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Consumer-resource dynamics are central to the understanding of behavioral, nutritional, and population ecology. Nevertheless, many critical gaps in knowledge remain about the consumer-resource dynamics of large herbivores because their large body size, expansive space use, and slow life histories hinder experimental manipulation. The growth rate of moose (*Alces alces*) populations across the Intermountain West and other areas of North America has been declining over the past thirty years, but recent (30 to 80 years) translocations of moose have resulted in some relatively small, rapidly growing populations. These translocations therefore created a natural experiment whereby the relationship between resources and the behavior, nutritional, and demography of large-herbivore consumers was evaluated.

In chapter one, I integrated a suite of field, laboratory, and remote-sensing techniques with life history theory to understand the role of resource limitation in declining moose recruitment. I found that simple browse surveys and fecal-based measures of forage quality and pregnancy were correlated with recruitment, indicating that these tools can be used to monitor resource limitation. Further, I found that recruitment was dictated ubiquitously by inter-annual variation in weather and regional differences in climate (i.e., average, long-term weather conditions), signifying that all populations were near nutritional carrying capacity. In chapter two, I show how metabolic allometries and state-dependent foraging behavior alter energy-endocrine profiles in large herbivores. Consequently, this chapter both contributes to knowledge about the behavior of large herbivores and illustrates that applying laboratory models of energy-endocrine relationships to large-bodied, free-ranging animals may result in erroneous inference regarding their nutritional condition and proximity to carrying capacity.

My third chapter continues to explore how resource limitation influences the foraging behavior of moose by quantifying how diet selection changes as intraspecific competition intensifies and resources become increasingly limiting. Contrary to the Niche Variation Hypothesis, and in accordance with Optimal Foraging Theory, moose broaden their diet selection under resource limitation by increasing individual diet breadth rather than forming into groups of specialized individuals that collectively forage on a wide variety of foods. Although the Niche Variation Hypothesis has gained much attention over the past two decades, my work indicates that when inheritance of behavioral or morphological traits associated with foraging (i.e., dietary phenotype) is weak, populations forage in accordance with Optimal Foraging Theory and individual diet breadth broadens under resource limitation. My fourth chapter tested a long-standing hypothesis in ungulate ecology that predicts migratory behavior is socially learned and culturally transmitted across generations. This hypothesis, however, had not be tested empirically. Using GPS collar data, I compared the migratory propensity of individual moose and bighorn sheep (*Ovis canadensis*) that were translocated from migratory populations into novel landscapes with the migratory propensity of individuals residing in historical populations that had persisted for at least 200 years. I also compared the ability of individuals to track high-quality, green forage across topographic gradients—a behavior known as "green-wave surfing"—hypothesized to be a precursor to migration. Individuals failed to migrate when first translocated, but over time (decades) the surfing ability of translocated populations increased and individuals began migrating. Thus, my work demonstrates that the migrations of large herbivores are learned and culturally transmitted from generation to generation, indicating that conservation of migration corridors not only protects the landscapes that these iconic animals depend on, such

47 efforts also maintain the traditional knowledge that migratory animals use to bolster fitness and
48 sustain abundant populations.

BEHAVIORAL, PHYSIOLOGICAL, AND DEMOGRAPHIC CONSEQUENCES OF RESOURCE LIMITATION FOR LARGE HERBIVORES

by
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DEDICATION

To everyone who has supported my desire to work with wildlife and in wild places, especially my parents.

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CHAPTER ONE

CLIMATE AND WEATHER DETERMINE NUTRITIONAL CARRYING CAPACITY FOR LARGE HERBIVORE AT SOUTHERN RANGE LIMIT

ABSTRACT

Since the time of Aldo Leopold, wildlife managers have sought to prevent density-dependent declines in abundance by using harvest to maintain populations below carrying capacity. Concurrently, population ecologists have struggled to understand the factors underlying density-dependent and density-independent shifts in demography. Life-history theory predicts that nutritional reserves of large herbivores should be allocated to reproduction in a state-dependent manner because survival is highly conserved. Consequently, as populations approach carrying capacity and density-dependence intensifies, habitat condition should deteriorate first, followed by diminished animal nutrition, reduced recruitment, and lastly declines in adult survival. For individuals with few nutritional reserves, unfavorable weather conditions further curtail recruitment through its impact on the resource base. Hence, quantifying the sensitivity of recruitment to severe weather conditions provides a measure of proximity to carrying capacity. Recruitment rates in many moose (*Alces alces*) populations across the Intermountain West have declined over the past 30 years, even in areas lacking large carnivores, which suggests bottom-up limitation stemming either from density-dependent declines in forage quality or from long-term, unfavorable shifts in weather (i.e., climate). To develop a suite of tools that scientists and managers can use to monitor resource limitation in moose, I measured forage quantity with an index of willow (*Salix* spp.) browsing pressure, forage quality using fecal nitrogen concentration, pregnancy through fecal progestagen concentration, autumn nutritional condition of harvested

210 animals using the kidney fat index, and weather and plant phenology via remotely-sensing. I then
211 related these habitat and nutritional metrics to recruitment estimates established from aerial
212 surveys across six populations of moose. Additionally, I tested the hypothesis that moose
213 populations exhibiting greater calf recruitment were below carrying capacity and therefore
214 nutritionally buffered against the effects of unfavorable weather conditions. I found that
215 recruitment was correlated with measures of browsing pressure, fecal nitrogen, fecal
216 progrestagens, and the kidney fat index, indicating that resource limitation indeed underpinned
217 declines in recruitment, thereby identifying a low-cost set of tools for measuring resource
218 limitation. Recruitment was sensitive to inter-annual variation in weather, demonstrating that all
219 populations were in close proximity to nutritional carrying capacity and lacked the nutritional
220 reserves needed to buffer vital rates from the effects of severe weather. Further, average calf
221 recruitment over the past 10 to 20 years was determined by local climatic regimes (i.e., long-term
222 weather patterns). This study therefore demonstrates that life-history theory provides a useful
223 framework through which the reproductive effort of large herbivores can be linked to shifts in
224 nutritional condition stemming from habitat, weather, and climatic conditions, thereby providing
225 a "management paradigm" though which biologists can detect proximity to carrying capacity and
226 thus proactively preempt prolonged declines in recruitment.
227

228 **INTRODUCTION**

229 A major goal in population ecology is to understand the consumer-resource dynamics that
230 underlie shifts in demography. Concurrently, and in attempt to both maximize sustainable
231 harvest and prevent density-dependent declines stemming from resource limitation, wildlife
232 agencies manage annual harvest to keep large-herbivore populations from overshooting

ecological carrying capacity (e.g., Boertje et al. 2009). Nevertheless, wildlife ecologists and managers have struggled to link indicators of resource limitation to carrying capacity for over eighty years (Leopold 1933, MacNab 1985, Bowyer et al. 2014). Although recent advances in nutritional ecology provide a means of identifying a population's proximity to carrying capacity, these approaches require long-term monitoring of individual animals (Monteith et al. 2014b). Because such intensive studies are often financially and logistically prohibitive, low-cost tools are needed to incorporate measures of resource limitation into decisions regarding the management of large herbivore populations.

Large herbivores employ a conservative life-history strategy, wherein adults prioritize survival over reproduction (Stearns 1992, Gaillard et al. 1998). This life-history paradigm predicts that a sequence of density-dependent declines in vital rates occurs as populations approach carrying capacity (Bonenfant et al. 2002, Eberhardt 2002): declines first manifest in juvenile survival, then age of first reproduction and pregnancy, and lastly adult survival (Fig. 1A). Although population growth is most sensitive to adult survival, it is relatively invariant (Gaillard et al. 1998). Therefore, variability in recruitment and other vital rates early in the life cycle of large herbivores underpin population growth (Gaillard et al. 2000). The energy and nutrients large herbivores acquire from their habitats (i.e., their nutritional condition) dictates their survival and reproductive success, and ultimately, population growth (Keech et al. 2000, Cook et al. 2004, Monteith et al. 2014b). As such, nutritional condition provides a direct link between environmental conditions and population growth because it integrates both weather and habitat (Parker et al. 1999, Parker et al. 2009). Extending Eberhardt's (2002) life-history paradigm to include aspects of nutritional ecology would predict that declines in habitat condition should precede declines in nutritional condition, both of which should occur prior to

declines in recruitment and other vital rates (Fig. 1A). Thus, measures of habitat and nutrition provide a window through which a population's proximity to carrying capacity can be viewed.

Ecological carrying capacity is defined as a state of equilibrium between the size of a consumer population and its resources (Fig. 1A; McCullough 1979, MacNab 1985). Although valuable as a heuristic, ecological carrying capacity is difficult to quantify because abundance and quality of resources are ever-changing. The concept of nutritional carrying capacity, however, recognizes that equilibrium is rarely achieved because quantity and quality of forage vary across temporal scales (e.g., seasonally, annually, over decades; Mautz et al. 1978, McLeod 1997, McCullough 1999; Fig. 1B). Nutritional condition is influenced by both density-dependent (i.e., per capita forage availability) and density-independent (i.e., weather) factors, and shapes the population dynamics of large herbivores (Coulson et al. 2001, Monteith et al. 2014b). Hence, managers have recently come to appreciate that the impacts of unfavorable weather conditions can be mitigated by ensuring population densities are held below nutritional carrying capacity where greater nutritional reserves buffer vital rates from the effects of severe weather (Fig 1C, D; Bowyer et al. 2000, Bowyer et al. 2014). The degree to which weather influences vital rates therefore provides a measure of proximity to nutritional carrying capacity.

Climate warming and drying is increasingly threatening the persistence and growth of animal populations (Parmesan and Yohe 2003, Parmesan 2006). Relative to small-bodied species, large mammals (> 3kg) are highly sensitive to environmental change because of slow intrinsic growth rate and their diminished ability to use microhabitats (Cardillo et al. 2005, McCain and King 2014). Compared to those near the center of their geographic range, populations near range limit are more likely to experience weather conditions that shift patterns of plant phenology (Post and Stenseth 1999, Post et al. 2008) and challenge physiological limits

(Portner and Farrell 2008). Consequently, populations residing near the periphery of ranges often are characterized by more variable rates of population growth relative to those near the core of the range (Hanski 1982, Brown 1984). Indeed, large herbivores in temperate and Arctic regions are experiencing declines in recruitment and abundance across many of their southern range limits (Heffelfinger and Messmer 2003, Laliberte and Ripple 2004, Murray et al. 2006, Vors and Boyce 2009). By influencing forage quantity and quality, shorter springs triggered by severe winter snowpack and warmer, drier spring and summer weather lower nutritional carrying capacity, resulting in declines in recruitment and other vital rates (Fig. 1B; Post and Forchhammer 2008, Christianson et al. 2013). Thus, declines in recruitment along the southern range limits of temperate and Arctic herbivores may be linked to a changing climate.

