yearling survival was 6.43% lower than adult survival, thus our estimate was calculated as $S_y = S_a - 6.43\%$.

The resulting beta distributions of each vital rate were randomly sampled to produce 10,000 matrix replicates and estimates of λ. We then regressed λ on each vital rate, providing an estimate of the proportion of variation and slope in λ explained by each vital rate (r^2). We were unable to account for sampling variance due to the limited time-frame of the studies.

Covariate LSA—After assessing vital rate variability and its influence on λ, we evaluated the influence of the covariates on Jackson and Sublette λ through their relative effect on vital rates. To estimate the strength and variability of covariates on vital rates, we extended the LSAs (see Methods in main text) to incorporate the effects of covariates on the vital rates. We estimated rates of pregnancy, parturition, neonatal, overwinter juvenile, and overwinter adult survival as a function of the coefficient estimates of the covariates for 10,000 iterations, and populated 3 x 3 stage-structured, female-based, post-birth matrix models (same matrix-model protocol used in LSAs) with these predicted values. For the covariate LSA, we used estimates of adult survival from the winter model (January-May) only, because summer models failed to converge. We accounted for total annual mortality by subtracting the average rate of summer mortality (June-December) from each predicted estimate of winter survival. For vital rate responses that were not predicted by any covariate, we applied the beta distribution from the LSA to account for unexplained variation. Yearling survival was also set as a constant, estimated at 6.43% lower than adult survival ($S_y = S_a - 6.43\%$). Similar to the LSA, we then regressed λ on each covariate, providing an estimate of the amount of variation (r^2) and slope in λ explained by the covariate.

Figure S1. Minimum counts of moose (a) and annual estimates of Palmer Drought Severity Index derived from PRISM raster data (b) from the Jackson (yellow) and Sublette (blue) study areas from 1988-2015 in western Wyoming, USA. Minimum counts of moose by Wyoming Game and Fish Department were completed in February along aerial transects throughout the herd management units using a Bell-47 helicopter with 1 pilot and 2 observers.



APPENDIX S2. Tables and figures from analyses on Jackson moose in western Wyoming, USA, from 2005-2010. Legend for all covariate abbreviations in model selection tables is immediately below.

Variable	**Abbreviated Name**
Growing season length	Grow Seas Length
Spring length	Spring Length
Mean summer PDSI	Summer PDSI
Mean late-winter PDSI	Lt Winter PDSI
Monthly cumulative SWE	csum SWE
Relative wolf density	Wolf Dens
Relative grizzly bear density	Griz Bear Dens
Percentage of summer home range burned by the 1988 fires	Fire

Table S3. Results from AIC$_c$ model selection of all possible combinations of covariate influences on pregnancy status of Jackson adult (≥ 2.5 years) moose during February from 2005-2009, using GLMMs with year of observation as a random intercept. We constrained model selection to 1 covariate per model, because there were 10 failures (moose not pregnant at February capture). We omitted growing season length $_{t\text{-}1}$ from AIC$_c$ model selection, because it was collinear ($r > |0.50|$) with and had higher AIC values derived from univariate models than spring length $_{t\text{-}1}$.

Model	**Summer PDSI $_{t\text{-}1}$**	**Spring Length $_{t\text{-}1}$**	**Fire $_{t\text{-}1}$**	***k***	**logLik**	**AIC$_c$**	**Δ**	***w$_i$***
3	0.71			1	-28.01	62.30	0.00	0.49
1				0	-29.87	63.90	1.56	0.22
5		0.49		1	-28.98	64.30	1.95	0.18
2			-1.23	1	-29.48	65.30	2.95	0.11

Table S4. Results from AIC_c model selection of all possible combinations of covariate influences on Jackson neonatal moose survival (June-July) from 2005-2009, using GLMMs with the year of observation as a random intercept. We constrained model selection to 3 covariates per model, because there were 33 failures (neonatal moose not present with mother during July survey). We omitted monthly cumulative SWE, growing season length $_{t-1}$, and mean summer PDSI $_{t-1}$ from AIC_c model selection, because they were collinear ($r > |0.50|$) with and had higher AIC values derived from univariate models than mean late-winter PDSI $_{t-1}$.

Model	**Fire**	**Griz Bear Dens**	**Spring Length**	**Lt Winter PDSI $_{t-1}$**	**Wolf Dens**	k	**logLik**	AIC_c	**Δ**	w_i
2	-0.72					1	-44.59	95.50	0.00	0.19
4	-0.61	-0.34				2	-43.94	96.50	0.96	0.11
10	-0.90		-0.33			2	-43.98	96.60	1.03	0.11
6	-0.71			-0.24		2	-44.20	97.00	1.48	0.09
12	-0.81	-0.39	-0.39			3	-43.13	97.20	1.66	0.08

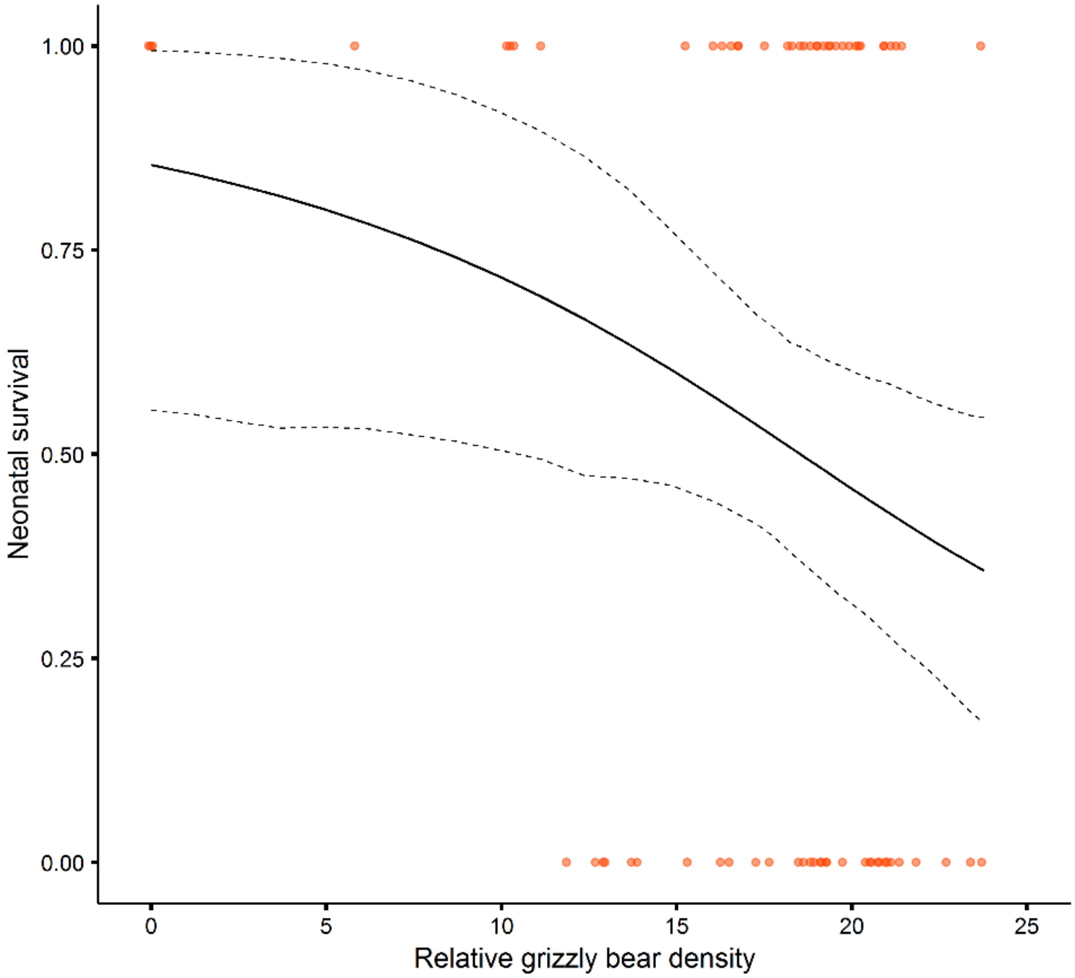
Table S5. Results from AIC$_c$ model selection of all possible combinations of covariate influences on Jackson overwinter juvenile survival (July-February) from 2005-2010, using GLMMs with year of observation as a random intercept. We constrained model selection to 1 covariate per model, because there were 8 failures (juvenile moose not present with mother during July survey). We omitted spring length $_{t-1}$, SWE (in utero), and mean late-winter PDSI $_{t-1}$ from AIC$_c$ model selection, because they were collinear (r >|0.50|) with and had higher AIC values derived from univariate models than growing season length $_{t-1}$ or SWE (first winter as a juvenile).

