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Understanding the Drivers of Body Condition in Female Elk: Implications for Nutritional Ecology on Changing Landscapes

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Chairperson: Mark Hebblewhite

ABSTRACT

Ungulate body condition is often understood to reflect the nutritional resources on the landscape but is ultimately influenced by more than forage because body condition integrates both energetic costs and benefits. Factors driving variation in female body condition can be classified in both individual vs. environmental and bottom-up vs. top-down frameworks. My research evaluates how individual vs. environmental and bottom-up vs. top-down frameworks explain variation in ingesta-free body fat (IFBF) in female elk (*Cervus canadensis*). I used seven years (2015-2021) of IFBF data from monitored and recaptured female elk (n = 139) in the Ya Ha Tinda (YHT) population in Alberta, Canada. I determined the best-fitting generalized linear mixed-effects model to explain IFBF as a function of factors in both frameworks. The top model included only prior summer calf survival as a predictor variable, with the second model (ΔAICc = 1.42) including both prior summer calf survival and average prior summer forage biomass. The final top model predicts that a female elk whose calf survives the previous summer will have 3.28 percent points (95% CI: 2.38, 4.19) lower body fat levels in winter compared to a female elk whose calf did not survive the summer. The importance of prior summer calf survival as an explanatory variable and the large size of its effect indicates that changes in energetic reproductive costs driven by predation influence variation in female body fat more significantly than bottom-up factors like forage in this system and emphasize the importance of individual variation. This research helps scientists and managers interpret variation in ungulate body condition data and understand the important effects of juvenile survival on adult ungulate female body condition in the context of expanding predator communities across North America.

Key Words: Ungulate nutritional ecology, body condition, energetic costs of reproduction, top-down vs. bottom-up, individual vs. environmental, elk, neonate predation

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Finally, I would like to specify that although I will be using the ‘I’ voice for this thesis manuscript, this research is the product of decades of long-term work and intellectual

contributions. I would like to recognize Mark Hebblewhite, Evie Merrill, Sara Williams, Hans Martin, and Jodi Berg as co-authors of this work.

INTRODUCTION

The body condition of reproductive females significantly affects ungulate pregnancy rates, overwinter survival, and even population growth, thereby influencing population dynamics (J. G. Cook et al. 2004, Tollefson et al. 2010, Monteith et al. 2014, Cook et al. 2016, Proffitt et al. 2016, Schooler et al. 2022). Body condition represents the physiological composite of the energetic costs and benefits that an individual experiences (R. C. Cook et al. 2004, Parker et al. 2009). Although body condition is often thought of as a representation of the nutritional quality of forage on a landscape, there may be differences between available forage and realized nutritional condition due to the multiple energetic costs and benefits that influence body condition. In the context of ungulate research and management, two non-exclusive frameworks can help understand and quantify the mechanisms that drive body condition to advance ecological knowledge and enable targeted management action.

The first framework for evaluating the drivers of body condition in ungulates examines the influences of individual vs. environmental factors. Body condition may be influenced by environmental factors such as habitat and forage selection, costs of avoiding predation risk, and energetic costs of movement (Parker et al. 1984, 2009, Creel et al. 2009, Hebblewhite and Merrill 2011, Watkins et al. 2023). Individual characteristics such as age and reproductive effort are also well known to influence body condition (J. G. Cook et al. 2004, Cook et al. 2016, Proffitt et al. 2016). For example, female elk (*Cervus canadensis*) that incur costs of lactation are typically in poorer body condition in autumn or winter across many studies (Middleton et al. 2013*a*, Simard et al. 2014, Proffitt et al. 2016, Watkins et al. 2023).

The second framework for evaluating the drivers of body condition examines the impacts of top-down and bottom-up ecological processes. The contrasting influences of ‘top down’ predator-determined ecosystem effects and ‘bottom-up’ nutrition-determined effects have been the subject of much ecological study (Sinclair et al. 2000, Hebblewhite and Merrill 2011, Paterson et al. 2022). These bottom-up and top-down forces drive population demography, life history tradeoffs, and metrics of nutritional condition like body condition (Griffin et al. 2011, Watkins et al. 2023). Evidence supports the important regulatory influences of both bottom-up (J. G. Cook et al. 2004, Watkins et al. 2023) and top-down forces on ungulate populations (Hebblewhite et al. 2018), ultimately underscoring that bottom-up and top-down influences interact in complex ways in ungulate ecosystems (Sinclair et al. 2000, Testa 2004). Evaluating ungulate body condition from the perspectives of both bottom-up vs. top-down and individual vs. environmental factors provides a more wholistic ecological understanding with direct implications for effective management and conservation action.

Although body condition has long been understood to serve as an important physiological indicator that influences demographic rates, much is still unknown about the factors influencing body condition. With the development of new methodology to quantitatively measure body condition with estimates like ingesta-free body fat (IFBF), research has demonstrated that body condition can be highly variable within populations (Bergman et al. 2018), but the specific drivers of this variation are still poorly understood. Bergman et al. (2018) studied variation in IFBF in female mule deer (*Odocoileus hemionus*) across Colorado and found that environmental effects explained 13% of the variation in IFBF, individual body metrics explained 4%, but 83% of the variation in IFBF remained unexplained (2018). Bergman et al. (2018) suggested that much of this unexplained variation may be explained by more difficult-to-collect individual data such as age and reproductive effort. Reproductive effort refers to the pregnancy and lactation of the past biological year up to the present, both of which significantly influence body condition in female ungulates (J. G. Cook et al. 2004, R. C. Cook et al. 2004, Proffitt et al. 2016, Watkins et al. 2023). Despite our understanding of the importance of reproductive effort on body condition, it is difficult to study the effects of reproductive effort on maternal body condition in wild populations, as a thorough understanding of reproductive history often requires long-term monitoring and recapturing known individuals (Gaillard 2013).

The effects of reproductive costs on female body condition include pregnancy and the cumulative costs of lactation and maternal care of young from neonate birth to winter. A few recent studies evaluated the effect of lactation status upon capture or harvest on body condition of female ungulates and found that lactating females demonstrated significantly lower body condition than non-lactating females (Middleton et al. 2013*a*, Simard et al. 2014, Proffitt et al. 2016, Watkins et al. 2023). However, treating lactation status in winter as a simple binary variable may not provide a very informative metric of reproductive effort throughout the previous summer and autumn because of variation in weaning phenology and juvenile survival. Weaning in wild ungulate species typically occurs around 3-6 months of age, but there is considerable variation in individual timing and limited research on weaning behavior in the wild (Lent 1974). This weaning time frame means that individuals with surviving calves may no longer be lactating upon capture or harvest in winter. Additionally, the bulk of the energetic costs of lactation occurs during the summer, meaning the presence of a nursing calf is most energetically costly through summer and less costly over winter (Robbins et al. 1981, Cook et al. 2013, Watkins et al. 2023).