Across much of their southern range, moose (*Alces alces*) populations are experiencing suppressed reproduction and population declines (Murray et al. 2006, Lenarz et al. 2010, Monteith et al. 2014b, Ruprecht et al. 2016). A number of factors have been implicated in these declines, including reduced forage quality and changes in plant phenology (Monteith et al. 2015), heat stress (Lenarz et al. 2009), parasites and disease (Murray et al. 2006, Musante et al. 2010, Henningsen et al. 2012), and predation (Severud et al. 2015, Oates 2016). In the Intermountain West of North America, calf recruitment has declined over the last thirty years (Monteith et al. 2015). For populations inhabiting the Greater Yellowstone Ecosystem, predation of calves by grizzly bears (*Ursus arctos*) and wolves (*Canis lupus*) may underlie declines in calf recruitment (Oates 2016). Nevertheless, nearby populations outside of the Greater Yellowstone Ecosystem that lack grizzly bears and wolves have also declined (Fig. 2), suggesting that a more widespread mechanism is responsible.

Although climate warming and drying may synchronize population dynamics across space and time (Bjørnstad et al. 1999, Post and Forchhammer 2002), calf recruitment across the Intermountain West is variable and site-specific (Fig. 2). Such variation in recruitment may stem from interactions between climate and variation in local forage conditions stemming from variation in herbivory. Recent (past 30 to 70 years) colonization and translocation of moose across the Intermountain West (i.e., Wyoming, Idaho, Montana, and Utah; Brimeyer and Thomas 2004, Toweill and Vecellio 2004, Wolfe et al. 2010, DeCesare et al. 2014) has likely resulted in among-population variation in the quantity, quality, and composition of forage because both current and historical herbivory alter forage characteristics (Augustine and McNaughton 1998, Anderson et al. 2007). For example, increased browsing and grazing pressure often decrease the digestibility, protein content, and biomass of forage (Bryant et al. 1983, Danell et al. 1985, Bryant et al. 1992, McArt et al. 2009, Seaton et al. 2011). Concurrent with variation in browsing and grazing pressure, temperature and precipitation influence the digestibility, protein content, and biomass of forage (Craine et al. 2012, Zamin et al. 2017). Hence, nutritional carrying capacity is determined by both density-dependent (i.e., browsing and grazing pressure) and density-independent (i.e., climate and weather) factors that ultimately determine vital rates via their effects on forage quantity and quality (Figs. 1C, D; Bowyer et al. 2000, Monteith et al. 2014b). The variation in calf recruitment across the Intermountain West therefore provides an ideal opportunity for assessing how density-dependent and density-independent factors combine to determine nutritional carrying capacity.

I sought to (1) test and develop a suite of field, laboratory, and remote-sensing tools through which proximity to nutritional carrying capacity may be identified, and (2) apply these tools to illuminate the roles of density-dependence and density-independence in the ongoing

declines of moose recruitment across the southern extent of their range. Specifically, I first evaluated the relationship between indices of resource limitation and vital rates (i.e., pregnancy and recruitment). I then tested the hypothesis that populations experiencing high levels of calf recruitment were either (i) experiencing favorable climatic conditions, or (ii) were below nutritional carrying capacity, such that the effects of unfavorable weather conditions were mitigated by abundant forage and nutritional reserves. By integrating the aforementioned tool set and the life history paradigm for long-lived vertebrates, I offer a "management paradigm" useful for endangered species and harvest management plans (Fig. 2).

METHODS AND MATERIALS

Study area

I studied six populations of moose in Wyoming, northern Colorado, and northern Utah, USA (Fig. 2A), where habitats were characterized by riparian shrublands dominated by Booth's willow (*Salix boothii*), Geyer's willow (*Salix geyeriana*), and planeleaf willow (*Salix planifolia*). Within riparian shublands, several other willow species, deciduous shrubs (e.g., *Betula glandulosa*, *Rosaceae* spp.), cottonwoods (*Populus* spp.), and a number of grasses (*Poaceae* spp.), sedges (*Carex* spp.) and forbs (e.g., *Asteraceae*, *Onagraceae*) also were common. Moose also used habitats that interspersed riparian habitats (hereafter "uplands"; Baigas 2008, Becker 2008, Vartanian 2011, Oates 2016) characterized by mixed conifers (*Abies lasiocarpa*, *Picea engelmannii*, *Pinus contorta, Pseudotsuga menziesii*), aspen (*Populus tremuloides*), sagebrush (*Artemisia* spp.), mountain mahogany (*Cercocarpus* spp.), and bitterbrush (*Purshia tridentata*). Winters were characterized by deep snow (mean February snow depth 78±15 cm) and cold temperatures (mean February low temperature -15±1˚C), while summers were characterized by

low precipitation (mean July rainfall 4±1cm) and mild temperatures (mean July high temperature 23±2˚C; Western Regional Climate Center).

Study Design and Sampling

Climate, weather, and phenology— Climate and weather were summarized for winter, spring, summer, and winter seasons separately. I defined seasons using measures of plant phenology rather than arbitrary calendar dates by fitting a double logistic curve to annual patterns of plant phenology, which I quantified using a time series of remotely-sensed plant greenness (Normalized Difference Vegetation Index; MODIS product MOD09Q1; 250m x 250m pixel size, 8-day temporal resolution) spanning from 2001-2016. Using Normalized Difference Vegetation Index (NDVI) values, I estimated (1) start of spring as the point in time on the double logistic curve where green-up first occurs (1^{st}, 2^{nd} derivative), (2) end of spring as the point in time when the double logistic curve asymptotes (2^{nd}, 2^{nd} derivative), (3) start of autumn as the point in time when the maximum rate of plant 'brown-down' occurs (2^{nd}, 1^{st} derivative), and (4) the end of autumn as the point in time when NDVI returned to its annual minimum (4^{th}, 2^{nd} derivative; Fig. S1) (*sensu* Bischof et al. 2012). I defined spring as the period between start of spring and end of spring, summer as the period between end of spring and start of autumn, autumn as the period between start and end of autumn, and winter as the period between the end of autumn and start of spring. Further, I used estimates of seasonal periods to estimate plant phenology metrics important to the foraging ecology of large herbivores. Specifically, I estimated length of spring as the number of days between the start and end of spring, length of the growing season as the number of days between start of spring and start of autumn, and plant biomass by summing NDVI values throughout the growing season (Pettorelli et al. 2005, Pettorelli et al. 2007). I then

used my estimates of seasonal periods to summarize daily, rasterized (DayMet; 1km x 1km pixel size) measures of temperature, precipitation and snow water equivalence for each season in each study area (Thornton et al. 2014). All NDVI and DayMet metrics were then masked within high probability of use areas (see *moose space use* below) to quantify spatially and temporally explicit weather and phenology patterns.

Moose space use— To quantify forage quantity and diet quality as well as weather across the six study populations, I first estimated the spatial distribution of moose in each population. To estimate the spatial distribution of moose during winter and summer independently, I divided GPS collar locations (n=1,523,829 locations), representing three populations and 174 individual moose (Becker 2008, Baigas et al. 2010, Vartanian 2011, Oates 2016), into two datasets representing winter and summer space use. To identify the winter and summer space use of migratory individuals, I used net-squared displacement to identify spring and fall migration (Bunnefeld et al. 2011, Jesmer et al. 2018). All points occurring between the end of spring migration and the start of fall migration were considered to occur on summer range (and vice versa for winter). To identify the winter and summer ranges of non-migratory individuals (i.e., individuals that had a single range throughout the year), I defined each population's range as the 95% minimum convex polygon around all GPS-collar data (Calenge 2006), and averaged start of spring and start of winter dates for all pixels within the population's range. I then subset the GPS collar locations of non-migratory individuals into summer and winter locations according to my estimates of start of spring and start of winter.

Using random forests, I modeled second-order, seasonal habitat selection (Johnson 1980, Evans et al. 2011) and projected model predictions across all six populations to inform sampling

393 efforts. Rather than quantifying weather conditions across entire management areas (Fig. 2),
394 predictions of space use were used to constrain measures of weather to areas moose were most
395 likely to occupy. I parameterized random forest models with habitat covariates known to
396 influence moose space-use in the study region (Becker 2008, Baigas et al. 2010; see figure S2). I
397 used the National Land Cover Database (Homer et al. 2015) to define spatially explicit habitat
398 availability. Because moose select riparian habitat in the study area and the spatial resolution
399 (30m x 30m) of the National Land Cover Database often lumps narrow (<30m wide) riparian
400 habitat with surrounding cover classes (e.g., deciduous or conifer forest; Homer et al. 2015), I
401 also included topographic proxies of riparian habitat (i.e., the compound topographic index and
402 the topographic position index; Evans et al. 2014, Evans 2017). Like other classification and
403 regression tree methods, random forest models are sensitive to unbalanced sample sizes among
404 classes (in this case presence and psuedoabsence; Breiman 1984, Evans et al. 2011). Therefore, I
405 randomly selected GPS-collar locations from the two more location-rich databases to standardize
406 presence (collar locations, n = 51,515 in winter, n = 53,898 in summer). I then created an equal
407 number of psuedoabsences by plotting random points across the entire study region (i.e., the
408 bounding box illustrated in Fig. 2A). Overfitting is common with random forest models, so I
409 used the model selection function in the rfUtilities package (Evans and Murphy 2018) to reduce
410 the parameter set to include only highly informative parameters. I then fit random forest models
411 using either winter or summer locations to estimate and map seasonal habitat across the entire
412 study area (Liaw and Wiener 2002, Hijmans 2017) to constrain the search area in which I
413 collected fecal samples and ensure I measured climate and weather only within moose habitat.
414 Model performance was evaluated using a cross validation approach (i.e., "out of bag error";
415 Evans et al. 2011).

Forage quantity and diet quality— Using the habitat selection model, I reclassified the probability of use surface to only include high probability of use areas (i.e., the 0.5 quartile). I further divided high probability of use areas into "core habitat", defined as the 0.75 quartile), and "peripheral habitat", which I defined as the 0.50-0.75 quartile. Because willow is the primary forage for moose across the Intermountain West (Renecker and Schwartz 2007, Baigas 2008, Vartanian 2011), I used the National Land Cover Database and masked high probability of use areas to only include willow riparian habitat. I then identified 20 locations within core habitat and 20 locations within peripheral habitat using a spatially-balanced stratified random sampling algorithm (Stevens and Olsen 2004, Kincaid et al. 2012). At each location, I randomly selected a direction that allowed us to remain within willow habitat for a 200m live-dead index transect. The live-dead index provides a measure of browsing intensity, and therefore quantifies competition for, and quantity of, willow forage. Each live-dead transect consisted of measuring the height of the tallest dead stem from browsing, and the height of the tallest annual growth ring of the current year, for 20 willow plants spaced 10m apart (Keigley and Fager 2006).