Model	**Wolf Dens** **July-March**	**Grow Seas Length $_{t-1}$**	**Fire $_{t-1}$**	**SWE**	**Summer PDSI $_{t-1}$**	**Griz Bear Dens** **Summer and Fall**	***k***	**logLik**	**AIC$_c$**	**Δ**	***w$_i$***
33	-0.85						1	-17.13	41.00	0.00	0.46
1							0	-19.32	43.00	1.99	0.17
5		-0.54					1	-18.42	43.60	2.57	0.13
2			0.35				1	-19.00	44.70	3.74	0.07
17				0.14			1	-19.26	45.20	4.25	0.06
9					0.13		1	-19.27	45.30	4.27	0.06
3						-0.07	1	-19.30	45.30	4.34	0.05

Table S6. Results from AIC$_c$ model selection of all possible combinations (2 ΔAIC$_c$ shown) of covariate influences on Jackson adult (≥ 2.5 years) female moose overwinter (January-May) survival using Cox-Proportional Hazards models with a cluster term (i.e., robust "sandwich" estimator) around each individual. We constrained model selection to 4 covariates maximum per model, because there were 45 failures (moose mortalities). We omitted grizzly bear density (April-May), growing season length $_{t-1}$, and mean late-winter PDSI $_{t-1}$ from AIC$_c$ model selection, because they were collinear ($r > |0.50|$) with and had higher AIC values derived from univariate models than spring length $_{t-1}$ or cumulative SWE. A model with the interaction term of SWE × relative wolf density (not shown) did not compete with the top models (AIC$_c$ = 471.8; ΔAIC$_c$ = 3.3).

Model	**Wolf Dens**	**Fire $_{t-1}$**	**Summer PDSI $_{t-1}$**	**Spring Length $_{t-1}$**	**csum SWE**	***k***	**logLik**	**AIC$_c$**	**Δ**	***w$_i$***
29	0.32	-0.30	-0.25			3	-231.26	468.50	0.00	0.16
25	0.37	-0.32				2	-232.72	469.40	0.90	0.10
21	0.33		-0.26			2	-232.89	469.80	1.26	0.08
31	0.34	-0.28	-0.22	0.11		4	-231.06	470.20	1.62	0.07
27	0.39	-0.26		0.18		3	-232.07	470.20	1.62	0.07
19	0.41			0.24		2	-233.20	470.40	1.87	0.06

Figure S2. Estimated probability (± 95% CI) with observed covariate values (orange points) of survival of neonatal Jackson moose (*n* = 70) from June to July, modeled as a function of relative grizzly bear density from 2005-2009 in western Wyoming, USA, using a GLMM with the link logit function, and year of the observation as a random intercept.



APPENDIX S3. Tables and figures from analyses without IFBFat on Sublette moose in western Wyoming, USA, from 2011-2014. Legend for all covariate abbreviations in model selection tables is immediately below.

Variable	**Abbreviated Name**
Growing season length	Grow Seas Length
Spring length	Spring Length
Mean summer PDSI	Summer PDSI
Mean late-winter PDSI	Lt Winter PDSI
Monthly cumulative SWE	csum SWE

Table S7. Results from AIC$_c$ model selection of all possible combinations of covariate influences (IFBFat not included) on pregnancy status of Sublette adult ($\geq$ 2.5 years) moose during February from 2011-2014, using GLMMs with year of observation as a random intercept. We constrained model selection to 4 covariates maximum per model, because there were 47 failures (moose not pregnant during February capture). We omitted mean summer PDSI $_{t-1}$ from model selection, because it was collinear (r >|0.50|) with and had higher AIC values derived from univariate models than spring length $_{t-1}$ or growing season length $_{t-1}$.

Model	**Grow Seas Length $_{t-1}$**	**Spring Length $_{t-1}$**	***k***	**logLik**	**AIC$_c$**	**Δ**	***w$_i$***
1			0	-97.22	198.50	0.00	0.42
2	-0.16		1	-96.78	199.70	1.19	0.23
3		0.16	1	-96.79	199.70	1.22	0.23
4	-0.14	0.14	2	-96.48	201.20	2.69	0.11

Table S8. Results from AIC_c model selection of all possible combinations of covariate influences (IFBFat not included) on parturition status of Sublette adult (≥ 2.5 years) moose during February from 2011-2014, using GLMMs with year of observation as a random intercept. We constrained model selection to 2 covariates maximum per model, because there were 28 failures (neonatal moose not present with mother during June survey). We omitted spring length $_{t-1}$, growing season length $_{t-1}$, and mean late-winter PDSI $_{t-1}$ from AIC_c model selection, because they were collinear ($r >|0.50|$) with and had higher AIC values derived from univariate models than mean summer PDSI $_{t-1}$.

Model	**Summer PDSI $_{t-1}$**	**SWE**	***k***	**logLik**	**AIC_c**	**Δ**	**w_i**
2	0.61		1	-59.08	124.40	0.00	0.63
4	0.60	-0.04	2	-59.07	126.50	2.13	0.22
1			0	-61.92	128.00	3.55	0.11
3		-0.17	1	-61.70	129.60	5.23	0.05

Table S9. Results from AIC_c model selection of all possible combinations of covariate influences (IFBFat not included) on Sublette neonatal (June-July) moose survival from 2011-2014, using GLMMs with year of observation as a random intercept. We constrained model selection to 1 covariate maximum per model, because there were 10 failures (neonatal moose not present with mother during June survey). We omitted spring length $_{t-1}$, growing season length $_{t-1}$, and mean late-winter PDSI $_{t-1}$ from AIC_c model selection, because they were collinear (r >|0.50|) with and had higher AIC values derived from univariate models than mean summer PDSI $_{t-1}$ or SWE.

Model	**Summer PDSI $_{t-1}$**	**SWE**	***k***	**logLik**	**AIC_c**	**Δ**	**w_i**
2	-0.58		1	-29.27	64.80	0.00	0.53
1			0	-30.79	65.70	0.88	0.34
3		0.17	1	-30.67	67.60	2.79	0.13

Table S10. Results from AIC$_c$ model selection of all possible combinations of covariate influences (IFBFat not included) on Sublette overwinter (July-February) juvenile survival of moose from 2011-2014, using GLMMs with year of observation as a random intercept. We constrained model selection to 2 covariates maximum per model, because there were 28 failures (juvenile moose not present with mother during winter survey). We omitted mean summer PDSI $_{t-1}$, SWE (first winter as a juvenile), and SWE (in utero) from AIC$_c$ model selection, because they were collinear (r >|0.50|) with and had higher AIC values derived from univariate models than spring length $_{t-1}$ or mean late-winter PDSI $_{t-1}$.

Model	**Grow Seas Length $_{t-1}$**	**Lt Winter PDSI $_{t-1}$**	**Spring Length $_{t-1}$**	***k***	**logLik**	**AIC$_c$**	**Δ**	***w$_i$***
1				0	-30.90	66.00	0.00	0.45
2	-0.31			1	-30.40	67.30	1.24	0.24
3		-0.14		1	-30.81	68.10	2.05	0.16
5			-0.01	1	-30.90	68.30	2.24	0.15

Table S11. Results from AIC$_c$ model selection of all possible combinations of covariate influences (IFBFat not included) on Sublette adult female moose overwinter (January-May) survival from 2011-2014, using CPHs with a cluster term (i.e., robust “sandwich” estimator) around each individual. We constrained model selection to 2 covariates maximum per model, because there were 26 failures (moose mortalities). We omitted mean summer PDSI $_{t-1}$ from AIC$_c$ model selection, because it was collinear ($r >|0.50|$) with and had a higher AIC value derived from univariate models than spring length $_{t-1}$ or mean late-winter PDSI $_{t-1}$.

Model	**Spring Length $_{t-1}$**	**csum SWE**	**Grow Seas Length $_{t-1}$**	**Lt Winter PDSI $_{t-1}$**	***k***	**logLik**	**AIC$_c$**	**Δ**	***w$_i$***
9	-0.29				1	-130.47	262.90	0.00	0.27
10	-0.38	-0.22			2	-130.16	264.30	1.39	0.14
11	-0.30		-0.09		2	-130.37	264.70	1.81	0.11
13	-0.29			-0.03	2	-130.45	264.90	1.98	0.10
3			-0.04		1	-131.54	265.10	2.15	0.09
5				0.02	1	-131.56	265.10	2.18	0.09
2		0.02			1	-131.56	265.10	2.18	0.09
7			-0.05	0.04	2	-131.53	267.10	4.13	0.04
4		0.01	-0.04		2	-131.54	267.10	4.15	0.03
6		0.05		0.05	2	-131.54	267.10	4.16	0.03

Table S12. Top models derived from AIC_c model selection (IFBFat not included), with coefficient estimates and 85% confidence intervals that did not overlap zero for vital rates from the Sublette study (2011-2014) in western Wyoming, USA. Model Fit refers to either the area under the receiver operating characteristic curve (AUC) from GLMMs or concordance from CPHs. Negative beta coefficients from CPHs decrease the mortality hazard (positively relate to survival).