Despite the limitations of winter lactation status upon capture or harvest as a representation of the energetic costs of reproduction, the data collection necessary to use a more informative metric is effort and money intensive. Individual-specific juvenile survival can be used to investigate the full energetic cost of reproduction on maternal body condition, but juvenile survival must be monitored the season prior to body condition measurement, which necessitates the recapture of adult females. Only one study to date has utilized such intensive monitoring, capturing female mule deer in spring, recapturing in autumn, measuring body fat at each occasion, and monitoring fawn recruitment over the summer (Monteith et al. 2014). Monteith et al. (2014) found that the change in female body fat over summer was directly related to the number of fawns recruited, with females that recruited zero fawns experiencing a large gain in fat over summer and females that recruited three fawns experiencing a loss of fat throughout the summer. This dramatic result demonstrates the magnitude of energetic costs that female ungulates face in raising nursing young and emphasizes the increased information provided by summer juvenile survival data in understanding female ungulate body condition and reproductive effort. The importance of juvenile survival indicates that in populations that experience high levels of predation, female body condition may be positively impacted by neonate predation, as losing nursing young relieves females of the energetic cost of lactation (Middleton et al. 2013*b*, Berg et al. 2022). Monitoring of summer juvenile survival in connection with subsequent maternal body condition measurement has never been completed in elk, so the magnitude and importance of energetic reproductive costs in determining body condition remain unknown.

The effects of age on body condition are incompletely understood. Early research demonstrated decreased body condition in older elk based on organ fat deposits measured after death in Elk Island National Park, Alberta (Flook 1970). However, in Yellowstone National Park, Cook et al. (2004) found that body fat in female elk was unrelated to age, although they hypothesized that higher body condition of older females may have been augmented by lower rates of reproduction. New research in elk demonstrates an overall negative relationship between age and body condition, with the body condition of lactating females decreasing in a linear fashion with age and the body condition of non-lactating females decreasing quadratically (Watkins et al. 2023). This interaction between age and reproduction underscores the need for research on drivers of body condition that accounts for multiple sources of individual variation on body condition. Understanding the relationship between body condition and age is important so that population age-structure may be accounted for when interpreting body condition values, rather than interpreting body condition as solely a measure of habitat-induced variation in nutritional ecology. The effects of age and reproductive history on body condition are currently a major knowledge gap in our understanding of ungulate nutritional ecology.

Many ungulate species migrate seasonally from lower-elevation winter ranges to higher-elevation summer ranges. Migration provides a nutritional benefit to ungulates by increasing access to high quality forage through gradients in plant phenology (Hebblewhite et al. 2008*a*, Gaidet and Lecomte 2013). For example, high-elevation summer ranges for species like elk and mule deer (*Odocoileus hemionus)* provide higher-quality available forage (Hebblewhite et al. 2008*a*, Schuyler et al. 2021). Partial migration is a phenomenon observed in many species, including ungulates (Gaidet and Lecomte 2013, Berg et al. 2019) in which some, but not all individuals in a population migrate. Compared to non-migratory resident individuals, migrant animals are often in better body condition, have higher pregnancy rates, or have higher overwinter calf weights, consistent with the bottom-up nutritional benefits of migration (Hebblewhite et al. 2008*a*, Middleton et al. 2013*a*). However, migration may also be influenced by other top-down factors like predation or indirect predation risk effects if predation risk varies spatially between migratory strategies (Hebblewhite and Merrill 2009, Middleton et al. 2013*a*).

Partially migratory systems provide an excellent opportunity to better understand the dynamics of ungulate body condition by comparing migrants and residents that experience different conditions. The partially migratory Ya Ha Tinda (YHT) elk population adjacent to Banff National Park in Alberta, Canada includes three migratory strategies: resident, eastern migrant, and western migrant. Previous studies showed that in comparison to residents, migrant females were exposed to and obtained higher forage quality, had higher pregnancy rates, raised calves that were 20% heavier in winter, and had higher overall juvenile survival (Hebblewhite et al. 2008*a*, Martin et al. 2022). However, winter body condition (IFBF) measurements were higher on average for resident females than eastern migrants (Berg et al. 2022). Berg et al.

(2022) hypothesized this difference in body condition was due to demonstrated high predation on resident neonate calves, especially by grizzly bears. Summer is an incredibly important time for ungulates to recoup fat reserves as nutritional resources peak to prepare for winter when conditions are harsh, energetic costs of movement are high, and forage availability is low (Mautz 1978). Because lactation represents a significant energetic demand, resident females who lost their calves early were likely able to obtain higher body condition because they did not incur the costs of lactation throughout the summer (R. C. Cook et al. 2004, Berg et al. 2022, Watkins et al. 2023). However, Berg et al. (2022) only examined the population-level correlation between migratory strategies and their respective mean body fat levels and calf survival rates. This example highlights how available forage is not the only factor, and potentially not the most important factor, affecting measures of body condition, which integrate costs and benefits across individual and environmental as well as bottom-up and top-down factors.

With my research, I examined how variation in female late winter body condition in the YHT elk population is driven by factors in two frameworks: individual vs. environmental and bottom-up vs. top-down. I determined which factors are the most important drivers of female body condition, seeking to understand the relative importance of individual vs. environmental and bottom-up vs. top-down sources of variation in body condition. Within the individual vs. environmental framework, I hypothesized that individual and environmental factors would both contribute variation to body condition (IFBF), but that individual factors like age and reproductive effort would be the most important explanatory variables. Alternative hypotheses included that body condition would be best explained solely by individual factors or that body condition would be best explained solely by environmental factors. Within the bottom-up vs. top-down framework, I hypothesized that bottom-up and top-down factors would both contribute variation to body condition (IFBF), but that top-down factors like juvenile predation would be the most important explanatory variables. Alternative hypotheses include that body condition would be best explained solely by top-down factors or that body condition would be best explained solely by bottom-up factors. As body condition significantly influences demographic rates, a better understanding of the factors influencing body condition in female elk may yield an improved understanding of how ungulate energetic dynamics are regulated.

Study Area

My study area is defined by the summer and winter ranges of the Ya Ha Tinda (YHT) elk population, annually occupying a ~6000km^2 area in and adjacent to Banff National Park (BNP) in Alberta, Canada (Hebblewhite 2006). Elevation within the study area ranges from 1600m in valley bottoms to 3500m in alpine areas, and the climate is characterized by long, cold winters and short summer growing seasons (Hebblewhite 2006). There are three main ecoregions in the study area: montane regions including grasslands, willow areas (*Salix* spp.), and forests composed of lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmanni*), and aspen (*Populus tremuloides*); sub-alpine regions including Engelmann spruce, subalpine fir (*Abies lasiocarpa*), and lodgepole pine interspersed with willow-shrub riparian communities and grasslands; and alpine regions including avalanche terrain and alpine shrub-forb meadows (Hebblewhite 2006).

This YHT region of the Canadian Rockies is a multiple predator, multiple prey system that includes the full suite of large carnivores such as wolves (*Canis lupus*), grizzly bears (*Ursus arctos*), coyotes (*Canis latrans*), black bears (*Ursus americanus*), and cougars (*Puma concolor*). In fact, the YHT elk population experiences amongst the highest predation rates by large carnivores and lowest documented survival rates for both adults and calves in the literature (Griffin et al. 2011, Brodie et al. 2013). Other prey species include white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), moose (*Alces alces*), bighorn sheep (*Ovis canadensis*), and mountain goats (*Oreamnos americanus*) (Morgantini 1995). The density of large predators like grizzly bears and wolves are thought to decline moving eastward from the park boundary due to increasing human-caused mortality and increasing industrial and recreational activity (Berg et al. 2022). The YHT system is therefore a fascinating study ecosystem that represents a fully recovered Rocky Mountain ecological community, providing insight into predator-prey dynamics and other ecological processes that may become incredibly relevant for more southern ecosystems as large carnivores like grizzly bears and wolves continue to recover and expand their ranges (USFWS 2021, Sells et al. 2022).