To quantify diet quality, I measured the nitrogen content of fecal samples (see laboratory methods below) collected along transects on both summer and winter range. In winter, I collected fecal samples along live-dead transects in riparian habitat and opportunistically in upland habitats (e.g., aspen and conifer forests, sagebrush, and other xeric shrub communities). In summer I constrained sampling to core habitat and used spatially-balanced stratified random sampling to collect fecal samples within willow riparian habitat and upland habitat strata. I identified 20 locations within each stratum, and at each location I randomly selected a direction that would allow us to remain within the habitat strata for the entire 2-km sampling transect. I

used detection dogs to find fecal samples along transects during summer because fecal samples were scattered across vast summer ranges, hidden by thick vegetation, and were required to be less than approximately 48 hr old for DNA analysis (Dahlgren et al. 2012). During winter, visual detection of fecal samples was feasible because feces were concentrated on winter ranges, easy to detect in snow, and were frozen shortly after deposition by the cold winter conditions in the study area. All samples were collected according to a sterile protocol and placed in a -20^{o}C freezer within 8 hours.

Nutritional condition— Autumn nutritional condition of large herbivores determines pregnancy and overwinter survival of both juveniles and adults (Cook et al. 2004, Monteith et al. 2014b). I therefore quantified the autumn nutritional condition of moose by measuring the Kidney Fat Index of hunter-harvested kidneys (Riney 1955, Stephenson et al. 1998). In collaboration with the Wyoming Game and Fish Department and Colorado Parks and Wildlife, I instructed hunters on how to collect kidneys without disturbing attached fat. Renal fat forcefully removed from the kidney was indicated by cut marks in the fat or kidney as well as air bubbles within the renal membrane caused by tearing fat away from the membrane. I noted any signs of fat disturbance and excluded all disturbed kidneys from further analysis.

Laboratory Methods

Genetic Analyses—To assess diet quality and pregnancy, I used multi-locus genotypes derived from fecal samples to identify individual moose and their sex. I extracted DNA from fecal samples using a sterile protocol and the QIAamp DNA Stool Mini Kit (Qiagen, Inc.; Adams et al. 2011, Woodruff et al. 2014). Through an iterative trial-and-error process, I optimized

multiplex PCR conditions such that nine microsatellites and a sex marker (Table 1) were amplified in a single PCR reaction (Table 2). Fecal DNA is often highly degraded and fecal contamination may interfere with microsatellite amplification, resulting in genotyping errors (Pompanon et al. 2005). I therefore employed a multiple tubes approach, wherein a minimum of three PCR reactions were conducted for each fecal sample (Taberlet et al. 1996). Microsatellite fragment lengths were then quantified by Cornell University's Biotechnology Resource Center using an ABI 3730xl DNA Analyzer (Applied Biosystems). Each fragment analysis was genotyped by two independent observers using GeneMarker® (SoftGenetics, LLC). If fewer than five microsatellites amplified during the first three PCR attempts, the sample was discarded. If five or more microsatellites amplified during the first three PCR, I used program Reliotype (Miller et al. 2002) to estimate the number of additional genotypes needed to identify a reliable genotype for a given fecal sample. This process was iterated until a reliable genotype was identified or a sample was genotyped nine times, after which the sample was discarded. Because genotypic data derived from fecal DNA are prone to genotyping error, I used program GIMLET (Valière 2002) to estimate genotyping error rates (Table 1) and create a final consensus genotypes. I then used package AlleleMatch in Program R to identify individual moose from the genotypic data (Galpern et al. 2012). I used the probability that two genotypes were indeed unique individuals and not simply siblings with similar genotypes (i.e., $Psibs<0.05$) as a conservative measure of individual identification (Waits et al. 2001). All pairwise combinations of loci were tested for significant linkage disequilibrium, and Hardy-Weinberg equilibrium was evaluated within each population using Genepop version 4.6 (Raymond and Rousset 1995, Rousset 2008).

485 *Fecal nitrogen, fecal progestogens, and pregnancy-specific protein B* — Fecal nitrogen and fecal
486 progestagens were quantified only for fecal samples of known individuality and sex. I quantified
487 fecal nitrogen in winter for both males and females, but because lactation status influences
488 nitrogen assimilation and excretion (Monteith et al. 2014a), fecal nitrogen was assessed only for
489 males during summer. Fecal nitrogen analyses were performed by the Washington State Habitat
490 Lab (Washington State University, Pullman, WA, USA). Six pellets from each fecal sample were
491 chosen at random and oven-dried at 55˚C, ground in a Wiley Mill, passed through a 1.0mm
492 screen and homogenized. The Dumas method of combustion was used to determine fecal
493 nitrogen using a Truspec CN analyzer (LECO corp., St. Joseph, MI, USA). Fecal nitrogen is
494 reported on a percent dry matter basis (Hodgman et al. 1996).
495 Fecal progestagen assays were performed by the Smithsonian Conservation Biology
496 Institute (Front Royal, VA, USA). Six pellets from each fecal sample were chosen at random and
497 freeze-dried for 24-48 hours in a Labconco Freeze-Dry system at -50˚C, then thoroughly
498 homogenized into a fine powder. Approximately 0.1g was weighed from each sample to control
499 for mass-induced bias in metabolite concentration (Millspaugh and Washburn 2003, Goymann
500 2012) and a pulse-vortex double extraction with 15mL 70% ethanol was performed. Ethanol
501 extracts were then stored at -20˚C until assay. Radioimmunoassays were performed on ethanol
502 extracts at previously validated dilutions progestagens (Wasser et al. 1991, Monfort et al. 1993)
503 using an in-house 3-H progesterone assay. All hormone extracts were run in duplicate in each
504 assay, and only those with intra-assay variation (%CV) below 10% were accepted.
505 Concentrations of fecal hormones are reported as ng per gram of dried feces.
506 To validate a threshold from which to determine pregnancy from fecal progestogen
507 concentrations, I compared fecal progestagen concentrations of live-captured female moose with

serum-based measures of pregnancy-specific protein B (n=67). I also estimated the nutritional condition of moose using ultrasonography and body condition scoring (n=153). Although methods of live capture, serum collection, determining the presence of pregnancy-specific protein B, and assessment of nutritional condition are described elsewhere (i.e., Jesmer et al. 2017), I briefly summarize those methods here. Adult (>1 yo), moose were captured on winter range in February 2013 and 2014 via helicopter net-gunning (Barrett 1982, Krausman et al. 1985). Dr. Kevin L. Monteith and myself ultrasonography to determine the maximum depth of subcutaneous rump fat, and used a standardized protocol validated in other species to assign a body condition score (Stephenson et al. 1998, Cook et al. 2010). Subcutaneous rump fat was used to estimate percent ingesta-free body fat for moose with measurable fat. For animals without subcutaneous fat, body condition scores were used to estimate percent ingesta-free body fat based on the linear relationship between ingesta-free body fat and the body condition score of moose with measurable rump fat (Cook et al. 2010, Monteith unpublished data). I collected fecal samples (10–12 pellets) via rectal palpation, which I immediately froze at -20˚C until assayed for fecal nitrogen and fecal progestagen concentrations. A blood sample (20ml) was collected via jugular venipuncture. Blood samples were centrifuged and serum was pipetted into 5ml cryovials and stored at -20˚C until analyzed for the presence of protein-specific protein B. The commercially available BioPRYN wild assay was used to determine pregnancy-specific protein B concentrations was analyzed by BioTracking LLC (Moscow, ID, USA). Capture and handling methodologies followed the recommendations of the American Society of Mammalogists (Sikes et al. 2011) and were approved by the Institutional Animal Care and Use Committee at the University of Wyoming (Permit # A-3216-01).

Statistical Analyses

Confounding variables— Prime-aged (~5-10 yo) large herbivores typically exhibit greater nutritional condition and higher vital rates than older and younger age classes (i.e., <3 yo >11; Boertje et al. 2007, Monteith et al. 2014b). Additionally, and because moose reduce foraging while increasing locomotive and reproductive costs during the breeding season in autumn (Schwartz et al. 1984), date of harvest may obscure the influence of density-dependent and density-independent factors on kidney fat (i.e., nutritional condition). I therefore fit linear models to male and female kidney fat index values with age and Julian day of harvest as dependent variables, and used model residuals as a corrected measure of nutritional condition.

Plant phenology strongly influences fecal nitrogen concentrations through its impact on forage digestibility and crude protein concentration (Hamel et al. 2009). Forage quality for large herbivores is highest when plants are in an intermediate phenological state because this stage of growth balances digestibility and biomass (Fryxell 1991, Hebblewhite et al. 2008). I computed the date at which forage reached an intermediate phenological state across space and time by estimating the first derivative of the double logistic curve, a metric referred to as the Instantaneous Rate of Green-up (IRG; Bischof et al. 2012, Merkle et al. 2016). This process resulted in a single raster for each year with cell values corresponding to the Julian day in which IRG peaked. I then used the date and location a fecal sample was collected to extract temporally and spatially explicit NDVI and date of peak IRG values from the raster sets. I considered the difference in days between peak IRG and the date fresh fecal samples were collected, as well as raw NDVI values, as a measures of plant phenology (Aikens et al. 2017, Jachowski et al. in press). I then regressed fecal nitrogen concentrations against NDVI and days from peak IRG values to control for potential variation in plant phenology caused by differences in elevation,

554 topography, and the date fecal samples were collected across the study area. In this way, I
555 ensured that any differences forage quality observed among-populations was because of
556 differences in plant nutritional value rather than simply the phenological state of plants at the
557 time of fecal collections.

558 Measures of weather are often highly correlated. For example, warm summers tend to be
559 dry and result in drought conditions, whereas cool summers are correlated with greater
560 precipitation and better growing conditions for plants (i.e., increased NDVI; Trenberth and Shea
561 2005, Lamchin et al. 2018). Hence, measures of drought, such as the Palmer Drought Severity
562 Index (PDSI) that incorporate temperature, precipitation, and plant transpiration may encompass
563 a number of correlated climate variables (Palmer 1968, Heim 2002). I therefore summarized
564 PDSI within moose habitat and across seasons for the entire study area and used principal
565 components analysis to identify non-correlated parameters that together characterized inter-
566 annual variation in weather across the study area (Legendre and Legendre 2012).