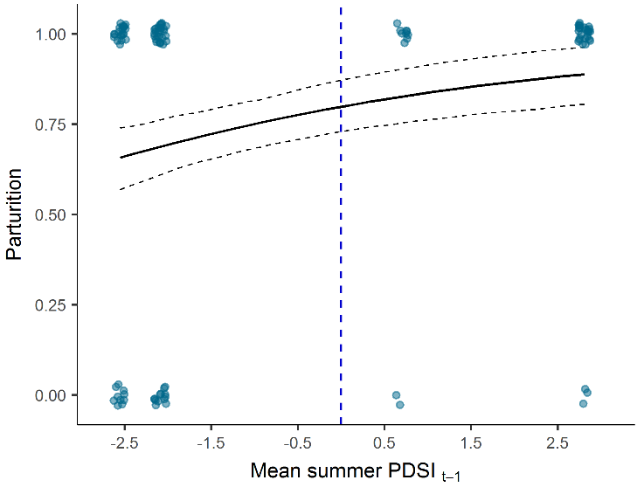
Vital Rate	**Model Type**	**Study**	**Parameter**	β	**Lower 85% CI**	**Upper 85% CI**	**Model Fit**
Pregnancy	GLMM logit	Sublette	**Intercept**				
Parturition	GLMM logit	Sublette	**Mean summer PDSI $_{t-1}$**	0.61	0.27	1.17	0.63[a]
Neonatal survival	GLMM logit	Sublette	**Mean summer PDSI $_{t-1}$**	-0.58	-1.25	-0.08	0.66[a]
Overwinter juvenile survival	GLMM logit	Sublette	**Intercept**				
Overwinter adult survival	CPH	Sublette	**Spring length t-1**	-0.29	-0.548	-0.03	0.59[b]

[a] AUC

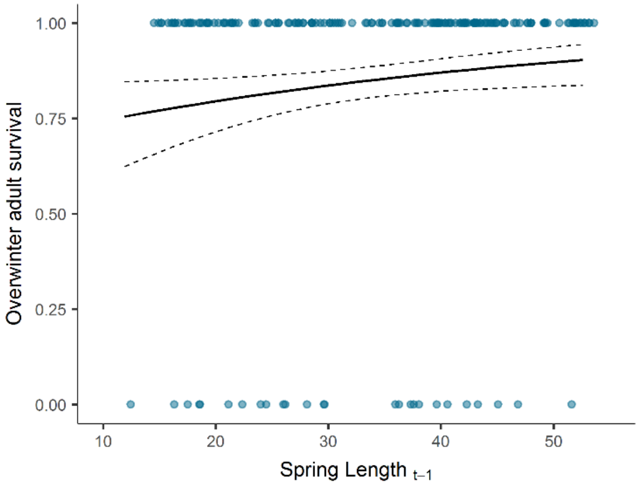
[b] Concordance

Figure S3. Top models (IFBFat not analyzed) for Sublette moose from 2011-2014 showing estimated probability (± 85% CI) with observed covariate values (blue points) of (*a*) parturition of adults as a function of mean summer PDSI $_{t-1}$ (vertical blue line represents drought threshold; positive values are wetter conditions), and (*b*) overwinter (January-May) survival of adult female moose, as a function of the spring length $_{t-1}$.

(a) Sublette (IFBFat not analyzed)



(b) Sublette (IFBFat not analyzed)



APPENDIX S4. Tables and figures from analyses including IFBFat on Sublette moose in western Wyoming, USA, from 2012-2014. Legend for all covariate abbreviations in model selection tables is immediately below.

Variable	**Abbreviated Name**
Growing season length	Grow Seas Length
Spring length	Spring Length
Mean summer PDSI	Summer PDSI
Mean late-winter PDSI	Lt Winter PDSI
Monthly cumulative SWE	csum SWE
IFBFat	Ingesta-Free-Body-Fat

Table S13. Results from AIC$_c$ model selection of all possible combinations of covariate influences (including IFBFat) on pregnancy status of Sublette adult (≥ 2.5 years) moose during February from 2012-2014, using GLMMs with year of observation as a random intercept. We constrained model selection to 4 variables maximum per model, because there were 40 failures (moose not pregnant during February capture). We omitted mean summer PDSI $_{t-1}$ from model selection, because it was collinear (r >|0.50|) with and had higher a AIC value derived from a univariate model than spring length $_{t-1}$.

Model	**IFBFat**	**Grow Seas Length $_{t-1}$**	**Lt Winter PDSI $_{t-1}$**	**Spring Length $_{t-1}$**	***k***	**logLik**	**AIC$_c$**	**Δ**	***w_i***
2	1.42				3	-63.14	132.50	0.00	0.32
4	1.44	-0.28			4	-62.41	133.10	0.66	0.23
6	1.42		-0.08		4	-63.07	134.40	1.98	0.12
10	1.41			0.05	4	-63.11	134.50	2.06	0.11
8	1.44	-0.29	0.03		5	-62.41	135.20	2.79	0.08
12	1.45	-0.29		-0.02	5	-62.41	135.20	2.79	0.08
14	1.41		-0.08	0.03	5	-63.06	136.60	4.11	0.04
16	1.44	-0.30	0.02	-0.02	6	-62.40	137.40	4.96	0.03

Table S14. Results from AIC$_c$ model selection of all possible combinations of covariate influences (IFBFat included) on parturition status of Sublette adult (≥ 2.5 years) moose during February from 2012-2014, using GLMMs with year of observation as a random intercept. We constrained model selection to 2 covariates maximum per model, because there were 26 failures (neonatal moose not present with mother during June survey). We omitted spring length $_{t-1}$, growing season length $_{t-1}$, and mean late-winter PDSI $_{t-1}$ from AIC$_c$ model selection, because they were collinear (r >|0.50|) with and had higher AIC values derived from univariate models than mean summer PDSI $_{t-1}$.

Model	**IFBFat**	**Summer PDSI $_{t-1}$**	**SWE**	***k***	**logLik**	**AIC$_c$**	**Δ**	**w_i**
4	1.47	0.83		4	-41.66	91.70	0	0.78
2	1.39			3	-44.30	94.90	3.12	0.16
6	1.38		-0.01	4	-44.30	97.00	5.29	0.06
3		0.63		3	-53.87	114.00	22.25	0.00
7		0.61	-0.08	4	-53.81	116.00	24.3	0.00
1				2	-56.48	117.10	25.34	0.00
5			-0.28	3	-56.01	118.30	26.52	0.00

Table S15. Results from AIC$_c$ model selection of all possible combinations of covariate influences (IFBFat included) on Sublette neonatal moose survival (June-July) from 2012-2014, using GLMMs with year of observation as a random intercept. We constrained model selection to 1 covariate maximum per model, because there were 7 failures (neonatal moose not present with mother during July survey). We omitted mean summer PDSI $_{t-1}$ and SWE (in utero) from AIC$_c$ model selection, because they were collinear (r >|0.50|) with and had higher AIC values derived from univariate models than mean late-winter PDSI $_{t-1}$.

Model	**Lt Winter PDSI $_{t-1}$**	**IFBFat**	**Spring Length**	**Grow Seas Length $_{t-1}$**	***k***	**logLik**	**AIC$_c$**	**Δ**	***w$_i$***
5	-1.43				1	-20.43	47.20	0.00	0.41
2		-1.06			1	-20.54	47.40	0.23	0.36
9			-0.74		1	-21.84	50.00	2.84	0.10
1					0	-23.03	50.20	3.04	0.09
3				-0.38	1	-22.75	51.80	4.64	0.04

Table S16. Results from AIC$_c$ model selection of all possible combinations of covariate influences (IFBFat included) on Sublette overwinter (July-February) juvenile survival from 2012-2014, using GLMMs with year of observation as a random intercept. We constrained model selection to 1 covariate maximum per model, because there were 12 failures (juvenile moose not present with mother during winter survey). We omitted mean late-winter PDSI $_{t-1}$, SWE (first winter as a juvenile), and SWE (in utero) from model selection, because they were collinear ($r > |0.50|$) with and had higher AIC values derived from univariate models than mean summer PDSI $_{t-1}$.

Model	**Grow Seas Length $_{t-1}$**	**IFBFat**	**Summer PDSI $_{t-1}$**	**Spring Length $_{t-1}$**	k	**logLik**	**AIC$_c$**	**Δ**	w_i
1					0	-26.40	57.1	0.00	0.40
3	-0.33				1	-25.92	58.4	1.33	0.20
2		0.16			1	-26.30	59.2	2.08	0.14
5			-0.11		1	-26.35	59.3	2.19	0.13
9				-0.06	1	-26.39	59.3	2.26	0.13

Table S17. Top models from AIC_c model selection including IFBFat with coefficient estimates and 85% confidence intervals that did not overlap zero for vital rates of Sublette moose from 2012-2014 in western Wyoming, USA. “Model Fit” refers to either the area under the receiver operating characteristic curve (AUC) from GLMMs or concordance from CPHs. Negative beta coefficients from CPHs decrease the mortality hazard (positively relate to survival). We did not detect important covariates for overwinter juvenile survival of Sublette moose.