The YHT elk population spends winters on the Ya Ha Tinda Ranch, a ~20km^2 high elevation montane rough fescue (*Festuca campestris*) grassland along the Red Deer River. In the summer, the elk population exhibits partially migratory behavior. Most of the population remains on winter range, but a portion migrates eastwards onto multiple-use provincial lands, and a small number migrate north or west into sub-alpine and alpine areas in BNP. Historically, most of the YHT elk population migrated westward into BNP and the population achieved far greater total abundance, with the total population increasing to a peak of 2,200 individuals in 1992 (Morgantini 1995). In the past two decades, the population declined to around 450 individuals by 2016 and migratory behavior has decreased overall with the appearance of an alternate eastern migration (Hebblewhite 2006, Eggeman et al. 2016). In 2001-2004, the ratio of migrants to residents was 3:1 (Hebblewhite 2006), and by 2013-2016 the ratio of western migrants to eastern migrants to residents was 1:5:10 (Berg et al. 2021).

METHODS

Data Collection

I used seven years (2015-2021) of elk capture data collected at the YHT (N=274). Elk were captured using ground darting following approved University of Montana Institutional Animal Care and Use Committee protocols (AUP# MH-004-16, 066-21). Elk were fitted with GPS or VHF collars and several individual metrics were measured, including chest girth, maximum rump fat, lactation status, pregnancy status, and age. Maximum rump fat thickness (cm) was measured with ultrasound by two trained technicians (Sonovet system with 5.0-MHz, 7.0-cm probe, Universal Medical Systems, Bedford Hills, NY, USA). Pregnancy status was determined via pregnancy specific protein-B levels in blood serum samples. Vestigial canines were extracted to determine age through cementum annuli examination. Rump fat thickness and chest girth were used to calculate percentage of ingesta-free body fat (IFBF) according to MAXFAT methods for elk outlined by Cook et al. (2010).

This data set is unique because many (N=139) of these captures were recaptures of previously radio-collared or marked female individuals for which we have previous data. This prior knowledge allowed me to investigate how different factors influence body condition in a mechanistic way. Summer calf survival was monitored through mark-resight calf:female surveys throughout the study period (Bonenfant et al. 2005, Hebblewhite et al. 2018). For 3 years (2014-2016), neonate survival to 90 days was tracked via VHF ear tags (Berg et al. 2022). Migratory strategy was classified through a combination of net-squared displacement and visual inspection (Eggeman et al. 2016).

Statistical Methods

To address my research objective, I determined the best fitting linear mixed-effects model to explain body condition and interpreted the most important explanatory variables in the context of an individual vs. environmental framework as well as a bottom-up vs. top-down framework. Individual factors include prior summer calf survival (i.e., reproductive effort), age and pregnancy status. Environmental factors include average prior summer forage biomass, average prior summer wolf predation risk, and average prior summer grizzly predation risk. Bottom-up factors included average prior summer forage biomass, and top-down factors included prior summer calf survival, average prior summer wolf predation risk, and average prior summer grizzly predation risk (Table 1, see *Covariate Section* below). I first examined univariate relationships between each covariate and IFBF with linear regression to understand basic relationships. For the age covariate, I also considered different linear and non-linear functional forms of the relationship between age and IFBF and used Akaike's information criterion adjusted for small sample size (AICc) to select the best functional form.

I built candidate models with all possible combinations of additive fixed effects and included interactions with ecological rationale or evidence in univariate data exploration. I also tested a random effect for individual and year and looked for effects of date of capture. I standardized (subtracting the mean and dividing by standard deviation) all continuous predictor variables to allow for coefficient comparison between categorical and continuous variables. I examined all predictor variables for collinearity and avoided including variables with a correlation coefficient of $r > 0.6$ in the same model. I then used Akaike information criterion adjusted for small sample size (AICc) for model selection.

I predicted that calf survival, age, and predation risk would produce negative model coefficients as they are energetic costs (Parker et al. 2009). I predicted that forage biomass would have a negative model coefficient as forage quality is inversely related to forage biomass according to the forage maturation hypothesis, and forage quality is an energetic benefit (Hebblewhite et al. 2008*a*). I also predicted that pregnancy would have a positive model coefficient as autumn body condition strongly predicts the probability of successful breeding in elk (R. C. Cook et al. 2004), so females who are in very poor body condition are least likely to be pregnant.

Individual Covariates

Individual covariates include individual-level prior summer calf survival, age, and pregnancy status. Vestigial canines were extracted during capture to determine age through cementum annuli examination. Pregnancy status was determined via pregnancy specific protein-B levels in blood serum samples collected during captures.

Prior summer calf survival (also a top-down covariate) was represented by a combination of individual juvenile:female resight data collected during the entire study period (2015-2021) and direct VHF calf survival monitoring collected for years 2015-2016 (Bonenfant et al. 2005, Berg et al. 2022). The VHF calf survival monitoring was conducted from calf birth (captured using VITs) to 90 days of life, and I classified calves as 'survived summer' or 'did not survive summer' based upon their status at the end of this 90-day period, which occurred in late August. The individual juvenile:female resight data consisted of visual observations of marked females to determine whether or not the female had a calf at the time of observation. I examined observations from August, September, and October and considered a female's calf to have 'survived summer' if she was observed with a calf at least once during this period and 'did not survive summer' if she was observed at least once during this period and did not have a calf at any point.

Environmental Covariates

For the environmental factors forage biomass, wolf predation risk, and grizzly bear predation risk, I defined the summer period as April 24 – October 19 based upon the 25th and 75th quartile dates for migratory departure and return. Values for all three covariates were extracted from 2,500 randomly sampled summer locations for each individual elk-year.

Forage biomass values (also a bottom-up covariate) were generated from a dynamic herbaceous (graminoids and forbs) biomass model previously developed for the study area (Hebblewhite et al. 2008*a*). This model predicts biomass in 16 day intervals from data from ~1000 vegetation plots, spatial covariates of landcover type, topographic variables, and time-varying MODIS NDVI at 250m resolution (Hebblewhite et al. 2008*b*). Hebblewhite et al.

confirmed the inverse relationship between forage biomass and dry matter digestibility as indicated by the forage maturation hypothesis (2008). Therefore, higher forage biomass values are interpreted as lower forage quality values (Williams et al. 2023). The mean forage biomass value from all 2500 summer period locations was used to represent average forage quality exposure for each individual elk-year.

Wolf predation risk values (also a top-down covariate) were generated from wolf resource selection functions weighted by pack size developed for the study area using GPS and VHF data from 2002-2005 with updated landcover information through 2018 (Hebblewhite and Merrill 2007). An independent out-of-sample K-folds cross validation of the wolf predation risk model was conducted using locations of wolf-killed adult and calf elk from 2001-2020 to confirm predictive accuracy given the long time period since model creation (Williams et al. 2023). For this analysis, the mean wolf predation risk value from all 2,500 locations per individual elk-year was used to represent the average risk exposure of that individual in that summer period.