567

568 *Modeling approach*— Qualitative estimates of thresholds in fecal progestagens for determining
569 pregnancy in moose and other large herbivores have been reported (Monfort et al. 1993,
570 Schwartz et al. 1995, Garrott et al. 1998, Murray et al. 2012), yet a quantitative evaluation is
571 lacking. Classification and regression tree (CART) analysis was developed specifically to
572 estimate threshold values for classifying data into distinct categories (e.g., pregnant versus non-
573 pregnant; Breiman 1984). Classification and regression tree analysis, however, is sensitive to
574 unbalanced sample sizes and currently there is no method for calculating confidence intervals for
575 threshold estimates. I therefore combine classification and regression tree analysis with a Monte
576 Carlo resampling approach to create a distribution of progestagen thresholds from which I

577 estimated a threshold and confidence intervals (Robert et al. 2010). I quantified a fecal
578 progestagen threshold for determining pregnancy in moose by comparing the presence of
579 pregnancy-specific protein B in serum to fecal progestagen concentrations in live-captured
580 moose (n=67). I identified the statistical distribution of fecal progestagen values for pregnant and
581 non-pregnant individuals (Delignette-Muller and Dutang 2015). I then sampled progestagen
582 values (n=30) from statistical distributions for both pregnant and non-pregnant individuals,
583 thereby achieving balanced samples, and estimated progestagen thresholds for determining
584 pregnancy (Therneau et al. 2015). This procedure was iterated one thousand times to create a
585 distribution of threshold values from which I estimated a final threshold value as the median of
586 the distribution and threshold confidence intervals as the 2.5 and 97.5 percent quantiles of the
587 distribution.

588 I used structural equation modeling (SEM) to assess a number of hypothesized pathways
589 by which density-dependent and density-independent factors influence recruitment (Grace 2008).
590 Hypothesized pathways were generated from knowledge of the nutritional ecology and life-
591 history paradigm for large herbivores. Specifically, the slow life history of large herbivores
592 results in significant lags between changing environmental conditions and shifts in vital rates
593 (Gaillard et al. 2000). Because of these lag effects, recruitment measured in any given winter
594 may be influenced by conditions experienced two years prior by impacting autumn nutrition and
595 pregnancy (Cook et al. 2004, Taillon et al. 2013). Similarly, preceding summer conditions may
596 influence the nutritional condition of females and their forage base, thereby impacting lactation,
597 maternal care, and thus recruitment (Gaillard et al. 1997, Hurley et al. 2017, Lukacs et al. 2018).
598 Given the hierarchical nature of my data, multiple hypotheses regarding the pathways (i.e.,
599 pregnancy and lactation) through which recruitment is determined, the different timescales at

which pathways operate, and potential collinearity among predictor variables, SEMs provide an ideal approach for evaluating my suite of monitoring tools and the relative roles of density-dependent and density-independent factors (Grace 2006). I used linear regression to evaluate relationships between measures of forage quantity, diet quality, nutritional condition, pregnancy, and calf recruitment when relationships could not be directly assessed in the SEM.

To evaluate the sensitivity of recruitment in each population to density-independent factors (e.g., temperature, precipitation, snow pack, plant phenology), and thus assess proximity to nutritional carrying capacity (Fig. 1), I fit generalized mixed-effect models to a time series of calf recruitment (Fig. 2). First, I fit piecewise regression models and mixed effects models with random slopes and random intercepts with autoregressive (AR1) and auto regressive moving average (ARMA) error structures (Muggeo 2008, Pinheiro et al. 2014) to evaluate temporal autocorrelation in calf recruitment. I then used forward stepwise model selection and Akaike's Information Criterion (AIC_C) to identify the most parsimonious parameter set (Burnham and Anderson 2002). I then again used AIC_C to assess whether populations with higher recruitment were less sensitive to density independent factors by competing models with random intercepts and models with random intercepts and random slopes. Predictive power of models was evaluated through leave-one-out cross validation (Kuhn et al. 2015).

RESULTS

Moose Distribution, Climate and Weather— Of the 28 variables identified a priori, model selection identified seven variables that accounted for most of the variation in moose occurrence during winter: (1) distance to willow, (2) distance to deciduous forest, (3) distance to mixed deciduous-conifer forest, (4) elevation, (5) amount of willow within 1-km radius, (6) latitude,

623 and (7) longitude. During summer, model selection identified the same variables as for winter,
624 but deciduous forest was replaced with barren ground (Fig. S2). Random forest predictions of
625 moose distribution had a mean (n = 100 permutations) out of bag error of <1% in both winter
626 and summer, indicating that the distribution model performed well and accurately predicted
627 patterns of presence-absence with 99% accuracy.
628 Principal components analysis (PCA) of climate and weather variables extracted from
629 within high-probability of use areas identified three primary axes of variation. The three PCA
630 axes combined to explain 62% of the variation in climate across the region. PC1 accounted for
631 24.1% of the variation and reflected variation in temperature and precipitation (Fig. 3), which
632 were strongly and negatively correlated. PC2 explained 21.5% of the variation and described
633 phenology (Fig. 3), specifically the length of spring, which was highly and negatively correlation
634 with higher spring temperature. PC3 accounted for 16.3% of variation and provided a measure of
635 drought as quantified by the Palmer Drought Severity Index (PDSI) and overwinter snowpack as
636 measured by cumulative snow water equivalent (SWE), which were not correlated.
637
638 *Genetics (individuality and sex)*— Surveys of fecal transects resulted in the collection 1,176
639 samples. The multiple tubes and multiple consensus approach resulted in low genotyping error
640 rates, with allelic dropout and false alleles constituting most of the error (Table 2). All loci were
641 polymorphic (range = 3-7; Table 3) and were not out of linkage Hardy Weinberg equilibrium.
642 Full genotypes were established for 709 of 1,176 (60%) samples, representing 198 individuals
643 (sex ratio = 50:50; 99 males and 98 females; Table 43). Number of individuals identified in each
644 study area ranges from 1-19 (Table 4).
645

Forage Quantity and Quality— Average diet quality (fecal nitrogen) of males in winter was markedly lower and less variable (mean = 1.17 +/- 0.03) than diet quality of males in summer (mean = 2.85 +/- 0.68; Fig. 4). Average diet quality was ubiquitously low and nearly identical for males and females (mean = 1.17 +/- 0.02) in winter (Fig. 4). Because I sampled diets during the middle of winter and after plant green-up had peaked in summer, fecal nitrogen was not influenced by plant phenology as indexed by NDVI or days from peak IRG (Fig. 4; all $P>0.05$). As assessed by the live-dead index, quantity of preferred forage (i.e., willow) varied among populations and species (planeleaf, range = 1.44-3.43 cm; Booth, range = 10.80-15.61 cm). Additional measures browse condition, such as plant height and percent browsed leaders, were strongly associated with the live-dead index (Fig. 5), indicating that these less time intensive measures accurately depict browse condition.

Kidney Fat Index— In collaboration with the Wyoming Game and Fish Department and Colorado Parks and Wildlife, I collected undisturbed kidneys from 665 individual moose. After excluding kidneys that lacked age or harvest date information, the final data set of autumn nutritional condition included 422 kidneys (males, n = 321; females, n = 101). The nutritional condition (kidney fat index) of males declined as the breeding season progressed (i.e., with Julian day of harvest, $\beta = -0.033$ [-0.037, -0.028], $P < 0.001$; Fig 6A) and as individuals aged ($\beta = -0.057$ [-0.087, -0.025], $P < 0.001$; Fig. 6B). Therefore, I used model residuals as a measure of nutritional condition corrected for age and progression of the breeding season. Female kidney fat did not decline with the progression of the breeding season ($\beta = -0.005$ [-0.016, 0.006], $P = 0.36$; Fig. 6C) or with age ($\beta = -0.005$ [-0.043, 0.056], $P = 0.84$; Fig. 6D), so I did not adjust values of the kidney fat index for females.

669

670 *Fecal Progestagens (pregnancy)*— Concentration of fecal progestagens varied from 237.4 ng/g
671 to 12,703.5 ng/g in pregnant females, and 216.9 ng/g to 2,943.6 ng/g in non-pregnant females
672 (pregnancy determined via the presence of pregnancy-specific protein B in serum samples). My
673 classification and regression tree and Monte Carlo resampling approach resulted in a fecal
674 progestagen threshold of 2,291.3 ng/g for determining pregnancy from individual fecal samples
675 (Fig. 7A). My Monte Carlo approach allowed me to estimate a confidence interval (1,340.9-
676 3344.9 ng/g) for the threshold (Fig. 7A). I therefore considered the pregnancy status of any
677 female with a fecal progestagen concentration that fell within the bounds of my confidence
678 interval to be ambiguous and I excluded these samples from further analysis. By excluding
679 samples with ambiguous pregnancy status (n = 16), I eliminated false negatives (from 5.6% to
680 0%) and reduced false positives by 2.4% (from 18.5% to 16.1%). Altogether, my approach
681 resulted in a single-sample fecal pregnancy test that was 90.2% accurate (Fig. 7A). Serum-based
682 PSPB accuracy is 95.5% (Huang et al. 2000), meaning non-invasive pregnancy estimates are
683 nearly as accurate as serum-based measures.
684

685 *Measuring Resource Limitation*— Structural equation models revealed that inter-annual
686 variation in weather acted to influence calf recruitment by influencing the nutritional condition
687 of females. Recruitment was influenced by autumn nutritional condition (KFI) of females two
688 years prior because KFI increased with increased plant biomass (iNDVI; 6.70), increased spring
689 temperature (5.78), increased length of spring (0.54), reduced summer drought (0.42), and
690 reduced growing season precipitation (-1.36), and lower recruitment the preceding year (-1.51;
691 Fig. 8; Table S2). Although pregnancy did not increase with increased autumn nutritional

condition, recruitment did increase as pregnancy increased (0.60; Fig. 8; Table S2). Thus, recruitment was influenced by weather conditions with a two year lag through its impact on pregnancy. Similarly, weather conditions influenced the ability of females to support calves via lactation, and influenced summer forage conditions experienced by weaned calves. Nutritional condition during the autumn immediately preceding winter calf classification increased with decreased precipitation during the growing season (-1.49), cooler temperatures during the growing season (-1.11), increased over-winter snow pack (SWE; 1.41), and increased temperature during spring (1.67). Autumn nutritional condition at a one year lag, however, was negatively correlated with recruitment (-0.48).

Estimates of female diet quality during summer were not included in the structural equation model of calf recruitment because the lactation status of females was unknown (Monteith et al. 2014a). Separate structural equation models were therefore used to estimate the effects of weather on diet quality of females during winter and males during winter and summer. Although I did not detect any influence of weather on the diet quality of females in winter (Fig. 9A; Table S3), the diet quality of males in both winter and summer increased with increased growing season precipitation, increase growing season temperature, increased plant biomass, decreased winter severity (SWE), decreased spring temperatures, decreased spring length, and increased drought (PDSI; Fig. 9B, 9C; Table S3). Thus, male nutrition can be viewed as an indicator of environmental conditions.