Vital Rate	**Model Type**	**Study**	**Parameter**	$\boldsymbol{\beta}$	**Lower 85% CI**	**Upper 85% CI**	**Model Fit**
Pregnancy	GLMM logit	Sublette	IFBFat	1.42	1.07	1.91	0.83[a]
Parturition	GLMM logit	Sublette	IFBFat	1.47	1.05	2.39	0.82[a]
			Summer PDSI $_{t-1}$	0.83	0.33	1.75	
Neonatal Survival	GLMM logit	Sublette	Lt winter PDSI $_{t-1}$	-1.42	-2.87	-0.45	.55[a]
Overwinter juvenile survival	GLMM logit	Sublette	Intercept				
Overwinter adult survival	CPH	Sublette	IFBFat	-1.07	-1.34	-0.87	0.84[b]

[a] AUC

[b] Concordance

Table S18. Results from AIC$_c$ model selection of all possible combinations of covariate influences (IFBFat included) on Sublette adult ($\geq$ 2.5 years) female moose overwinter (January-May) survival from 2012-2014, using CPHs with a cluster term (i.e., robust “sandwich” estimator) around each individual. We constrained model selection to 2 covariates maximum per model, because there were 20 failures (i.e., moose mortalities). We omitted spring length $_{t-1}$, growing season length (first summer as a juvenile), and mean late-winter PDSI $_{t-1}$ from AIC$_c$ model selection, because they were collinear ($r >|0.50|$) with and had higher AIC values derived from univariate models than mean summer PDSI $_{t-1}$. Although AIC$_c$ selected mean summer PDSI $_{t-1}$ to be in the top model, we declared the addition of this parameter as uninformative, because the ΔAIC$_c$ of this additional parameter was < 1.0 compared with a more parsimonious model of only IFBFat, and both models occurred within 2 ΔAIC$_c$ of the top model.

Model	**IFBFat**	**Summer PDSI $_{t-1}$**	**csum SWE**	***k***	**logLik**	**AIC$_c$**	**Δ**	**w_i**
7	-1.12	-0.41		2	-79.78	163.60	0.00	0.53
3	-1.07			1	-81.23	164.50	0.89	0.34
4	-1.07		-0.04	2	-81.22	166.50	2.89	0.13
5		-0.29		1	-97.42	196.80	33.27	0.00
2			-0.08	1	-98.11	198.20	34.65	0.00
6		-0.30	-0.10	2	-97.32	198.70	35.10	0.00

APPENDIX S5. Results and Discussion

RESULTS

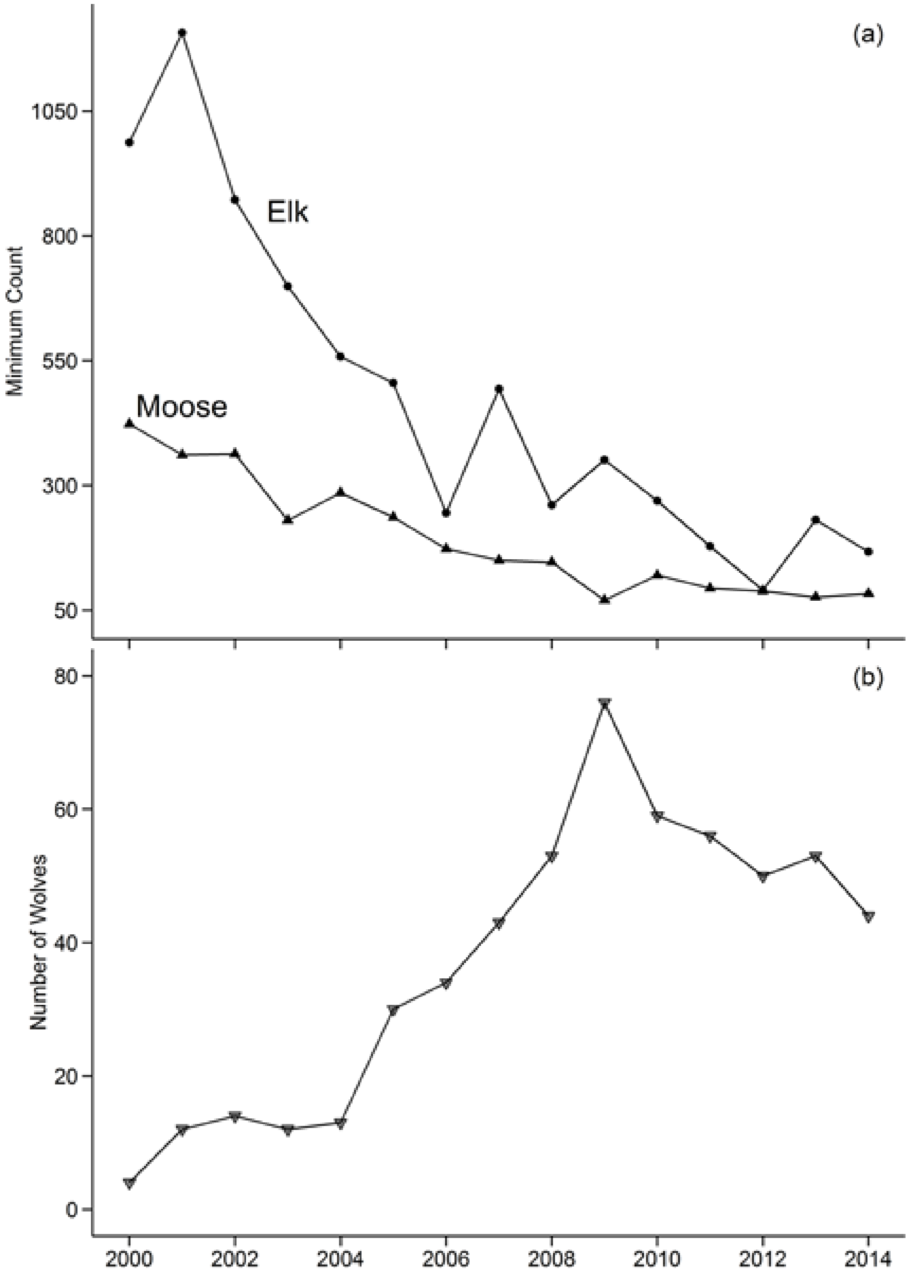
We detected a weak, negative effect of raising a neonate to July on overwinter adult survival of Jackson moose (CPH β = 0.77; 90% CI: 0.11, 1.4), although in Sublette, we detected a positive effect (CPH β = -1.09; 95% CI: -2.02, -0.16). Models testing the effect of raising a neonate to July on Jackson pregnancy, Sublette neonatal survival, and overwinter juvenile survival did not converge due to limited sample sizes of events (i.e., non-pregnant Jackson moose and Sublette juvenile mortalities).

DISCUSSION

Reproductive trade-offs—Increasing evidence points to the importance of reproductive trade-offs in population dynamics of ungulates (Testa & Adams 1998; Testa 2004a; Milner *et al.* 2013; Monteith *et al.* 2013). The positive effect of the 1988 fires on overwinter adult survival of Jackson moose (Fig. 2*a* in main text) may be linked to a dynamic between the cost of lactation, predation of neonates, and altered maternal condition. We found a negative, albeit weak, effect of rearing a neonate to July on subsequent overwinter survival of adult females (see also Testa 2004b). The majority of Jackson moose incurring the cost of lactation were rearing calves in unburned home ranges. Those moose that lost neonates in burned areas were possibly released from the cost of lactation during early summer, allowing them to recover lost somatic reserves in preparation for the following winter. Despite better forage quality in unburned home ranges (Vartanian 2011), moose rearing young would still be burdened by drought, which was negatively related to overwinter adult survival. Additionally, wolves during winter may have targeted female moose with juveniles (see also Testa 2004b). A study of forage quality by McArt *et al.* (2009) in the same study area as Testa (2004b) suggested that females with calves entering winter were particularly likely to be Nitrogen-limited from poor forage quality during summer. In our study, reproductive moose simultaneously dealing with the negative effects of drought of forage quality and the cost of lactation during summer may have further degraded their nutritional condition entering winter, making them more vulnerable to wolf predation.

Prey selectivity of wolves—Prey selectivity of generalist predators interacts not only with vulnerability, but also with relative prey abundance (Huggard 1993; Molinari-Jobin *et al.* 2004). Elk are primary prey for wolves in the GYE, partially due to their relatively high abundance (Smith *et al.* 2004; Metz *et al.* 2012). Although larger, alternative prey such as bison and moose are hunted, they exist at relatively lower densities and are considerably more dangerous for wolves to hunt (Mech, Smith & MacNulty 2015). Garrott *et al.* (2007) found that wolves in Yellowstone National Park prey switched from elk to bison as the ratio of bison to elk increased, and as bison became more vulnerable during years of deep snow. In our study area, wolves began recolonizing Jackson around the year 2000, responding to an initially high abundance of elk with a lagged and exponentially numerical response (Fig. S4b). As the abundance of wintering elk declined sharply over the next decade, the ratio of moose to elk began to increase (Fig. S4a). Thus, it is possible that higher ratios of moose to elk facilitated prey switching of wolves from elk to moose during our study. Recent research in the Jackson study area supports this notion, with an interannual kill ratio of moose to elk ranging from 0.06 to 0.91 ($\bar{x}$ = 0.44 SE ± 0.18; *n* = 205; calculated from Stephenson et al. 2010:2014).

Figure S4. Species counts by biological year (June 1-May 31) of (*a*) Minimum counts of moose and elk in the Buffalo Valley (winter range) during February from 2000-2015 by Wyoming Game and Fish Department using aerial transects from a Bell-46 helicopter with 1 pilot and 2 observers, and (*b*) number of wolves counted in December 2000-2014 by US Fish and Wildlife Service and National Park Service, whose pack boundaries overlapped Grand Teton National Park and used the Buffalo Valley during winter in western Wyoming, USA.