Grizzly bear predation risk values (also a top-down covariate) were generated from grizzly bear resource selection functions for early and late hyperphagia from GPS data from 1999-2006 and weighted by estimates of grizzly bear abundance with updated landcover information through 2018 (Boulanger et al. 2018, Berg et al. 2022). As with wolf predation risk, an independent out-of-sample K-folds cross validation of the grizzly bear predation risk model was conducted using locations of grizzly-killed adult and calf elk from 2001-2020 to confirm predictive accuracy (Williams et al. 2023). As with wolf predation risk, the mean grizzly bear predation risk value from all 2,500 locations per individual elk-year was used to represent the average risk exposure of that individual in that summer period.

Migratory strategy is difficult to classify into either the individual vs. environmental or bottom-up vs. top-down frameworks as migratory strategy is an individual-level behavioral choice that vastly impacts the environmental characteristics to which an individual is exposed. Each female was classified as a western migrant, eastern migrant, or resident based upon movement data from the previous summer season using net-squared displacement and visual inspection (Eggeman et al. 2016). For my analysis, I included eastern and western migrants together in one ‘migrant’ category due to small sample size.

Table 1. Covariate categories for generalized linear modeling body condition of female elk in the Ya Ha Tinda population (Alberta, Canada)

Framework Category	**Covariate**
Individual	Calf Survival
	Age
	Pregnancy
Environmental	Forage Biomass
	Wolf Predation Risk
	Grizzly Predation Risk
	Migratory Strategy
Bottom-up	Forage Biomass
Top-down	Calf Survival
	Wolf Predation Risk
	Grizzly Predation Risk

RESULTS

The ingesta-free body fat (IFBF) percentage for all recaptured females (N = 139) from 2015-2021 was fairly normally distributed with a mean of 11.4%, median 11.9%, and ranged from 5.8% to 17.1%.

Univariate Results

Prior summer calf survival had a significant effect on IFBF through both VHF calf monitoring data and individual juvenile:female resight data. Using only VHF calf monitoring data, females whose calves survived at least 90 days the prior summer (mean = 9.2%) had significantly lower IFBF than females whose calves did not survive the prior summer (mean = 12.6%, P = 0.0001). Using individual resight data, females who were observed with a calf in August, September, or October (mean = 9.1%) had significantly lower IFBF than females who were observed never having a calf during the same time period (mean = 12.4%, P < 0.0001). The close similarity of the individual resight data with the direct VHF monitoring data confirms the utility of the mark-resight data in accurately measuring calf survival (i.e., means 9.2% and 9.1%, 12.6% and 12.4%). Females were most often observed one or two times during this period with one female observed a maximum of 21 times. The outcome of the season classification (calf or no calf) was not related to the number of times a female was observed (P = 0.97). Combining the two metrics for a total of 89 animal-years, the mean IFBF for a female whose calf survived until fall was 9.3% and the mean IFBF for a female whose calf did not survive until fall was 12.6% (Figure 1).

Univariate examinations revealed a generally negative relationship between IFBF and age, where IFBF was lower for very young individuals, high and variable for individuals 2-10 years old, and decreasing for individuals over 10 years old. Including all male and female elk for which age and IFBF data were available (N = 255), I considered and tested a linear model, negative quadratic model, a categorical model with age bins 2-9, 10-14, and 15-21 years, and a generalized additive model. The quadratic model fit the data best from a visual perspective and was selected as the top model by AIC as well with nearest ΔAIC = 3 (Figure 2). There also appeared to be an interaction between age and prior summer calf survival in predicting IFBF, where females whose calves survived the summer had a slightly positive relationship between age and IFBF whereas females whose calves did not survive the summer had a negative relationship between age and IFBF (Figure 3).

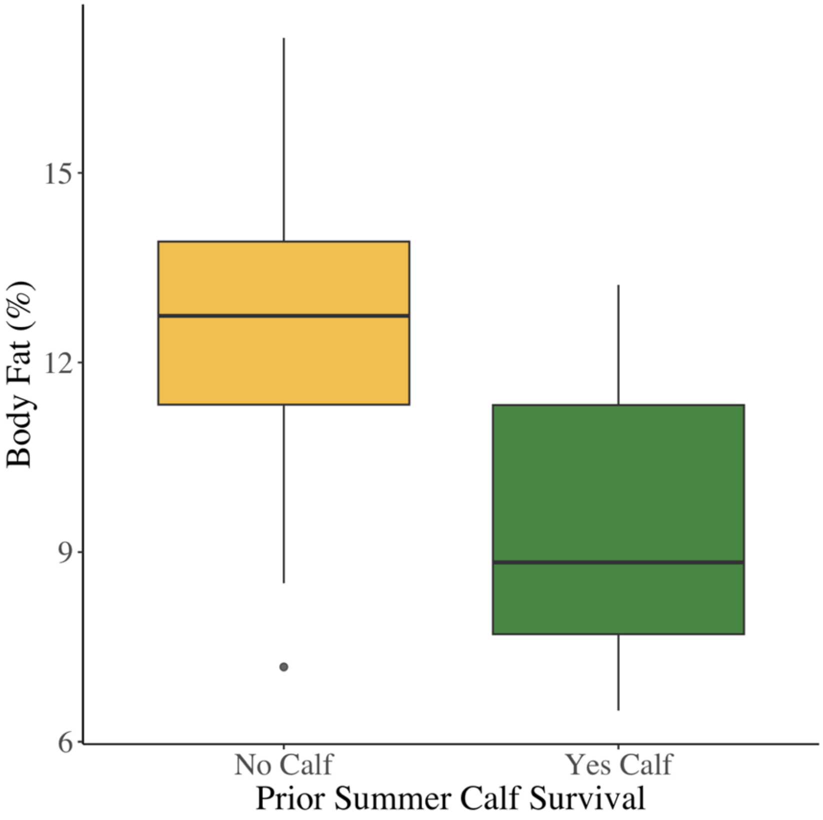

Figure 1. Ingesta-free body fat levels of female elk whose calves survived or did not survive the previous summer in the Ya Ha Tinda elk population in Alberta, Canada.