Male diet quality during summer was strongly and positively correlated with recruitment ($r = 0.79$ [0.61, 1.00], $P = 0.01$; Fig. 10A), positively correlated with pregnancy ($\beta = 3.10$ [1.13, 5.23], $P = 0.12$; Fig. 10B), and positively correlated with the nutritional condition of females in autumn ($r = 0.64$ [-0.08, 1.00], $P = 0.18$; Fig. 10C). Additionally, pregnancy was positively

715 correlated with recruitment (r = 0.33 [0.07, 1.00], P = 0.14; Fig. 10E) and browse condition (live-
716 dead Index) was positively correlated with recruitment (planeleaf r = 0.93, Booths r = 0.51).
717 Together, these results indicate that simple field-based measures of diet quality, pregnancy, and
718 browse condition can be used to understand resource limitation and thus proximity to nutritional
719 carrying capacity.
720
721 *Nutritional Carrying Capacity*— Recruitment rates of all six populations were equally sensitive
722 to inter-annual variation in weather, indicating each population was near its nutritional carrying
723 capacity. Further, average recruitment rates observed over the past 10 to 20 years were
724 determined by local climatic conditions (i.e., average weather over past 10 to 20 years).
725 Temporal autocorrelation of residuals was weak and unimproved by autoregressive error
726 structures (i.e., AR1, ARMA; Fig. S1). Forward stepwise model selection indicated that the
727 relationship between recruitment and inter-annual variation in weather was not improved by
728 allowing the intercept or slope for each herd to vary for any parameter (Table S4). The top model
729 set (i.e., models within 2 AICc) included four standard linear models and one model that treated
730 population as a random effect (Table 5). With the exception of the random intercept term, the
731 random intercept model was identical to the top overall model. The results of a log likelihood
732 ratio test indicated that including a random intercept did not improve model fit ($\chi^2 = 0.72$, P =
733 0.40), so I excluded the random effect model and model averaged the remaining four standard
734 linear models. Model-averaged parameter estimates indicated a strong, negative effect of winter
735 severity (i.e., SWE; Fig. 11A) during the previous year and a strong positive effect of extended
736 spring conditions (i.e., spring length; Fig. 11B) during the previous year (Table 3). The model
737 also indicated weak, non-significant (confidence intervals overlapped zero and P>0.10) effects of

738 drought severity (PDSI) and plant biomass (iNDVI) at both one and two year time lags (Table 3).
739 Predictive power of the model was high as demonstrated by leave one out cross validation (mean
740 average error = 7.67 calves/100 cows) and residual squared error ($R^2 = 0.54$; Fig. 11C).
741 Together, these results indicate that combing estimates of recruitment with freely available,
742 remotely-sensed data provides a means by which to quantify proximity to nutritional carrying
743 capacity.
744

745 **DISCUSSION**

746 The concept of nutritional carrying capacity has been increasingly accepted and applied over
747 recent decades because ecologist and managers recognize that density-dependent (i.e., per capita
748 resource availability) and density-independent factors (i.e., weather) interact in ways that cause a
749 single, long-term estimate of ecological carrying capacity of little use to managers (MacNab
750 1985, McLeod 1997, Monteith et al. 2014b). Nevertheless, readily accessible and low-cost tools
751 for measuring resource limitation and thus proximity to nutritional carrying capacity are lacking.
752 By integrating a suite of field, laboratory, and remote-sensing tools with concepts from
753 nutritional ecology and life-history theory (Eberhardt 2002, Parker et al. 2009, Bowyer et al.
754 2014), I developed a framework for measuring resource limitation in large herbivores (Fig. 1)
755 and applied this to six moose populations across the Intermountain West, USA to understand the
756 role of resource limitation in declines of calf recruitment (Fig. 2). Recruitment was correlated
757 with non-invasive measures of forage quantity, diet quality, and pregnancy, as well as estimates
758 of nutritional condition derived from hunter-harvested animals, indicating that resource
759 limitation indeed underpinned declines in calf recruitment across the Intermountain West and
760 that such measures represent a low-cost set of tools for measuring resource limitation.

761 Recruitment was sensitive to inter-annual variation in weather, demonstrating that all populations
762 were in close proximity to nutritional carrying capacity and lacked the ample nutritional reserves
763 (i.e., body fat and protein stores) needed to buffer vital rates from the effects of severe weather
764 (Bowyer et al. 2014). Further, average calf recruitment over the past 10 to 20 years were
765 determined by local climatic regimes (i.e., long-term weather patterns). Thus, recruitment was
766 spatially structured by regional climate and varied temporally in accordance with weather
767 conditions, thereby revealing that populations of moose in the region were resource limited—a
768 circumstance that can be detected using readily available measures of habitat condition, diet
769 quality, nutritional condition, and pregnancy.
770 Browsing alters the quantity, quality, and composition of plants (Bryant et al. 1983,
771 Augustine and McNaughton 1998), which in turn, influence the intraspecific competition,
772 nutrition, and demography of large herbivores (Boertje et al. 2007, McArt et al. 2009). Measures
773 of browse condition have been linked to the nutritional condition and demography of moose in
774 Alaska (Boertje et al. 2007, Seaton et al. 2011), yet the methods used in these studies (e.g.,
775 biomass removal) are often viewed as prohibited because they are labor intensive (pers comm,
776 WGFD). Hence, if less labor-intensive methods for monitoring browse condition were linked to
777 nutritional condition or demography, the ability of managers and ecologists to detect resource
778 limitations would be enhanced (Vartanian 2011, Paragi et al. 2015). The live-dead index simply
779 compares the height of the tallest leader that has died because of browsing to the height of the
780 tallest current annual growth ring (Keigley and Fager 2006), and this measure was strongly
781 correlated with calf recruitment in the Intermountain West (Fig. 10E). Further, the live-dead
782 index was highly correlated with the percent of willow stems on a transect that were browsed
783 (Fig. 5; also see Paragi et al. 2015). Thus, simple measures of browse intensity, such as the live-

784 dead index and percent browsed stems, offer a means by which resource limitation and thus
785 proximity to nutritional carrying capacity can be estimated.
786 Despite debate over the advantages and limitations of using fecal nitrogen as an indicator
787 of forage quality (Leslie and Starkey 1985, Hobbs 1987, Leslie and Starkey 1987), fecal nitrogen
788 explained much of the variation in recruitment (Fig. 5A), pregnancy (Fig. 5B), and nutritional
789 condition (i.e., body fat; Fig. 5C) observed across study populations (Fig. 2). The debate
790 surrounding limitations of fecal nitrogen was centered on the notion that plant defense
791 compounds (i.e., tannins) may cause fecal nitrogen to be artificially inflated in feces (Hobbs
792 1987). Nevertheless, free ranging herbivores rarely ingest the levels of tannins needed to cause
793 nitrogen precipitation in feces (Osborn and Ginnett 2001, Leslie et al. 2008). Clearly, given that
794 fecal nitrogen explained a substantial amount of the variation observed in recruitment,
795 pregnancy, and body fat (Fig. 5), fecal nitrogen provides a reliable measure of forage quality in
796 moose. Hence, my results indicate that nitrogen limitation was responsible for reduced
797 recruitment observed across the Intermountain West (Fig. 2).
798 Many large herbivores are classified as concentrate selectors, meaning their nutritional
799 condition and demography is more strongly influenced by quality of forage than quantity
800 (Hofmann 1989). Although the large body size of moose suggests that they should forage on
801 abundant, low-quality forage (Bell 1971, Jarman 1974), moose are indeed concentrate selectors
802 whose demography is linked to the digestibility and protein content of forage (White 1983,
803 McArt et al. 2009). I used the diet quality of males as an indicator of forage quality because
804 lactating females enhance nitrogen recycling to support milk production and conserve protein
805 reserves, which in turn influences the amount of nitrogen in feces (Monteith et al. 2014a). My
806 non-invasive sampling approach did not allow me to classify the lactation status of females from

807 which I collected fecal samples, so I measured summer diet quality using males as indicators of
808 forage quality. Indeed, fecal nitrogen increased when conditions that promote increased plant
809 quantity and quality of forage improved (e.g., extended spring conditions, temperature,
810 precipitation; Fig. 9). Male diet quality therefore reflected the nutritional landscape and provided
811 a simple, low-cost measure of resource limitation.

812 Quantifying nutritional reserves, such as body fat, is an ideal approach to measuring
813 resource limitation and proximity to nutritional carrying capacity because nutritional condition
814 integrates both density-dependent and density-independent factors (Parker et al. 2009, Monteith
815 et al. 2014b). The long-established kidney fat index (Riney 1955) is known to quantify the
816 nutritional condition of moose (Stephenson et al. 1998), yet citizen scientists (e.g., big game
817 hunters) are rarely used to collect kidneys because it is generally accepted that biologists trained
818 in kidney extraction are needed to ensure data quality (Anderson et al. 1990). I provide two lines
819 of evidence suggesting that hunter-harvested kidneys provided an accurate measure of body fat
820 and thus nutritional condition. First, and in accordance with the annual energetic cycle of male
821 moose (Schwartz et al. 1984), values of the kidney fat index declined predictably as the breeding
822 season progressed (Fig. 6A) and with age (Fig. 6B). Although declines in female kidney fat
823 index throughout the breeding season were not statistically significant (i.e., $P > 0.05$), average
824 kidney fat index declined with both progression of the breeding season and age as expected
825 according to annual energetic cycle of female moose (Parker et al. 2009). Second, as
826 demonstrated by my own nutrition-pregnancy assessments (Fig. 7B), as well as other research
827 (Keech et al. 2000, Cook et al. 2004), population-level nutritional condition as indexed by female
828 kidney fat was highly correlated with population-level pregnancy (Fig. 8). Together, these results
829 indicate that kidney fat measures derived from hunter-harvested animals, including males,

provide a viable means of indexing population-level nutritional condition and therefore resource limitation and proximity to nutritional carrying capacity.

Pregnancy is underpinned by nutritional condition and plays an important role in understanding the demography of large herbivores because juvenile recruitment strongly influences population growth rates (Gaillard et al. 2000, Cook et al. 2004). I improved upon previous work that established thresholds in fecal progestogens for assessing pregnancy (Monfort et al. 1993, Garrott et al. 1998, Cook et al. 2002, Murray et al. 2006, Murray et al. 2012) by combining classification and regression tree analysis (i.e., a statistical method designed to classify discrete variables by partitioning variance within a continuous variable) with Monte Carlo resampling methods to estimate both a threshold and confidence in the threshold. By establishing a single-sample pregnancy test and considering fecal progestogen values that fell within the 95% confidence interval of my threshold (2291.3 ng/g [1340.9 ng/g, 3344.9 ng/g]; Fig. 7A) to have undetermined status (Cook et al. 2002), I were able to link pregnancy rates derived from fecal progestogens to recruitment (Fig. 10D). My threshold aligns with that of previous thresholds developed for moose and elk beginning in approximately February (Monfort et al. 1993, Garrott et al. 1998, Murray et al. 2006), but was well below the threshold developed for moose in May (Murray et al. 2012). To use my threshold, I suggest collecting fecal samples in mid-winter (e.g., February), because circulating levels of progesterone and thus fecal progestogens increase throughout pregnancy (Monfort et al. 1993). My threshold will be inaccurate for fecal samples collected later in the year (e.g., May). By evaluating the relationship between nutritional condition as indexed by ultrasonographic measures of ingesta-free body fat (%IFBFat) and pregnancy (Fig. 7B), I demonstrated that estimates of pregnancy provide a course measure of population-level nutritional condition (Fig. 7C). Because nutritional condition

853 underlies pregnancy and recruitment, fecal-based assessments of pregnancy can be directly
854 linked to population growth rate (λ) as has been previously reported for mule deer (Odocoileus
855 hemionus; Monteith et al. 2014b; Fig. 7D). Thus, fecal-based estimates of pregnancy alone
856 provide a means by which nutritional condition, population growth rate, and proximity to
857 carrying capacity can be estimated.