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CHAPTER TWO

ANTIPREDATOR RESPONSE OF MOOSE DIMINISHES DURING PERIODS OF RESOURCE DEFICIT: A TEST OF THE STARVATION-PREDATION HYPOTHESIS

ABSTRACT

Quantifying how animals behave under the risk of predation is fundamental to understanding predator-prey dynamics. The starvation-predation hypothesis predicts that when prey experience resource deficits, they avoid starvation by foraging as much as possible, even when risk of predation is high. As winter progresses, ungulates experience resource deficits due to senescence of forage and increasing snow accumulation, and therefore should temper antipredator responses to avoid starvation. We tested this prediction by assessing antipredator response of moose (*Alces alces*) to wolf (*Canis lupus*) presence during winter in the Greater Yellowstone Ecosystem of North America. Using simultaneously-collected GPS locations of collared moose and wolves, we identified interactions (minimum distance at which a moose came to a wolf) at three distance categories (0-500m, 500m-1km, 1-1.5km). We assessed the antipredator response of moose by measuring speed, displacement, and habitat use 24 hours before and after interactions with wolves at each distance category. Additionally, we assessed how the progression of winter influenced movement rates and habitat use of moose before versus after interactions with wolves. Moose did not alter their movement rates or habitat use after encountering wolves at any distance category when time was ignored; however, when day-of-year was incorporated, we found that movement rates gradually diminished as winter progressed. Moose did not avoid their preferred foraging habitat (riparian areas) following encounters with wolves and, in early winter, more strongly selected riparian areas after wolf encounters. Our work demonstrates that antipredator response of moose to wolves is ephemeral as winter progresses, and supports theoretical predictions that prey experiencing resource deficits exhibit muted antipredator behavior. Our findings integrate antipredator responses with a long history of work on starvation-predation tradeoffs, suggesting that nutritional condition of prey may buffer against run-away risk effects in food webs featuring large mammals.

Key words: antipredator behavior, moose, predation risk, resource deficit, starvation-predation hypothesis, ungulate, winter, wolf.

INTRODUCTION

Animals often weigh the decision to forage or reduce predation risk (i.e., the risk of being killed) to maximize survival (Abrams 1984, Lima and Dill 1990, Matassa et al. 2016). Antipredator behavior of prey manifests through some combination of altered habitat selection, increased vigilance, higher movement rates, and reduced foraging (Beckerman et al. 1997, Heithaus et al. 2007, Winnie and Creel 2007). Because they come at the expense of energy gain, such behaviors can reduce the nutritional state of prey, indirectly reducing fitness (i.e., 'risk effects'; Preisser et al. 2005, Peckarsky et al. 2008, Boonstra 2013). Thus, improved understanding of the drivers of antipredator behavior may illuminate ties between individual behavior and population performance (MacLeod et al. 2014).

The influence of antipredator behavior on prey demography has become a central issue in predator-prey ecology (Lima and Dill 1990, Werner and Peacor 2003); however, understanding how risk effects are curtailed or exacerbated by resource limitation and other environmental factors is complex (Preisser et al. 2009). Specifically, feedbacks between predation risk and resource availability may attenuate risk effects, because reduced foraging by prey due to antipredator behavior increases resource abundance (Peacor 2002). Nevertheless, research has attributed reduced nutritional condition and growth of young to antipredator behavior as opposed to resource limitation (Boonstra et al. 1998, Dunn et al. 2010). Thus, contextual factors associated with antipredator behavior during periods of resource deficit warrant more attention due to their potential influences on prey demography.

Resource acquisition is necessary not only for tissue maintenance, but also for escaping or fending off predators. As a result, the nutritional state of an animal can influence the strength of antipredator response (McNamara and Houston 1986, McNamara and Houston 1990). For example, animals experiencing resource deficits should avoid starvation by foraging as much as possible, even at the cost of high predation risk. This is commonly known as the starvation-predation hypothesis, which has been supported across a wide variety of taxa, including tadpoles (*Rana catesbeiana*) (Anholt and Werner 1995), wildebeest (*Connochaetes taurinus*) (Sinclair and Arcese 1995), small mammals (Brown and Kotler 2004), and green sea turtles (*Chelonia mydas*) (Heithaus et al. 2007). In particular, the starvation-predation hypothesis should be well supported in environments characterized by high variability in resource availability. During winter, ungulates in temperate latitudes experience nutritional deficits as winter progresses due to senescence of forage and increasing snow accumulation (Parker et al. 2009), and therefore should temper antipredator responses to avoid starvation. Although the starvation-predation hypothesis predicts that antipredator behavior should change with prey condition, empirical tests remain rare, especially for wide-ranging predators and prey exposed to temporal variation in resource availability (but see Sinclair & Arcese 1995).

The response of elk (*Cervus canadensis*) to the recovery of gray wolves (*Canis lupus*) in the Greater Yellowstone Ecosystem (GYE) of North America (Fig. 1) is a prominent example of how ungulates adjust antipredator behavior in response to risk perception (Fortin et al. 2005, Winnie and Creel 2007, Gower et al. 2008). These studies have illustrated that antipredator responses (altered levels of habitat use, movement rates, and vigilance) of elk to the presence of wolves are likely to be ephemeral throughout winter (Liley and Creel 2008, Middleton et al. 2013). Elk are the primary prey of wolves throughout the GYE, although larger, alternative prey such as moose (*Alces alces*) and bison (*Bison bison*) are also hunted (Smith et al. 2004). Moose exposed to wolves in the GYE have experienced population declines (Oates 2016), although the extent to which antipredator behavior could have contributed to this decline is unclear. Moose are a key browser in this system, that have been shown to have cascading effects on willow and bird communities (Berger et al. 2001), creating the possibility that broader community-level consequences could result if foraging opportunities are reduced from avoiding encounters with predators.

We tested the starvation-predation hypothesis (McNamara and Houston 1990) through antipredator response of moose to wolves in the GYE during winter, a period of resource deficit. We expected antipredator response to weaken from early to late winter, because moose would be more averse to the risk of starvation than that of predation, and nutritional condition of ungulates decreases as winter progresses (Monteith et al. 2013). The potential links between antipredator behavior and prey demography underscores the importance of developing our understanding of how prey respond to predation risk.

METHODS

Study area— We monitored moose from February 2005-May 2010 in northwestern Wyoming (Fig. 1; 43.5202˚N, -110.2206˚W). The study area (approximately 1,050 km^2) consisted mostly of public land, including portions of Grand Teton National Park and the Bridger-Teton National Forest (43.5202˚N, -110.2206˚W). During winter, moose occupied mainly riparian areas, containing dense and expansive willow (*Salix* spp.) patches interspersed with cottonwood

(*Populus angustifolia*), Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), blue spruce (*Picea pungens*), and subalpine fir (*Abies lasiocarpa*). Homogenous and mixed-forests of aspen (*Populus tremuloides*) and conifers occurred throughout the study area. The climate is characterized by short, dry summers and long, cold winters with relatively deep snow (mean annual snowfall 339.09 SE ± 17.41 cm).

Large carnivores in the study area included gray wolves and cougars (*Puma concolor*), with grizzly (brown) bears (*Ursus arctos*) and American black bears (*U. americanus*) emerging from dens typically in mid to late April. Elk were the most common ungulate in the study area. Other ungulates included mule deer (*Odocoileus hemionus*), bison (*Bison bison*), pronghorn (*Antilocapra americana*), white-tailed deer (*O. virginianus*), bighorn sheep (*Ovis canadensis*), and mountain goats (*Oreamnos americanus).*

Collaring of wolves and moose—We captured a total of 51 adult (>2.5 years) female moose in January-March from 2005-2009 (details in Becker 2008, Vartanian 2011). We fit each individual with a GPS collar containing store-on-board technology (TGW-3700, Telonics, Inc., Mesa, Arizona, USA), with an hourly GPS-fix interval from 2005-2007, and every 3 hours from 2008-2010. We omitted all moose from analyses that died within 2 weeks of capture (*n* = 3). We used all locations from winter ranges between December 1st and April 30th, coinciding with accumulating snowfall throughout the season, before spring migration. We determined seasonal (summer and winter) ranges, and the onset of spring and fall migrations, using net-squared displacement calculations from GPS-fixes (Bunnefeld et al. 2011).We surveyed collared females from the air or ground each July for presence of a juvenile at mother’s heel. During the subsequent winter, we resurveyed these females once between February and March to confirm presence of juveniles.

From 2005-2010, we captured wolves (n = 20 individuals from 6 packs) by either helicopter darting during winter or padded leg-hold traps during summer, and fitted them with GPS (Global Positioning System) Argos collars. GPS collars acquired locations every 3 or 6 hours, depending on the transmitter. We omitted locations that were clearly erroneous or characteristic of dispersing individuals. We only used locations from 1 GPS-collared wolf (n = 14) per pack that best represented winter territory use based on our knowledge of the individual's hierarchy within the pack at any given time to represent pack-level movement during winter. We justified using one wolf to represent pack movement because cohesiveness is generally high during winter (Benson and Patterson 2015).