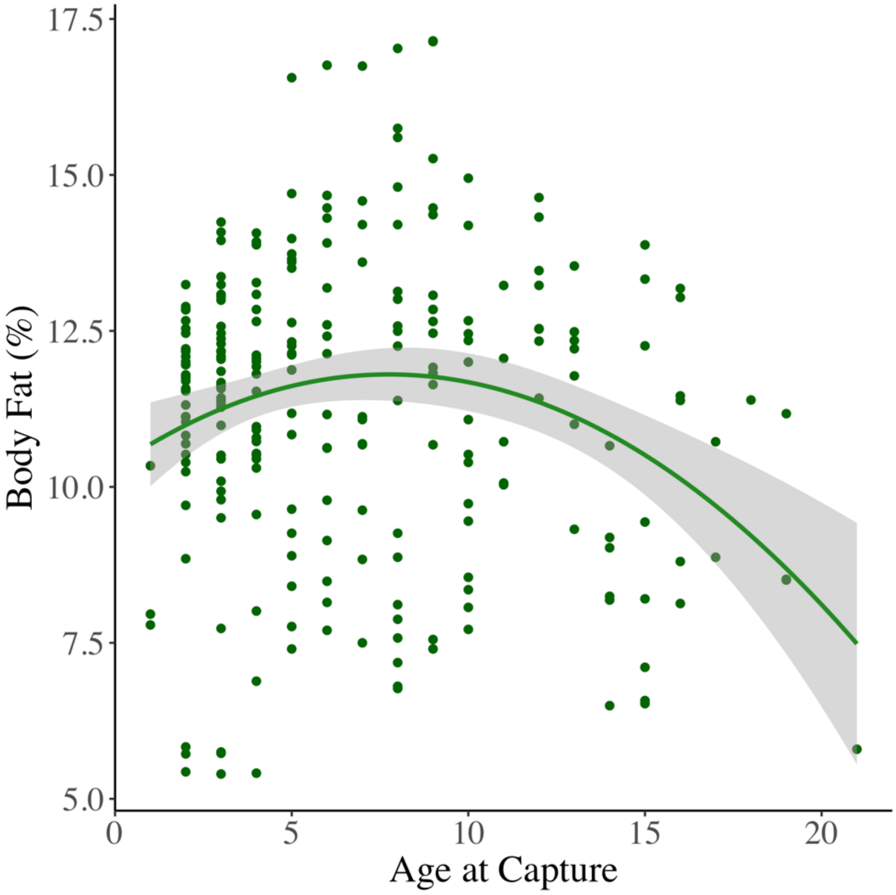

Figure 2. Ingesta-free body fat levels of female elk modeled as a negative quadratic function of age in the Ya Ha Tinda elk population in Alberta, Canada.

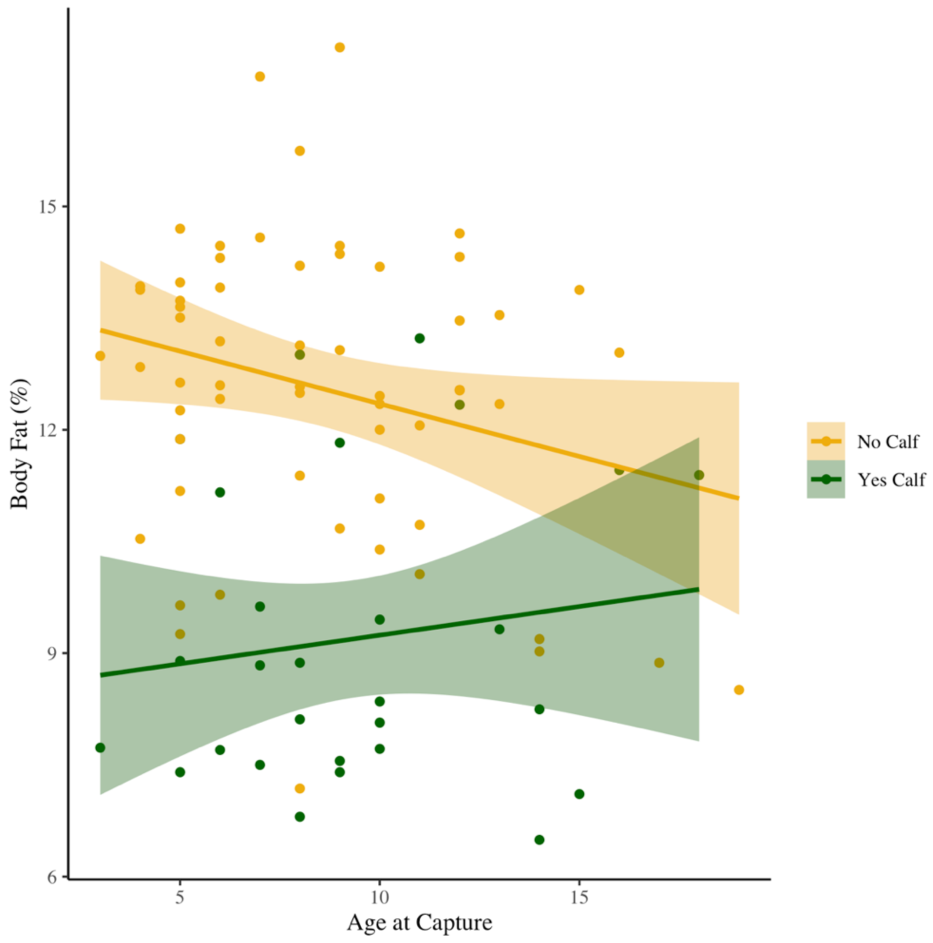

Figure 3. Ingesta-free body fat levels of female elk modeled as a function of age and split by those whose calves survived or did not survive the previous summer in the Ya Ha Tinda elk population in Alberta, Canada.

Of 118 females for which pregnancy data was available, only 7 were not pregnant. Pregnant females (mean = 11.5%) had slightly higher IFBF than not pregnant females (mean = 10.2%) but this difference was not statistically significant, perhaps because of small numbers of non-pregnant females (P = 0.21). The number of days between Jan 1. and capture date did not have any visually or statistically detectable effect on IFBF (P = 0.48).

Univariate examinations of forage biomass demonstrated a weak, negative linear relationship between average forage biomass summer exposure for an individual and that individual's body fat levels (P = 0.35, N = 40). Average wolf predation risk summer exposure for each individual displayed no visible or statistical relationship with body fat (P = 0.85, N = 40). Average grizzly bear predation risk summer exposure demonstrated a weak, positive linear relationship with body fat (P = 0.15, N = 40) that aligns with the positive maternal body fat impacts of direct grizzly predation on elk calves.

IFBF was marginally significantly lower (P = 0.056, N = 107) for migrant individuals (mean = 10.7%) than resident individuals (mean = 11.7%) and western and eastern migrants had similar IFBF values with means 10.9% and 10.6%, respectively (Figure 4). When examining differences between migratory strategies and interacting migratory strategies with prior summer calf survival, it becomes apparent that higher resident body condition is driven by patterns of calf survival (Figure 5).