858 Recruitment is sensitive to variation in weather when populations are near nutritional
859 carrying capacity because density-dependent declines in nutritional reserves (i.e., fat and protein
860 stores) are further depleted by stressful weather conditions (e.g., severe winters, drought) that
861 limit intake of energy and nutrients (Parker et al. 2009). Consequently, quantifying sensitivity of
862 recruitment to weather provides a measure of proximity to carrying capacity (Bowyer et al. 2000,
863 Bowyer et al. 2014). Across the Intermountain West, moose recruitment varied with winter
864 severity (i.e., snow water equivalent; Fig. 8, 11A) and a measure of plant phenology that reflects
865 the duration that high-quality forage is available (i.e., length of spring green-up; Fig. 8, 11B),
866 indicating that all populations were near nutritional carrying capacity. Calf recruitment during
867 the current year was influenced by weather conditions experienced during the previous two years
868 (Fig. 8, Table 3). The low mass-specific metabolic rate and slow life-history of large herbivores
869 facilitates carryover of nutritional reserves from season to season and year to year (Mautz et al.
870 1978, Parker et al. 2009, Harrison et al. 2011), indicating that recruitment is influenced by the
871 weather and foraging conditions experienced one and two years prior to estimates of recruitment
872 (Parker et al. 2009, Monteith et al. 2014b). With respect recruitment during a given winter,
873 lactation and maternal care during the previous summer (i.e., during the neonate stage) is
874 determined by both forage quality and the nutritional reserves of dams (Taillon et al. 2013).
875 Pregnancy, however, is largely determined by summer forage quality and hence autumn nutrition

876 of dams two years prior to a given estimate of recruitment (Cook et al. 2004). In the
877 Intermountain West, calf recruitment declined as snow water equivalent accumulated (i.e. as
878 winter became more severe) the year prior to recruitment estimates (Fig. 11A). Recruitment
879 increased, however, as the length in which high-quality spring forage was available (Fig. 11B).
880 Further, average recruitment (i.e. the intercept for each herd in figures 11A and 11B) in a region
881 was associated with regional differences in climate (i.e., average weather over the past 10 to 20
882 years), indicating that much of the variation in calf recruitment among populations stemmed
883 from different local carrying capacities determined by regional climate. Hence, variation in calf
884 recruitment across the southern extent of moose range emerged from both regional differences in
885 climate that determined long-term nutritional carrying capacity as well as density-dependent
886 declines in nutritional condition that caused populations to be sensitive to density-independent
887 factors (i.e., weather; Fig 1).
888 Female large herbivores prioritize adult survival over reproduction (Bårdsen et al. 2011,
889 Monteith et al. 2013), resulting in population growth rates being strongly influenced by calf
890 recruitment even in harvested populations (Gaillard et al. 1998, Gaillard et al. 2000, Eberhardt
891 2002). For this reason, managers have adopted calf recruitment surveys as a monitoring tool for
892 detecting carrying capacity in large herbivore populations (Fig. 1A). Nevertheless, lag effects
893 between weather and calf production refute the notion that declines in calf recruitment can be
894 used as an 'early warning' for declines in population size (Fig. 1B). Because nutrition lies at the
895 nexus between density-dependent (i.e., per capita resource availability) and density-independent
896 (i.e., weather conditions), declines in habitat and nutritional condition may serve as more
897 appropriate early warning signal (Fig. 1A). By applying a suite of field, laboratory, and remote-
898 sensing tools to a framework derived from life-history theory and nutritional ecology, I offer a

899 “management paradigm” wherein measures of browse (or grazing) conditions, diet quality,
900 nutritional condition, pregnancy, and climate and weather can be combined to provide a low-cost
901 means for monitoring resource limitation and nutritional carrying capacity.

902 **Table 1.** Names of microsatellite (ms) and sex identification markers, their primer sequences, GenBank accession number, and the
903 references from which marker information was derived.
904

Marker	**Type**	**Forward** 5'-3'	**Reverse** 5'-3'	**GenBank Accession #**	**Reference**
BL42	ms	CAAGGTCAAGTCCAAATGCC	GCATTTTTGTGTTAATTTCATGC	DQ136013	Bishop et al. (1994)
BM1225	ms	TTTCTCAACAGAGGTGTCCAC	ACCCCTATCACCATGCTCTG	DQ136013	Bishop et al. (1994)
BM203	ms	GGGTGTGACATTTTGTTCCC	CTGCTCGCCACTAGTCCTTC	DQ136013	Bishop et al. (1994)
BM2830	ms	AATGGGCGTATAAACACAGATG	TGAGTCCTGTCACCATCAGC	DQ136013	Bishop et al. (1994)
BM4513	ms	GCGCAAGTTTCCTCATGC	TCAGCAATTCAGTACATCACCC	DQ136013	Bishop et al. (1994)
BM848	ms	TGGTTGGAAGGAAAACTTGG	CCTCTGCTCCTCAAGACAC	DQ136013	Bishop et al. (1994)
BM888	ms	AGGCCATATAGGAGGCAAGCTT	CTCGGTGAGCTCAAAACGAG	DQ136013	Bishop et al. (1994)
BM4208	ms	TCAGTACACTGGCCACCATG	CACTGCATGCTTTTCCAAAC	DQ136013	Bishop et al. (1994)
FCB193	ms	TTCATCTCAGACTGGGATTCAGAAAGGC	GCTTGGAAATAACCCTCCTGCATCCC	LO1533	Buchanan and Crawford (1993)
KY1/KY2	sex ID	GCCCAGCAGCCCTTCCAG	TGGCCAAGCTTCCAGAGGCA	FJ434496, FJ434497	Brinkman and Hundertmark (2008)

905

906 **Table 2.** Type and frequency of genotyping error rates for multilocus genotypes established from
907 moose feces. Allelic dropout indicates when an animal that is heterozygous at a given locus is
908 genotyped as a homozygote (i.e., one allele 'drops out'). False alleles indicate individuals that a
909 truly homozygous individual is genotyped as a heterozygote. Homozygous allele shifts signify
910 base pair additions that occur during the PCR process.
911
912

Population	Locus	Dropout	False Allele	Homozygote Allele Shift	Population	Locus	Dropout	False Allele	Homozygote Allele Shift
Bighorn	KY	0.059	0.000	0.000	*Snowy Range*	KY	0.000	0.000	0.000
	BM2830	0.125	0.440	0.000		BM2830	0.093	0.022	0.000
	BL42	0.000	0.080	0.000		BL42	0.010	0.045	0.000
	FCB193	0.000	0.000	0.000		FCB193	0.000	0.014	0.000
	BM4208	0.000	0.000	0.000		BM4208	0.024	0.000	0.000
	BM848	0.000	0.077	0.000		BM848	0.018	0.000	0.000
	BM4513	0.017	0.000	0.000		BM4513	0.010	0.000	0.000
	BM203	0.000	0.000	0.000		BM203	0.000	0.000	0.000
	BM888	0.000	0.000	0.000		BM888	0.015	0.000	0.000
	BM1225	0.000	0.000	0.000		BM1225	0.000	0.038	0.013
Jackson	KY	0.027	0.000	0.000	*Sublette*	KY	0.000	0.000	0.000
	BM2830	0.026	0.021	0.000		BM2830	0.192	0.006	0.000
	BL42	0.005	0.083	0.000		BL42	0.000	0.000	0.000
	FCB193	0.000	0.014	0.000		FCB193	0.000	0.000	0.000
	BM4208	0.000	0.000	0.000		BM4208	0.060	0.023	0.000
	BM848	0.019	0.048	0.000		BM848	0.011	0.091	0.000
	BM4513	0.013	0.022	0.000		BM4513	0.000	0.000	0.000
	BM203	0.107	0.021	0.007		BM203	0.000	0.000	0.000
	BM888	0.026	0.000	0.000		BM888	0.000	0.014	0.000
	BM1225	0.041	0.028	0.000		BM1225	0.036	0.000	0.000
North Park	KY	0.017	0.022	0.000	*Uinta*	KY	0.000	0.000	0.000
	BM2830	0.000	0.018	0.011		BM2830	0.039	0.000	0.000
	BL42	0.021	0.000	0.000		BL42	0.000	0.063	0.000
	FCB193	0.077	0.000	0.000		FCB193	0.000	0.000	0.000
	BM4208	0.080	0.047	0.000		BM4208	0.000	0.000	0.000
	BM848	0.000	0.000	0.000		BM848	0.000	0.000	0.033
	BM4513	0.020	0.000	0.058		BM4513	0.000	0.000	0.000
	BM203	0.000	0.019	0.000		BM203	0.000	0.000	0.000
	BM888	0.400	0.000	0.000		BM888	0.000	0.000	0.019
	BM1225	0.000	0.000	0.000		BM1225	0.000	0.000	0.000

913

914 **Table 3.** Number of alleles per locus and their size range.