Encounters and habitat use—We tested antipredator response of moose during winter by comparing their movement rates and habitat use 24 hours before and after encounters with wolves. We tested moose antipredator response during winter only, because predation risk of adult female moose is largely attributed to wolves. Data were not available for grizzly bears, which are present during other seasons and are also predators of adult moose. We defined the sampling unit of interactions between moose and wolves as the minimum distance between a collared moose and wolf (hereafter, "encounter"), and binned encounters into 3 distance categories: 0 to 500 m (hereafter, "500 m"), 500 m to 1 km (hereafter, "1 km"), and 1 km to 1.5 km (hereafter, "1.5 km") (Fig. S1; Table S1). We assumed that moose were unlikely to detect wolves beyond 1.5 km, based on aerial behavioral observations of moose to wolf presence in other studies (Mech et al. 2015). To identify encounters, we intersected the GPS-fix time and coordinates of wolves and moose. We set a time buffer around each GPS-fix of each species to detect all encounters occurring within 70 minutes of the GPS-fix times of moose. For 24 hours before and after encounters, we measured speed (meters traveled between successive locations divided by the time length of the fix interval) and total distance traveled (displacement) of each moose. To maintain sampling independence and allow movement rates and displacement of moose to return to pre-encounter levels, we omitted encounters that occurred more than once within 48 hours. Additionally, we required that the wolf was further away from the moose than the distance category at which the encounter occurred for 48 hours prior to the hour at which the encounter happened. For example, if an encounter occurred at 600 m and a GPS-collared wolf approached closer than that distance over the next 48 hours, we omitted the 600 m encounter from analyses (Fig. S1).

Antipredator responses of ungulates are expressed not only through increased movement rates, but also through habitat use shifts (Creel et al. 2005, Middleton et al. 2013, Ford et al. 2014, Donadio and Buskirk 2016). We assessed whether habitat use of moose changed 24 hours after encounters with wolves using a vegetation raster (30 m spatial resolution) for Teton County (Cogan and Johnson 2013). Moose are obligate browsers, and consume few species of woody plants during winter (Houston 1967, Vartanian *unpublished*). In our study area, moose diet during winter consisted of 59% (SE ± 0.04) shrub (*Salix* spp.), 22% (SE ± 0.04) conifer (*Abies* spp., *Pinus* spp.), and 15% (SE ± 0.01) deciduous trees (*Populus* spp., *Betula* spp.) (Vartanian *unpublished*), therefore, we calculated distance to vegetation classes deemed important to moose: riparian vegetation (i.e., homogenous stands of *Salix* spp., and intermixed with species of *Populus*, *Pseudotsuga*, *Picea*, and *Abies*), conifer, and aspen.

Modeling Approach—We used a mixed-model framework to assess shifts in speed, displacement, and habitat use of moose in response to wolf encounters. We constructed models for each distance category using a paired-design, testing the moose response (i.e., before=0, versus after=1) as a main effect with speed (log transformed) and displacement (log transformed) as dependent variables, and the sampling unit of the encounter as a random intercept. To assess whether antipredator response attenuated as winter progressed, we tested for the interaction between day-of-year (hereafter, "DOY") and speed, as well as displacement. In the presence of wolves, female moose with juveniles are likely to be more cautious than those without juveniles (White and Berger 2001, Dussault et al. 2005); therefore, we tested a subset of females confirmed to have a juvenile present (from winter surveys) for differences in antipredator response.

We analyzed habitat use of moose with a use-versus-availability design at the third-order scale (Johnson 1980) 24 hours before and after wolf encounters with Generalized Linear Mixed-effects Models (GLMMs). We fit binomial GLMMs with the logit link function and with each encounter as a random intercept. For all GLMMs of habitat use, we defined availability by estimating a kernel Brownian bridge (Horne et al. 2007) contour at the 99% level from the 48 hours of locations (24 h before and 24 h after an encounter). Within the extent of the kernel contour, we extracted distance-to-habitat type from the true ("used") locations, as well as from randomly sampled ("available") locations, and ensured that each encounter had ≥ 100 random locations to minimize bias (Northrup et al. 2013). We tested habitat selection for distance to riparian, conifer, and aspen forests in each distance category, interacting moose response (before=0, after=1; main effect) with each habitat-type. We also tested habitat use between early- versus late-winter time periods by categorizing encounters that occurred earlier than DOY 59 as 'early' winter, and encounters ≥ DOY 60 as 'late' winter. We then ran GLMMs for each period to determine if habitat shifts in response to wolf encounters were different in early versus late winter. We allowed covariates to be in the same model if Pearson correlation coefficients between the pair was < 0.5. We checked global models (i.e., only main effects of distance-to habitat type) for each distance category against the models containing the response to the encounter to ensure directions of covariates (positive versus negative) were consistent. We inspected Variance Inflation Factors (VIFs) for covariates and retained them if VIFs in the global model were < 3.0. We interpreted covariates with 95% bootstrapped (500 simulations) confidence intervals that did not overlap zero as important. We used R version 3.3.0 (R Core Team 2016) for all data extraction and analyses.

RESULTS

We detected 119 unique encounters among 25 individual moose and 6 wolf packs (Table S1). Neither speed nor displacement of moose increased significantly following wolf encounters for any distance category when DOY was ignored. However, when DOY was incorporated into GLMMs, moose increased speed and displacement within the 500 m distance category during early winter, gradually diminishing as winter progressed (Fig. 2*a*-*b*; Table S1). Encounter sample size for the 500 m category during early winter (January-February) was limited (n = 3), therefore, we combined observations between 0-1 km (n = 22) to avoid type II error; significance still held (β = -0.01; 95% CI: -0.01 -0.0002). Due to limited number of encounters for moose with juveniles at heel (n = 12), we grouped all of these encounters into one distance category of 0-2 km. For mothers with juveniles, we did not detect a difference in speed, displacement, or their interactions with DOY following wolf encounters (Table S1).

Following wolf encounters within the 500 m and 1 km distance categories, moose more strongly selected riparian habitat (Fig. 2*c*; Table S2). We detected weak selection for conifer (β = -3.73, 90% CI: -6.85, -0.68) following encounters within the 0-500 m distance category. For early versus late winter, we grouped encounters between 0 and 1 km due to limited sample size (n = 3) of early winter encounters within the 500 m distance category. Following wolf encounters within 1 km, moose selected more strongly for riparian habitat during early winter, but showed no change in late winter (Table S2).

DISCUSSION

Antipredator responses of moose to wolves weakens as resource deficit increases during winter. Movement rates (speed and displacement) of moose did not change following wolf encounters during late winter, when resource deficits are greatest. Only during early winter did movement rates increase following wolf encounters, and then only at close proximity (< 500 m). Our findings support the starvation-predation hypothesis, in which resource-limited prey should be less responsive to predation risk, choosing to forage in riskier places or times to avoid starvation (McNamara and Houston 1990). The unwillingness of moose to abandon preferred habitats adds further support for the predation-starvation hypothesis. Moose did not avoid their preferred foraging habitat (riparian), following encounters with wolves and, in early winter, they more strongly selected riparian areas. Predators can strongly shape the antipredator behaviors of their prey, with the potential for risk effects and even trophic cascades (Donadio and Buskirk 2016). Our findings suggest that the risk of starvation, long known to mediate foraging behavior, has the potential to dampen or altogether negate such demographic effects of antipredator behavior.

Our results are consistent with prior work on the antipredator behavior of ungulates (Latombe et al. 2014, Nicholson et al. 2014, Vander Vennen et al. 2016, Wikenros et al. 2016), with some notable exceptions. Elk are the primary prey of wolves in the GYE, and are more vigilant (Liley and Creel 2008), select conifer cover (Fortin et al. 2005), and increase movement rates following wolf encounters within 1 km (Middleton et al. 2013) to 5 km (Proffitt et al. 2009). In contrast, moose increased movement rates in response to wolves only during early winter, and habitat use did not shift from preferred habitats. Riparian habitat may have served as refuge from wolves, despite the predictability of moose occurrence in these areas. Additionally, moose were less sensitive than elk to the spatial proximity of wolves, responding only when wolves approached within 500 m. These findings are consistent with predictions made by Creel (2011), that large-bodied prey and obligate feeders should show weakened antipredator responses to cursorial predators because levels of predation risk should be inversely related to body size. Further, mixed feeders (i.e., elk) should also exhibit stronger antipredator behavior compared with dietary specialists (i.e., moose), because the former have greater flexibility in resource and habitat use, enabling them to adjust their exposure to predation risk (Creel 2011). By comparison, elk are predicted to respond more strongly to predation risk because their diet breadth enables more flexibility of habitat use (Creel 2011). Further, compared with elk, moose are more likely to stand their ground when approached by wolves (Mech et al. 2015), similar to other large-bodied, alternative prey such as bison (MacNulty et al. 2014). Although moose may be generally less responsive to predation risk to wolves, our detection of a heightened behavioral response during early winter suggests that antipredator behavior is more dynamic among ungulates than has been appreciated previously.

Numerous factors can influence antipredator behavior, such as habitat structure, predator hunting mode, sociality of prey, and nutritional condition. For example, moose with calves in regions of boreal forest have been shown to select conifer cover more strongly when in the proximity of wolves (White and Berger 2001, Dussault et al. 2005). In sub-Saharan Africa, browsers are more sensitive to habitat cues associated with ambush predators (Valeix et al. 2009, Thaker et al. 2011). Weak antipredator responses of moose to wolves may be explained by a link between summer drought (leading to reduced forage quality) and lower adult survival in late winter when resource deficits are greatest (Oates 2016). In late winter, moose likely were in compromised nutritional condition, and unwilling to leave foraging habitats or increase movement rates in response to wolf encounters. The diverse array of antipredator responses suggest that a combination of environmental factors influences how ungulates manage predation risk.