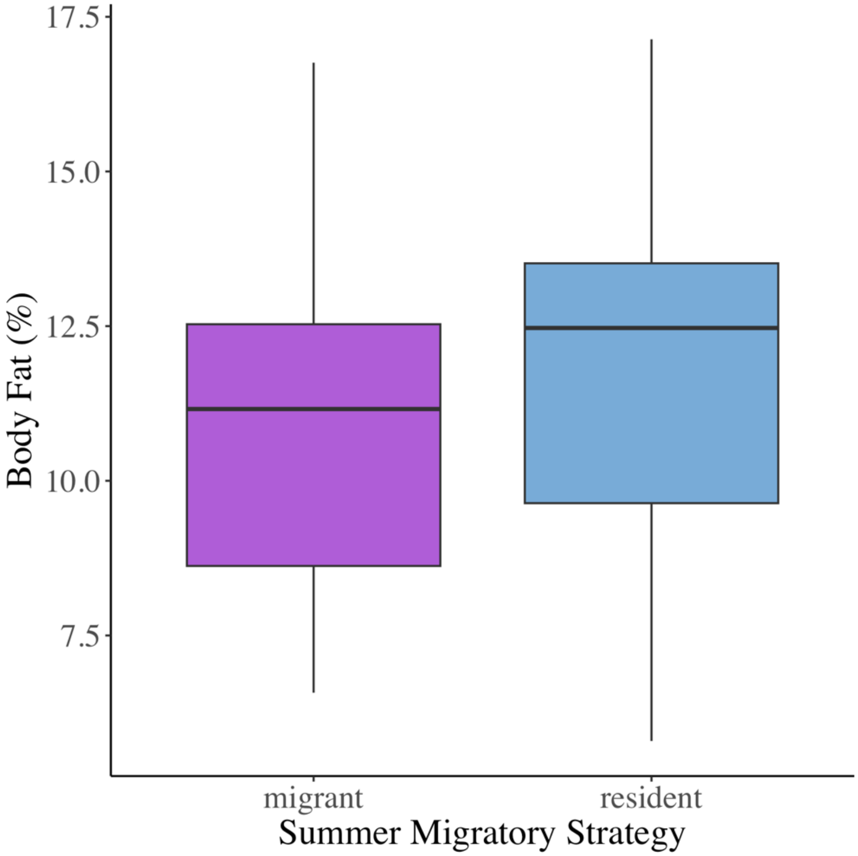

Figure 4. Ingesta-free body fat levels of female elk who exhibited a migratory or resident summer strategy in the Ya Ha Tinda elk population in Alberta, Canada.

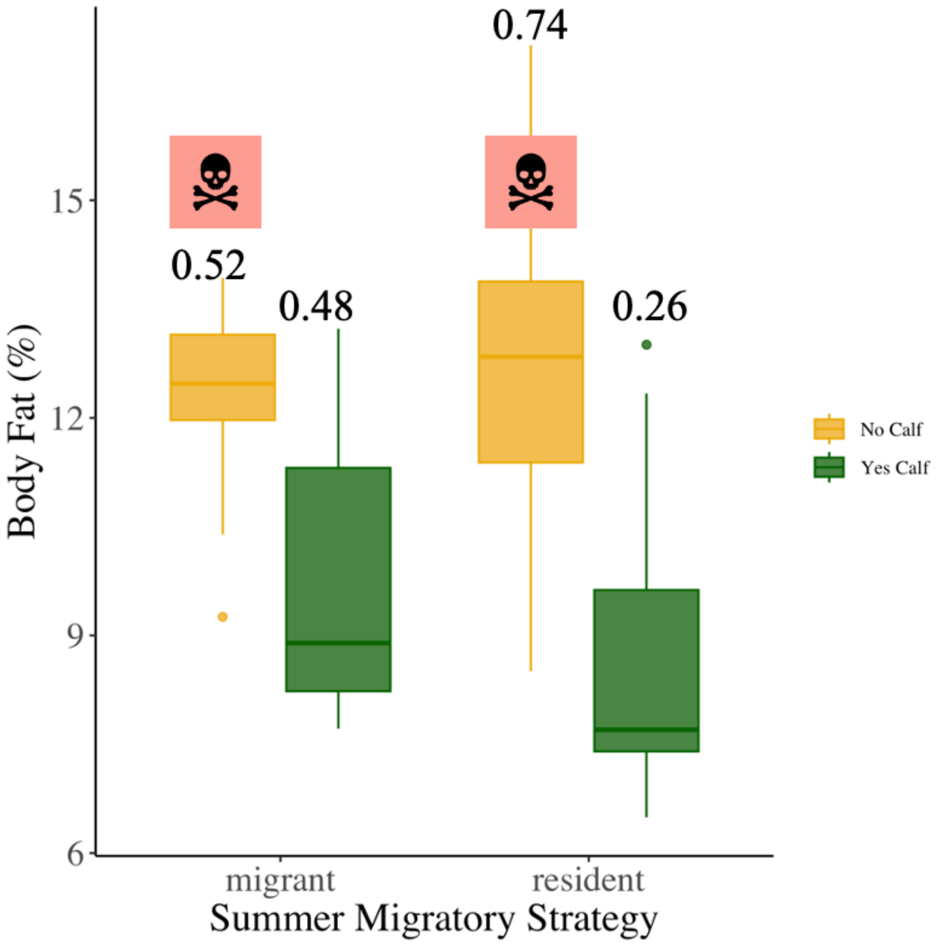

Figure 5. Ingesta-free body fat levels of female elk who exhibited a migratory or resident summer strategy categorized by female elk whose calves survived the summer prior to fat measurement (green) or whose calves did not survive the previous summer (yellow) in the Ya Ha Tinda elk population in Alberta, Canada. Plots are labeled with the proportion of female elk with surviving or not surviving calves within each migratory strategy, demonstrating that 74% of resident females' calves did not survive the summer compared to 52% of migratory females losing their calves.

Model Selection Results

Collinearity screening yielded a few fairly high correlation coefficients. Capture date and capture year had a correlation coefficient of r = 0.56 but were not included in any models together. This correlation also makes sense as individuals captured in the same year were captured close together in time. Migratory status was highly correlated with wolf and grizzly predation risk with correlation coefficients of r = 0.81 and r = 0.71, respectively, so these variables were not included in the same models and migratory strategy could be strongly interpreted as reflecting differences in predation. Wolf predation risk was moderately correlated with forage biomass and grizzly predation risk with correlation coefficients of r = 0.51 and r = 0.56, respectively. These variables were included in the same models and interactions were tested to possibly account for these correlations.

Model selection was carried out on a subset of 40 observations of all complete cases for all covariates of interest. Considering all possible fixed effects, 29 candidate models were considered. The top model via AICc model selection was a linear model with solely prior summer calf survival as an explanatory variable, with the second model (ΔAICc = 1.42) including both prior summer calf survival and average prior summer forage biomass and two other models within 3 AICc (Table 2). To consider the addition of random effects for individual and year, an additional 12 candidate models were considered with the addition of a random effect for individual, year, and both added to the top four models selected in the fixed-effects selection. None of these models produced a lower AICc than our top model, so I did not include any random effects in my final model, and I did not explore annual variation in other ways. I also considered a model averaging approach with coefficient shrinkage for covariates that did not appear in all four top models (Table 3). Because the other three covariates besides prior calf survival only appeared once, their coefficient estimates were quite small with high standard errors, reducing the overall utility of a model averaging approach.

I re-estimated the final model including solely prior summer calf survival as an explanatory variable on a subset of 89 observations of complete cases for prior summer calf survival. My final top model had reasonably normally distributed residual values and appeared to meet linear model assumptions. The final top model included a negative coefficient on prior summer calf survival of -3.28 (95% CI: -4.19, -2.38), predicting that a female elk whose calf survives the previous summer will have 3.28 percentage points lower body fat levels in winter compared to a female elk whose calf did not survive the summer. The final top model had a multiple R^2 value of 0.37, indicating that our model explains approximately 37% percent of the variation in female body fat.

Table 2. Top 4 candidate models considered for overall modeling framework for generalized linear modeling body condition of female elk in the Ya Ha Tinda population (Alberta, Canada). Repro = prior summer calf survival, age = age in years (integer), mig = prior summer migratory strategy, herb = average summer forage biomass exposure.

Models	**K**	**ΔAICc**	**AICc Wt**
repro	**3**	**0**	**0.30**
repro + forage	4	1.42	0.15
repro + age	4	2.34	0.09
repro + mig	4	2.38	0.09

Table 3. Model averaging coefficients estimates based on top 4 candidate models considered for overall modeling framework for generalized linear regression modeling body condition of female elk in the Ya Ha Tinda population (Alberta, Canada). Repro = prior summer calf survival, age = age in years (integer), mig = prior summer migratory strategy, herb = average summer forage biomass exposure.