915

Locus	Range	Alleles
BL42	256-264	6
BM1225	231-247	4
BM203	231-242	6
BM2830	104-110	4
BM4513	128-138	6
BM848	343-363	6
BM888	187-192	3
BM4208	139-169	6
FCB193	105-123	6
KY1	210	1
KY2	174	1

916

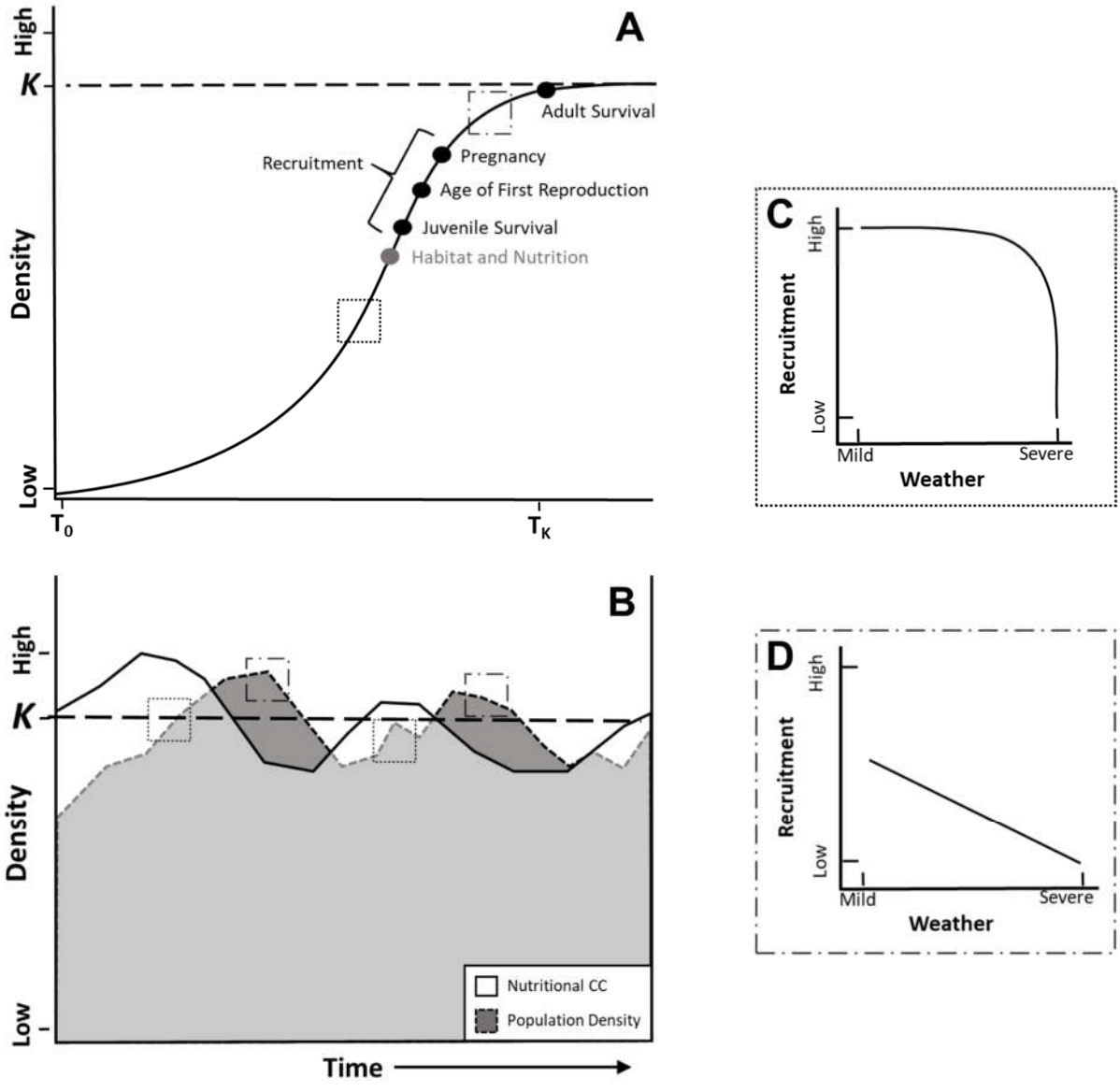
Table 4. Number of individual moose identified per herd, per season via fecal DNA.

Herd	Summer		Winter		Total
	M	F	M	F	
Jackson	2	1	11	13	27
Sublette	3	8	5	5	21
Bighorn	11	15	19	5	50
Snowy Range	9	9	1	4	23
Uinta	15	14	7	7	43
North Park	8	9	8	8	33

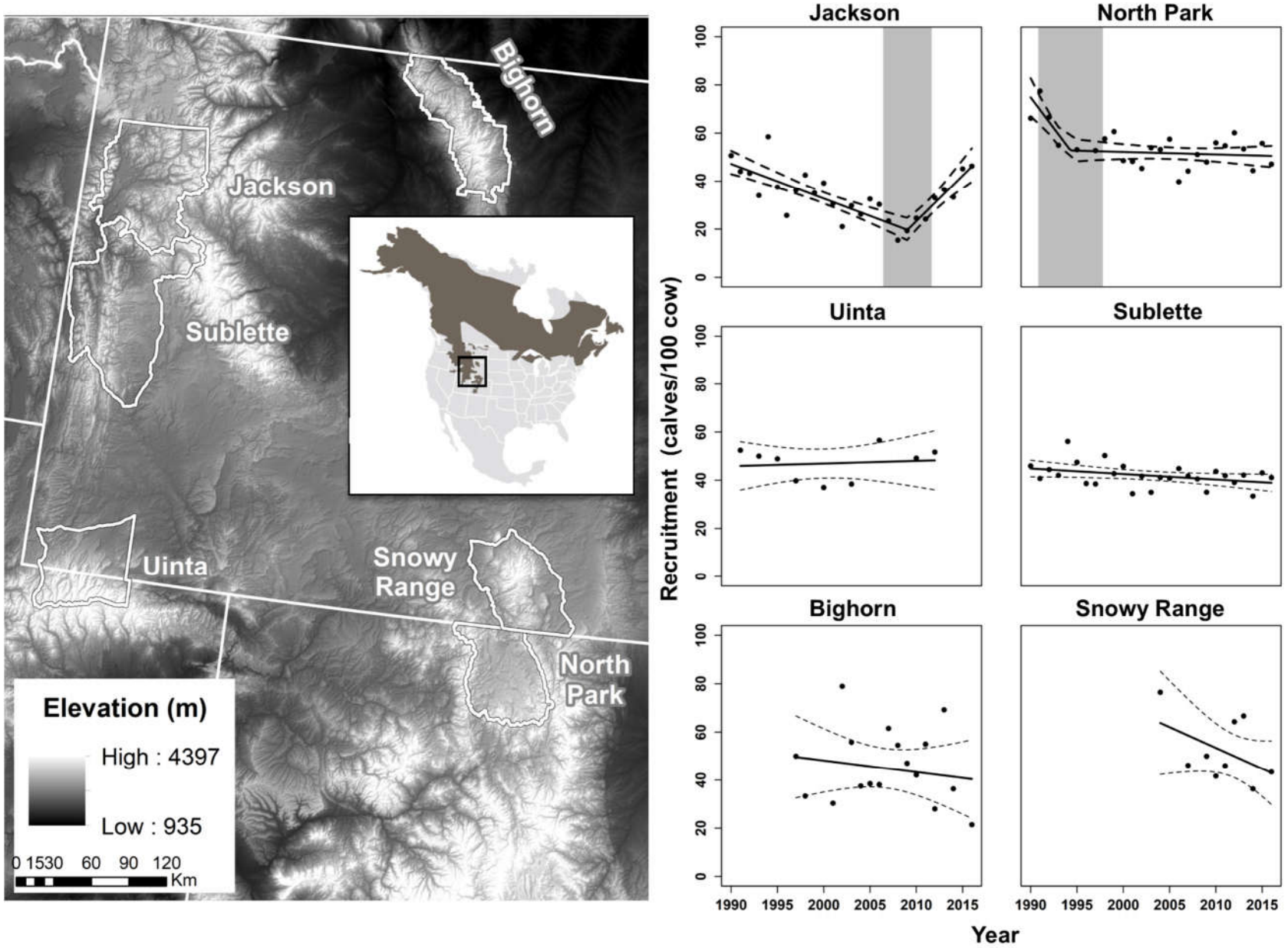
Table 5. Model-averaged parameter estimates, 95% confidence intervals, p-values, and model importance weights from models describing the effects of climate and inter-annual variation in weather on calf recruitment. A full list of a priori models can be found in Table S3.

Parameter	Estimate	95% CI		p-value	Importance Weight
		lower	upper		
Winter Severity (SWE) $_{t-1}$	-5.61	-8.02	-3.20	<0.001	1.00
Spring Length $_{t-1}$	4.47	1.82	7.11	<0.001	1.00
Drought (PDSI) $_{t-1}$	1.60	-0.98	4.18	0.22	0.77
Plant Biomass (iNDVI) $_{t-1}$	0.90	-1.83	3.62	0.52	0.44
Plant Biomass (iNDVI) $_{t-2}$	-0.34	-2.05	1.38	0.70	0.20

Fig. 1. Conceptual figure illustrating (A) the life history paradigm for long-lived vertebrates (black text; Bonenfant et al. 2002, Eberhardt 2002), wherein a sequence of declines in life-history traits are expected to occur as populations approach carrying capacity (*K*), and (B) the dynamism of nutritional carrying capacity and its contrast to classical carrying capacity (*K*; McCullough 1999). Panel A has been modified to include habitat and nutrition (gray text) as factors that influence variation in life history, thereby providing a "management paradigm" for large herbivores. When a population is below carrying capacity (C; dotted boxes), individuals have ample nutritional reserves and recruitment and other vital rates are buffered from the negative effects of severe weather. In contrast, when populations are at or above carrying capacity (D; dashed boxes), individuals have relatively few nutritional reserves and vital rates are sensitive to weather conditions.



939 **Fig. 2.** Study region (left) and trends in calf recruitment from 1990 to present across the study area (right). Vertical grey polygons
940 illustrate 95% confidence intervals for a change in slope estimated from piecewise regression.
941



942

Fig 3. Biplot of principal components analysis (PCA). Three PCA axes combined to explain 62% of the variation in climate across the region. PC1 accounted for 24.1% of the variation and reflected inter-annual variation in temperature and precipitation, which were strongly and negatively correlated (Fig. S9). PC2 explained 21.5% of the variation and described phenology, specifically the length of spring, which was highly and negatively correlation with higher spring temperature (Fig. S9). PC3 accounted for 16.3% of variation and provided a measure of drought as quantified by the Palmer Drought Severity Index (PDSI) and overwinter snowpack as measured by cumulative snow water equivalent (SWE), which were not correlated.