Shifts in resource availability are fundamental to assess the direction and strength of antipredator behavior (Preisser et al. 2009). Seasonal resource shortages characterize temperate (Parker et al. 2009) and tropical ecosystems (Owen-Smith 2008), suggesting that state-dependent antipredator responses should be widespread. Our findings integrate antipredator responses with a long history of work on starvation-predation tradeoffs (Abrams 1984, Brown 1992, Ovadia and Schmitz 2002), suggesting that nutritional condition of prey may buffer against run-away risk effects in large mammal systems.

Several caveats of our study are warranted. As a retrospective study, we were unable to collect data on vigilance, which may reduce forage intake despite moose occupying riparian habitat. Additionally, the temporal resolution of our GPS collars (fixes every 1-3 hours) may have been too coarse to detect all antipredator responses of moose to wolves, which could have been more acute and persistent through winter than we reported (Creel et al. 2013). Regardless, we were still able to detect differences in movement rates and habitat use predicted by the starvation-predation hypothesis. Additionally, our paired study design accounts for relative decreases in movement as winter progresses (Appendix S1: Fig. S2). These circumstances, as well as our record of observed encounters throughout winter (Appendix S1: Fig. S3), lead us to believe that our results accurately represent antipredator behavior of moose.

Research has shown that wolves can alter the behavior of their prey through predation risk (Fortin et al. 2005, Liley and Creel 2008), and numerous studies have advanced our knowledge of mechanisms of predation risk and risk effects across taxa (Lima and Dill 1990, Werner and Peacor 2003, Peckarsky et al. 2008, Schmitz 2008, Fortin et al. 2015). We caution, however, against generalizations of predators inducing ecosystem-level changes through fear, especially in multi-species ungulate assemblages. Although wolves and elk have been the focus of antipredator research in the GYE, moose have largely been overlooked, despite the strong influence of their browsing on shrub communities (Brandner et al. 1990, Berger et al. 2001). Our work suggests that the impact of herbivory in the GYE, and the extent to which it is reduced by predation risk, is more dynamic than currently is appreciated. In systems with multiple ungulate prey, species- or population-specific factors such as body size, diet specialization (Creel et al. 2014), and resource limitation (Owen-Smith 2008) are likely to interact to mediate the strength of antipredator responses across prey taxa, leading to outcomes of species interactions that are complex and difficult to predict.

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FIGURES & TABLES

Figure 1. Map of Jackson study area, with locations of moose on winter range (December-April) with wolf pack territories (colored polygons) estimated from 95% dynamic Brownian bridge movement models. Overlapping packs not shown: Teton and Antelope.

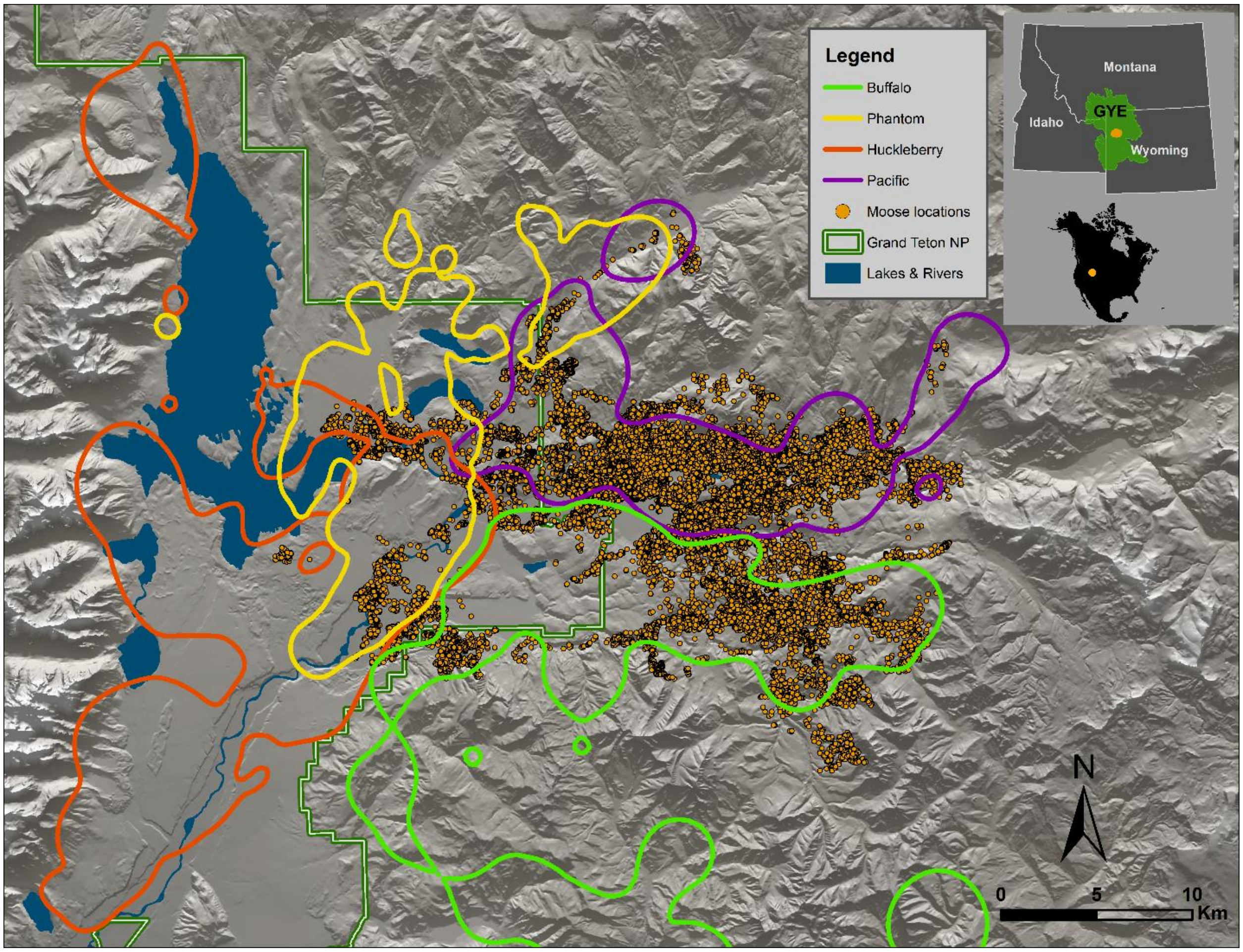
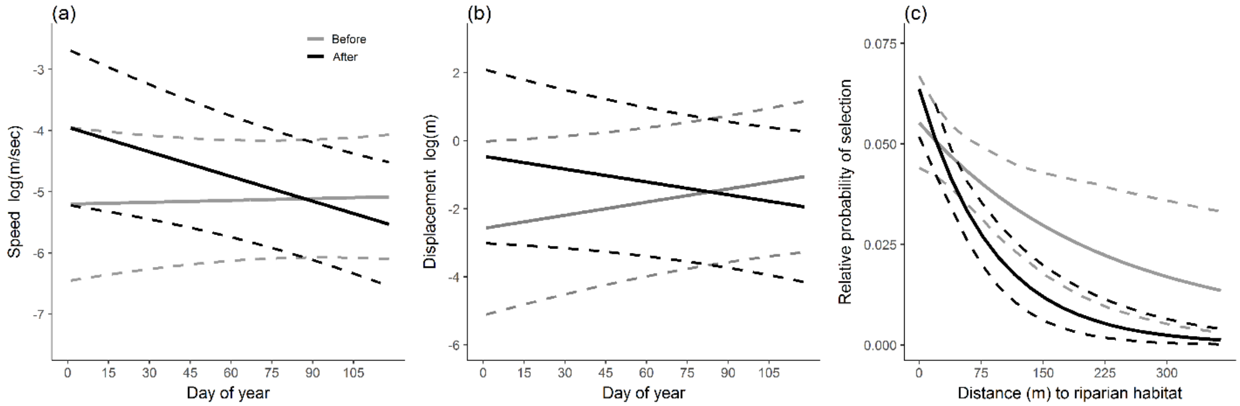


Figure 2. Predicted relationships (solid lines) and 95% CIs (dashed lines) from the 500m distance category of (a) speed, (b) displacement, both with an interaction between DOY and moose response, and (c) relative probability of selection of riparian habitat 24 hours before (gray lines) and after (black lines) encounters with wolves during winter (January-April) in northwest Wyoming from 2005-2010.



APPENDIX S1. Figures and Tables

Table S1. Model results from all distance categories of encounters with coefficient estimates and 95% confidence intervals.