Covariate	**Estimate**	**SE**
repro	-4.30	0.66
herb	-0.07	0.32
age	-0.02	0.32
mig	0.03	0.76

DISCUSSION

My research aimed to understand the drivers of female body condition within two ecological frameworks: individual vs. environmental and top-down vs. bottom-up. Prior summer calf survival had the strongest and most consistent effects as an explanatory variable for ingesta-free body fat (IFBF) in female elk, appearing in all four top models. Calf survival represents an individual variable as annual reproductive effort varies from female to female based on the survival of young, but also a top-down variable as calf survival is a product of direct predation in almost all cases. Conceptually, reproductive effort as an individual variable is driven by the amount of energy a female spends on reproduction in a given year. Reproductive effort is driven by whether a female becomes pregnant, how many fetuses she delivers, and how long they live and nurse, incurring energetic costs from lactation. These energetic costs are significantly impacted by predation on juveniles, but not entirely determined, especially for species that can produce more than one juvenile per year (Monteith et al. 2014). Juvenile predation is more intuitively understood as a top-down force impacting populations, but for species like elk who typically produce one juvenile per year, annual reproductive effort as an individual variable and individual-specific calf survival driven by predation converge upon the same quantity and effect.

Herbaceous forage biomass, age, and migratory strategy also appeared to modestly explain variation in IFBF in female elk because they appeared in the top four models. The negative relationship between forage biomass and IFBF reflects the intermediate forage maturation hypothesis and the intuitive positive relationship between forage quality and body fat. However, this effect was smaller and provided less explanatory power than prior summer calf survival. The negative relationship between age and IFBF also reflects an intuitive relationship of body condition senescence as individuals age. The univariate examinations of this relationship demonstrated that a negative quadratic model best fit this relationship (Figure 2), although the quadratic component was not selected in the multivariate model selection process, perhaps because reduced sample size reduced the power to detect a curvilinear relationship. This negative quadratic relationship indicates that very young individuals have slightly lower body condition, prime age individuals have high and variable body condition, and older individuals eventually begin to decrease in body condition. Visual inspection suggests that this decrease begins around a threshold of 10 years of age and accelerates past around 15 years of age. Additionally, the interaction between prior summer calf survival and age (Figure 3) suggests that calf survival impacts female elk slightly differently depending on their age. Females whose calves survived summer show a flat or positive relationship between body condition and age, whereas females whose calves did not survive summer show a clear negative relationship with age, indicating that perhaps younger females are able to physiologically recover more effectively or quickly after losing their calf. Migratory strategy also demonstrated importance as an explanatory variable. Although much of the difference in mean body fat between migratory strategies can be explained by differing calf survival rates (Figure 5), perhaps migratory strategy could also be capturing variation in forage, predation, or other behavioral or environmental variation that is not accounted for elsewhere in the model.

The drivers of female body fat demonstrate interactions between bottom-up and top-down regulation in this ecosystem. Berg et al. (2022) clearly demonstrate that calf survival is a result of predation in this system, primarily from grizzly bears (0.31 mortality rate from bears). By killing juveniles and cutting off the energetic costs of reproduction for female elk, grizzly bears significantly increase the body fat of female elk. Through this mechanism, the top-down influence of predation washes out the bottom-up influence of forage on female body fat. These results support my hypothesis that top-down factors explain the most variation in female body fat in comparison with bottom-up factors. The high absolute IFBF values in the YHT population reflect the high documented predation rates (Berg et al. 2022) and indicate a population that is regulated by predation and not nutritionally limited (J. G. Cook et al. 2004, Brodie et al. 2013, Eacker et al. 2016).

Comparison of our IFBF values and calf survival to other elk populations also supports our interpretation of high calf predation rates driving high IFBF values. For example, across ~2500 elk calves monitored in 12 study areas for the 3-month neonatal period, only Yellowstone National Park (with wolf and grizzly bear predation) had similar or slightly lower calf survival (0.31, Griffin et al. 2011) compared to our neonate survival rates at YHT (0.39, Berg et al. 2022). Furthermore, comparing IFBF values from the YHT across elk populations suggests our population has relatively high levels of IFBF in elk populations (Figure 6, White et al. 2011). This broad comparison suggests that comparisons of IFBF values may reflect differences in neonate predation rates as much as, if not more than, differences in bottom-up forage resources.

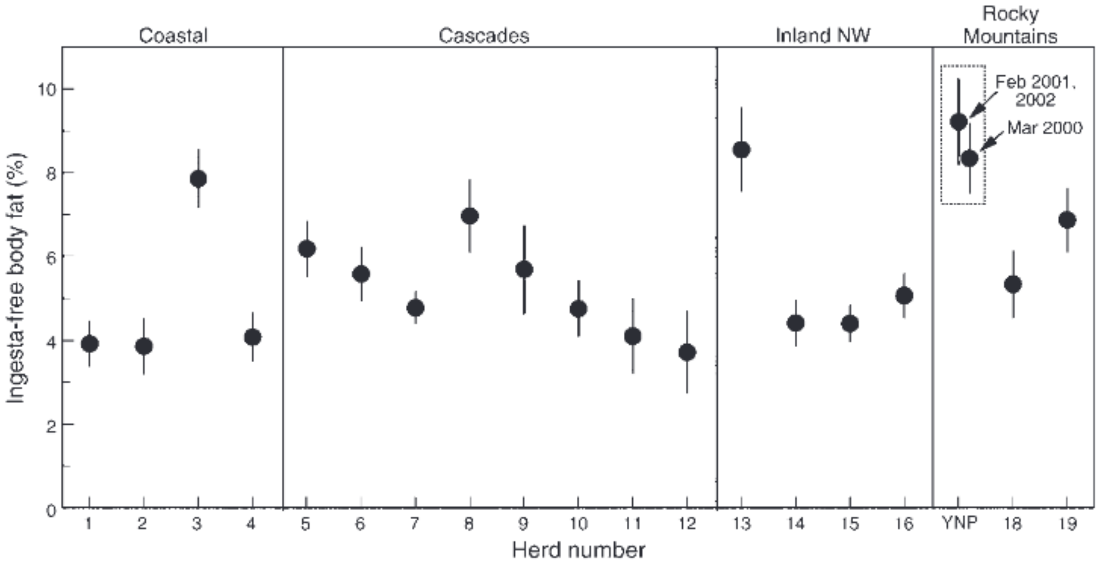

Figure 6. Mean late-winter and early-spring ingesta-free body fat values for female elk in 19 populations across the western U.S. (White et al. 2011).

Hebblewhite et al. estimated the nutritional carrying capacity for the YHT population to be ~ 1600 individuals (2006). Additionally, Martin et al. found evidence for density-dependent declines in pregnancy rates for resident female elk when the population was at high abundance greater than 1600 individuals (2022). As a result of density-independent predation from wolves and density-dependent predation from grizzly bears in this rich multi-prey, multi-predator system, the YHT population currently sits at ~500 individuals, far below the estimated carrying capacity (Hebblewhite and Merrill 2011, Hebblewhite et al. 2018). My results support and emphasize this understanding that the YHT population is currently regulated by predation well below carrying capacity with no nutritional limitation. As such, the top-down signals of direct predation drive female body fat dynamics rather than bottom-up signals of forage.