Model (units)	**Encounters**	**Distance range**	**Moose**	**Wolf packs**	**Parameter**	**Estimate**	**Lower 95% CI**	**Upper 95% CI**
DOY*log of Speed (m/sec)	17	0-500m	13	4	DOY*encounter response	-0.014	-0.025	-0.005
	48	500m-1km	16	6		-0.003	-0.009	0.004
	55	1-1.5km	20	5		0.001	-0.003	0.006
DOY*log of displacement (m)	17	0-500m	13	4	DOY*encounter response	-0.025	-0.034	-0.016
	48	500m-1km	16	6		0.005	-0.001	0.010
	55	1-1.5km	20	5		0.001	-0.004	0.004
Log of speed (m/sec)	17	0-500m	13	4	encounter response	0.027	-0.317	0.357
	48	500m-1km	16	6		-0.137	-0.310	0.050
	55	1-1.5km	20	5		-0.013	-0.197	0.172
Log of displacement (m)	17	0-500m	13	4	encounter response	-0.037	-0.378	0.256
	48	500m-1km	16	6		-0.003	-0.172	0.163
	55	1-1.5km	20	5		-0.236	-0.377	-0.087
Log of speed with calf presence (m/sec)	12	0-2km	3	3	encounter response	-0.213	-0.549	0.133
Log of displacement with calf presence (m)	12	0-2km	3	3		0.047	-0.416	0.499
DOY*log of speed with calf presence (m/sec)	12	0-2km	3	3	DOY*encounter response	-0.004	-0.021	0.015
DOY*log of displacement with calf presence (m)	12	0-2km	3	3	DOY*encounter response	0.010	-0.012	0.028

Table S2. Model Results of habitat use from all distance categories of encounters with coefficient estimates and 95% CIs.

Habitat use model	**Encounters**	**Distance range**	**Moose**	**Wolf packs**	**parameter for distance-to (m)**	β	**Lower 95% CI**	**Upper 95% CI**
All winter January-April	17	0-500 m	13	4	riparian*encounter response	-7.38	-13.36	-2.31
					conifer*encounter response	-3.73	-6.94	0.67
					aspen*encounter response	0.51	-1.16	2.33
	48	500 m-1 km	16	6	riparian*encounter response	-3.84	-6.40	-0.19
					conifer*encounter response	-0.27	-2.59	1.36
					aspen*encounter response	-0.06	-0.72	0.81
	55	1-1.5 km	20	5	riparian*encounter response	-1.38	-4.26	0.75
					conifer*encounter response	-1.73	-4.10	0.55
					aspen*encounter response	-0.03	-1.11	1.13
Early winter January-February	22	0-1 km	12	3	riparian*encounter response	-6.00	-10.21	-2.38
					conifer*encounter response	-0.63	-2.91	1.68
					aspen*encounter response	-0.51	-2.14	1.20
Late winter March-April	43	0-1 km	16	5	riparian*encounter response	-2.89	-7.82	1.68
					conifer*encounter response	-1.66	-4.35	0.94
					aspen*encounter response	0.40	-0.42	1.19
All winter January-April	12	0-2 km	3	3	riparian*encounter response	-12.73	-18.91	-7.73
					conifer*encounter response	-2.41	-6.83	0.98
					aspen*encounter response	-2.23	-6.73	2.07

Figure S1. Example of a wolf-moose encounter (a) at 600 m distance, the minimum distance the wolf came to the moose which was then identified as an 'encounter' in the 1 km distance category. For 24 hours before and after each encounter, we assessed antipredator response of moose changes in movement rates (speed, displacement) and habitat use of moose.

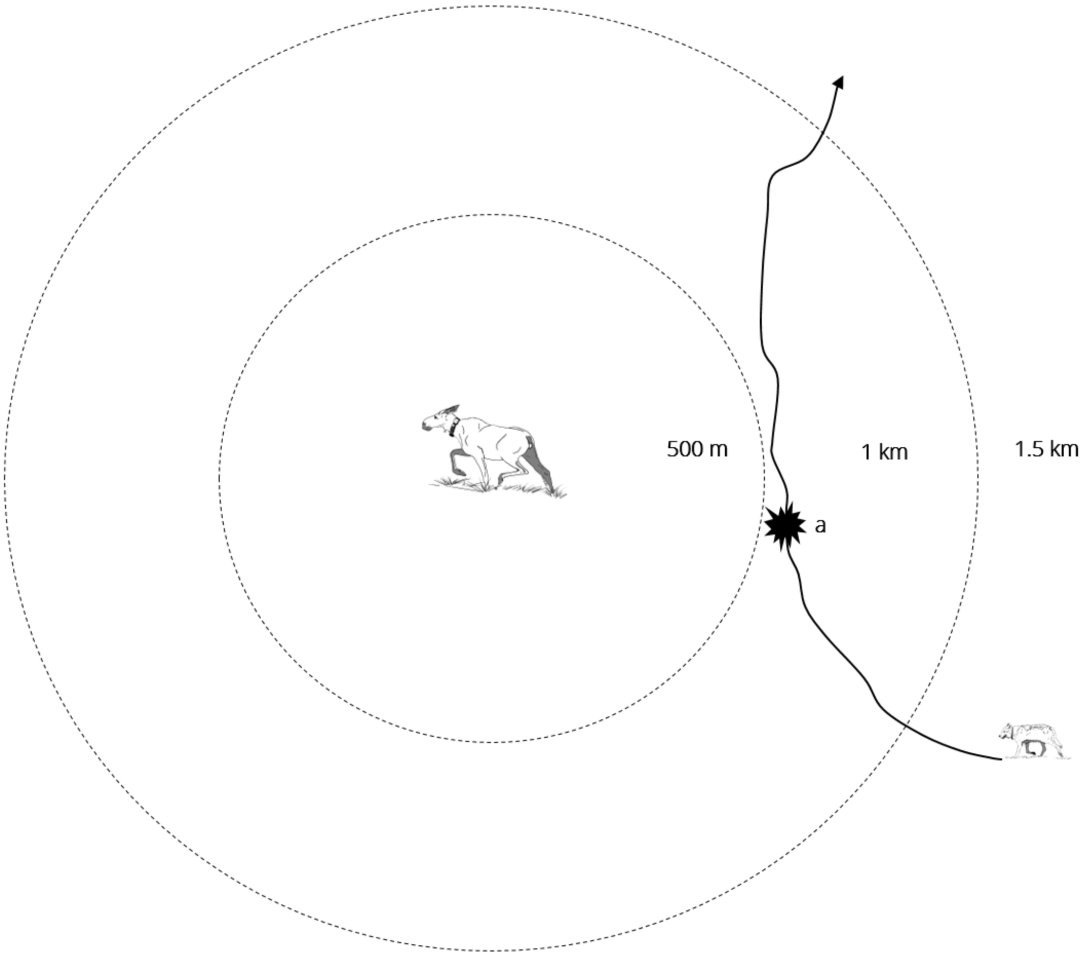


Figure S2. Mean speed (meters per hour) per day between GPS-collar relocations among all moose (*n* = 49) from December 1st to April 30th in 2005-2010.

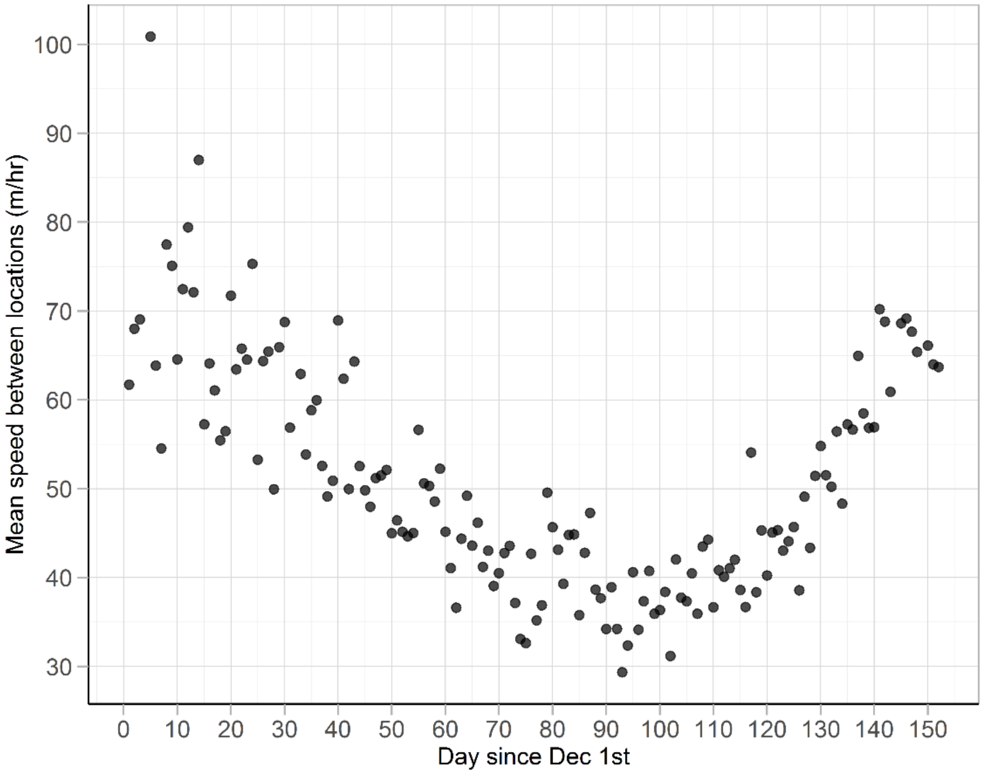


Figure S3. Histogram of the number of encounters (*n* = 119) per DOY used for analyses of moose antipredator response to wolves at the encounter distance categories 500 m, 1 km, and 1.5 km in Buffalo Valley of NW Wyoming from 2005-2010.