The interplay of bottom-up and top-down forces varies between ecosystems with different nutritional dynamics and predator communities. The YHT elk population is on the northern side of elk range with the full guild of Rocky Mountain predators and heavy snowpack and moisture to provide for vegetation, supporting top-down predator regulation and a lack of nutritional limitation. Conversely, elk populations much further south in New Mexico such as those on the Vermejo Park Ranch. experience very different conditions with reduced predator communities (no grizzly bears or wolves) and a much more arid system where annual precipitation has a more pronounced impact on the available nutritional resources (Watkins et al. 2023). In contrast to our findings, Watkins et al. found that bottom-up effects of summer precipitation drove female IFBF as well as pregnancy rates and calf:cow ratios (2023). The Vermejo elk population lives at the opposite ends of both the predation and nutritional spectrums from the YHT population. Vermejo elk likely occur at a population abundance far closer to carrying capacity, and therefore exhibit the opposite bottom-up drivers of IFBF. I expect that these shifts between bottom-up and top-down regulation, driven by shifts in predation and forage, appear as both differences in absolute IFBF values as well as the relative differences between females with and without juveniles. In top-down regulated systems with high predation and high forage availability such as the YHT, absolute IFBF values are high (White et al. 2011) and there are large differences in IFBF between females with and without surviving young, as the energetic release from lactation allows females to gain very large amounts of fat. In bottom-up regulated systems with lower predation and lower forage availability such as the Vermejo, we observe lower absolute IFBF values and smaller differences in IFBF between females with and without surviving young, as the energetic release from lactation does not create as meaningful of a difference in the face of nutritional limitation (Watkins et al. 2023).

It is also important to note here that these top-down influences reflect the direct costs of juvenile predation, rather than indirect costs of predation risk. In contrast to early work that provided evidence for the costs of antipredator responses (Creel et al. 2009), my research aligns with other recent work finding no or negligible costs of indirect predation risk (Paterson et al. 2022). Paterson et al. (2022) examined the potential for indirect costs of predation from wolves and mountain lions to impact female elk body fat and pregnancy rates. In accordance with my research, they found no meaningful changes. These findings may be explained by the multi-scale tradeoffs that elk must make to balance their needs for forage and predator avoidance on a landscape with wide-ranging predators like wolves (Hebblewhite and Merrill 2009).

Many factors that I examined demonstrated neutral or insignificant relationships with female IFBF. Pregnancy status suffered from very low sample size for not pregnant individuals and was therefore not informative (i.e. almost all females are pregnant anyway). The date of capture of each individual during winter was also unrelated to IFBF, indicating that at least during the window of capture (Feb. 10 – March 13), there were no detectable declines in body fat through time across the population. The predation risk covariates for both wolf and grizzly bears did not demonstrate significant relationships with IFBF, providing evidence that the indirect effects of predation do not have a measurable impact on female body fat. Although there was some indication of variation in IFBF by year, which may be driven by annual variation in the environment or annual sampling variation, the random effect for year did not substantially improve the model. Similarly, adding a random effect for individual to control for non-independence of measurements of the same individual in different years did not improve the model. The individual effect was likely ineffective because there were only 7 repeat measures of previously measured individuals, an artifact of modest sample size of difficult-to-collect data. The lack of impact of these other factors points again towards the importance of the top-down influence of juvenile predation driving what was traditionally considered a bottom-up indicator: body fat.

The importance of prior summer calf survival as a driver of female body fat levels also underscores the life history tradeoffs that female elk make between reproduction and their own condition. Because body fat levels are important in determining pregnancy rates, overwinter survival, and even population growth (J. G. Cook et al. 2004, Monteith et al. 2014, Watkins et al. 2023), these maternal tradeoffs may have important implications for population demography. In the Ya Ha Tinda population in particular, the differences in female body fat values due to differing calf predation rates between migratory strategies may have consequences for the demographic balancing of this partially migratory population (Martin et al. 2022).

Returning to the individual vs. environmental framework, the primary importance of prior summer calf survival supports the hypothesis that individual factors are most important in explaining variation in female body condition. In comparison to the findings of Bergman et al. (2018) which focused on explaining variation in IFBF in female mule deer, my top model was able to explain 37% of the variation in IFBF in female elk based on individual reproductive history as opposed to Bergman et al.'s (2018) 13% explained variation from environmental variables, ultimately supporting their hypothesis that individual factors contribute more variation to female ungulate IFBF. However, age was less important than hypothesized, perhaps due to a small number of individuals over the 10 year threshold where the most significant age effects were observed. Ultimately my results support contributions from both individual and environmental factors, but individual factors contributed more relative information. This relationship could also shift towards explanation from environmental factors in systems with a higher degree of annual variation or environmental stochasticity.

The relative contributions of individual and environmental sources of variation in body condition have important implications for ungulate managers and scientists. The interpretation or comparison of IFBF values must account for neonate survival. To compare relative condition or nutritional resource availability between individuals or groups, it is very necessary to also compare neonate survival to avoid spurious conclusions. In the context of predator recolonization and range expansion in the lower 48, it may be particularly important to examine juvenile survival alongside ungulate body fat data. For example, expanding grizzly bear range in Montana could decrease juvenile elk survival, causing increased mean body fat values in comparison with historical ranges. Without examining juvenile survival, these increasing body fat values could lead to the false conclusion that forage quality has increased, when in reality they merely reflect a shift in predation.

This research has also illuminated the limitations of using lactation status at time of capture in winter to control for differing reproductive energetic costs between individual female elk. The bulk of the energetic burden of lactation occurs over the summer with weaning occurring in fall or winter, meaning that females who lactated all summer but whose calves died in fall or who weaned their calves in fall may be classified as non-lactating at capture (Robbins et al. 1981, Watkins et al. 2023). During winter captures on the Ya Ha Tinda population, lactation status at time of capture was also recorded. These data allowed me to compare the information offered by both metrics. Lactation status at capture only indicated a surviving calf for 21% of females whose calves survived the summer, meaning 79% of females whose calves lived through the summer (the time period of greatest energetic burden) would have been classified as "Not Lactating" if lactation was the only information source used. Relying solely on lactation status leaves much potential for misclassification and can therefore underestimates the explanatory power of juvenile survival for body fat dynamics in female ungulates. To best capture and quantify the energetic costs of reproduction on an individual basis, the length of survival of each juvenile would be most useful, but this data would be costly and difficult to collect (Monteith et al. 2014).

The energetic dynamics of large herbivores like elk are complex products of complex ecological systems. The energetic costs of reproduction are significant for female ungulates in all ecosystems, but their importance as drivers of body fat reserves varies as a function of broader ecosystem regulation tradeoffs between bottom-up and top-down drivers. In the high predation Ya Ha Tinda elk population, individual variation in reproductive effort driven by the top-down effects of juvenile predation is the most important source of variation in female body fat reserves. As predation regimes change in mountain ecosystems in the lower 48, scientists and managers must expect changes in ungulate body fat dynamics and ecosystem regulation. Body condition data is a valuable tool for researchers and managers to understand the energetic dynamics of ungulate populations, but it is incredibly important to interpret body condition values in the broader context of ecological regulation and individual variation.

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