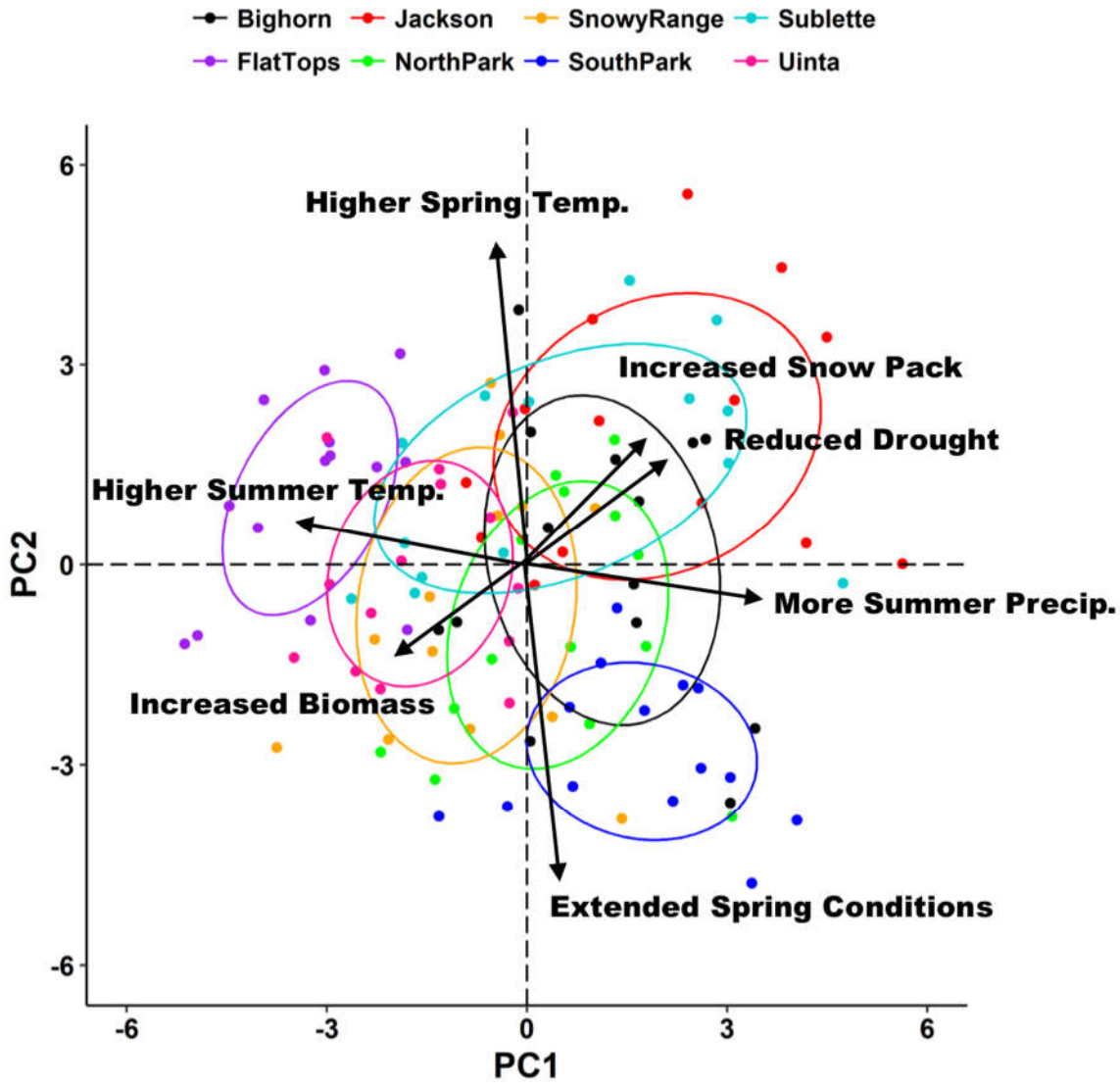
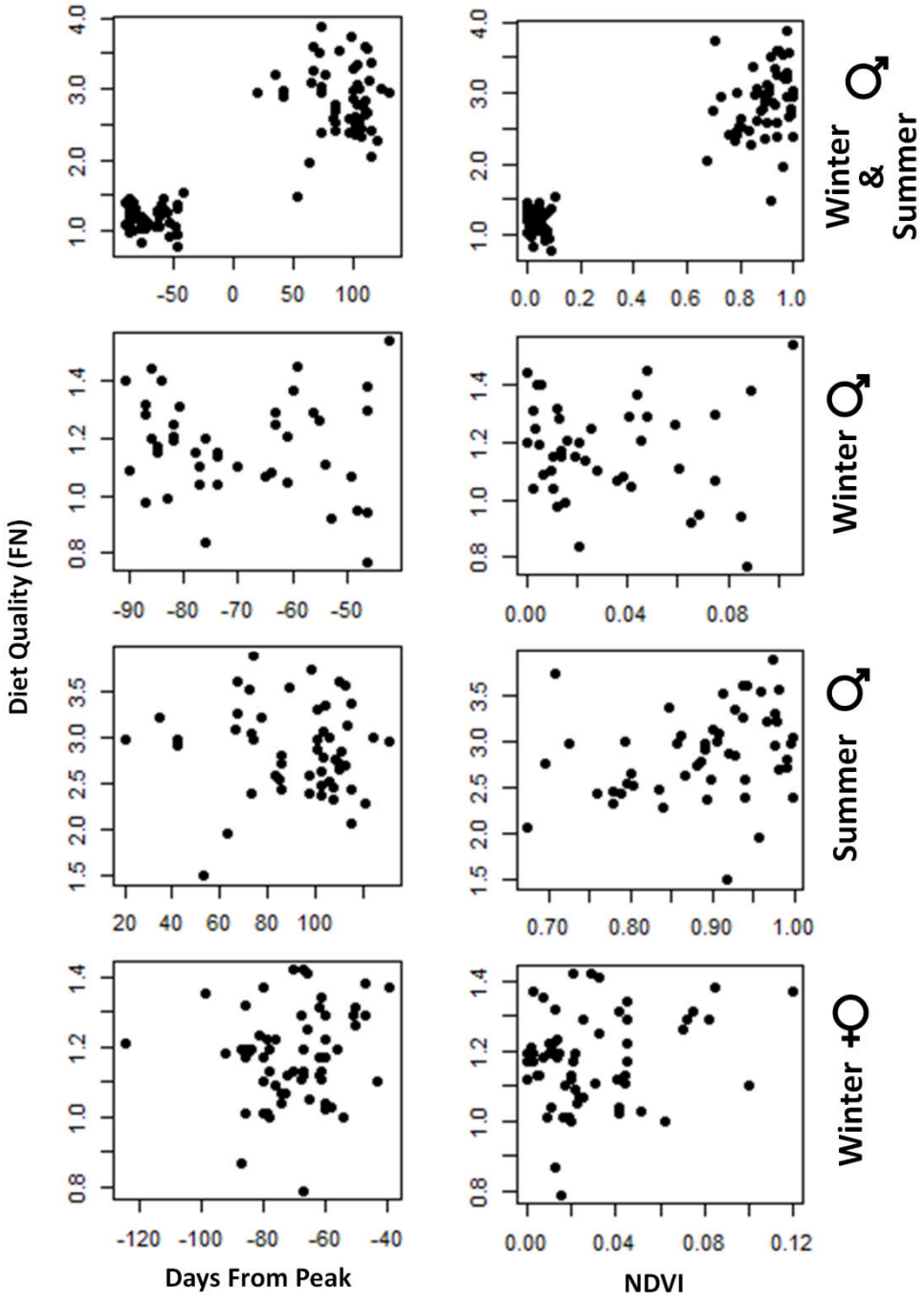
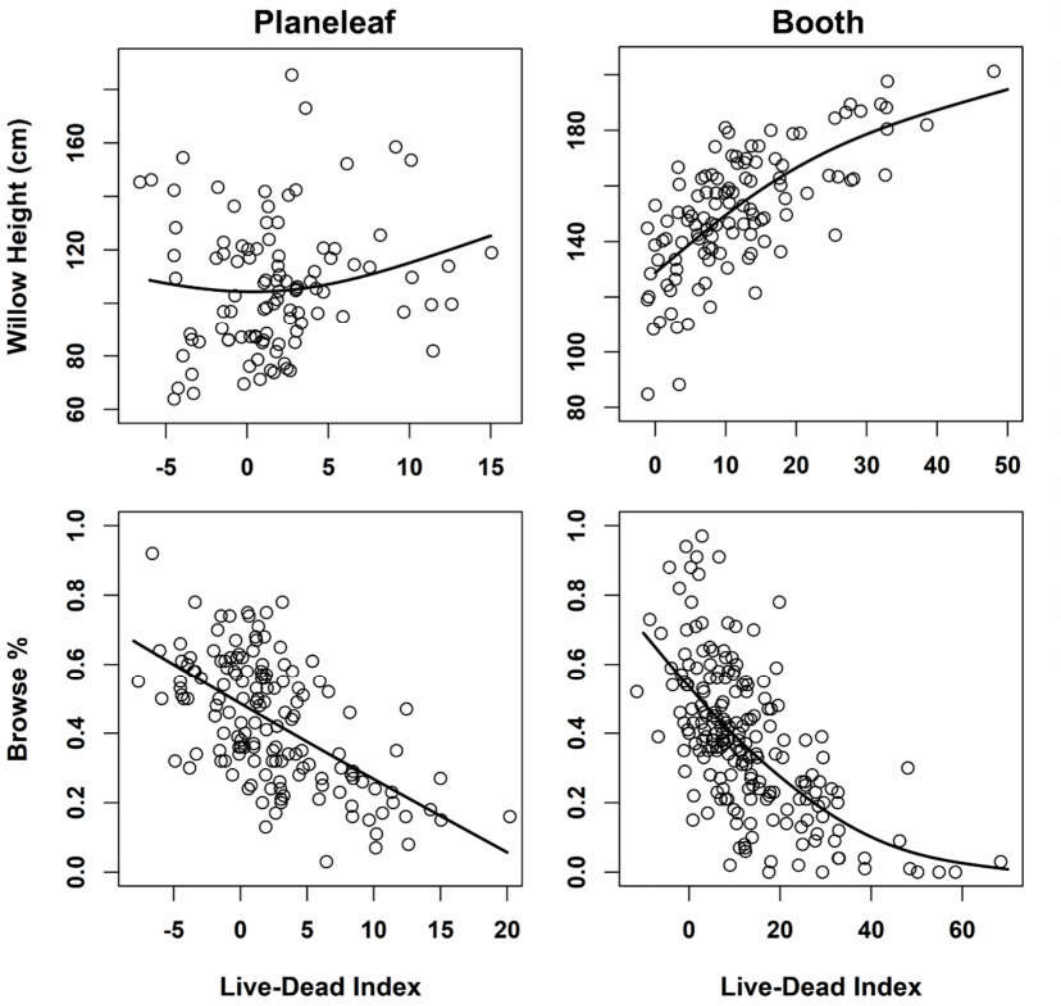


Fig 4. Relationship between the seasonal diet quality (fecal nitrogen) and plant phenology as measured by the normalized difference vegetation index (NDVI; right panels) and days from peak rate of vegetation green-up (left panels). Forage quality is highest when days from peak rate of green-up equals zero. Because fecal samples were collected during the middle of winter (days from peak green up < 40) and after peak summer green-up (days from peak green up > 20), no relationship between diet quality and phenology was detected (all P>0.05).



961 **Fig 5.** Relationship between the live-dead Index and alternative measures of browse condition
962 such as willow height and percent browsed stems. Because planeleaf willow (*Salix planifolia*)
963 and Booth willow (*Salix boothii*) have different growth forms and compensatory growth rates,
964 data for the two species are presented separately. Alternative measures of browse condition, such
965 as willow height and percent stems browsed, provide managers with simpler, alternative
966 measures of resource limitation.
967



968

Fig 6. Relationship between male (A, B; n = 321) and female (C, D; n = 102) kidney fat index, progression of the breeding season (i.e., date of harvest), and age according to tooth cementum annuli.

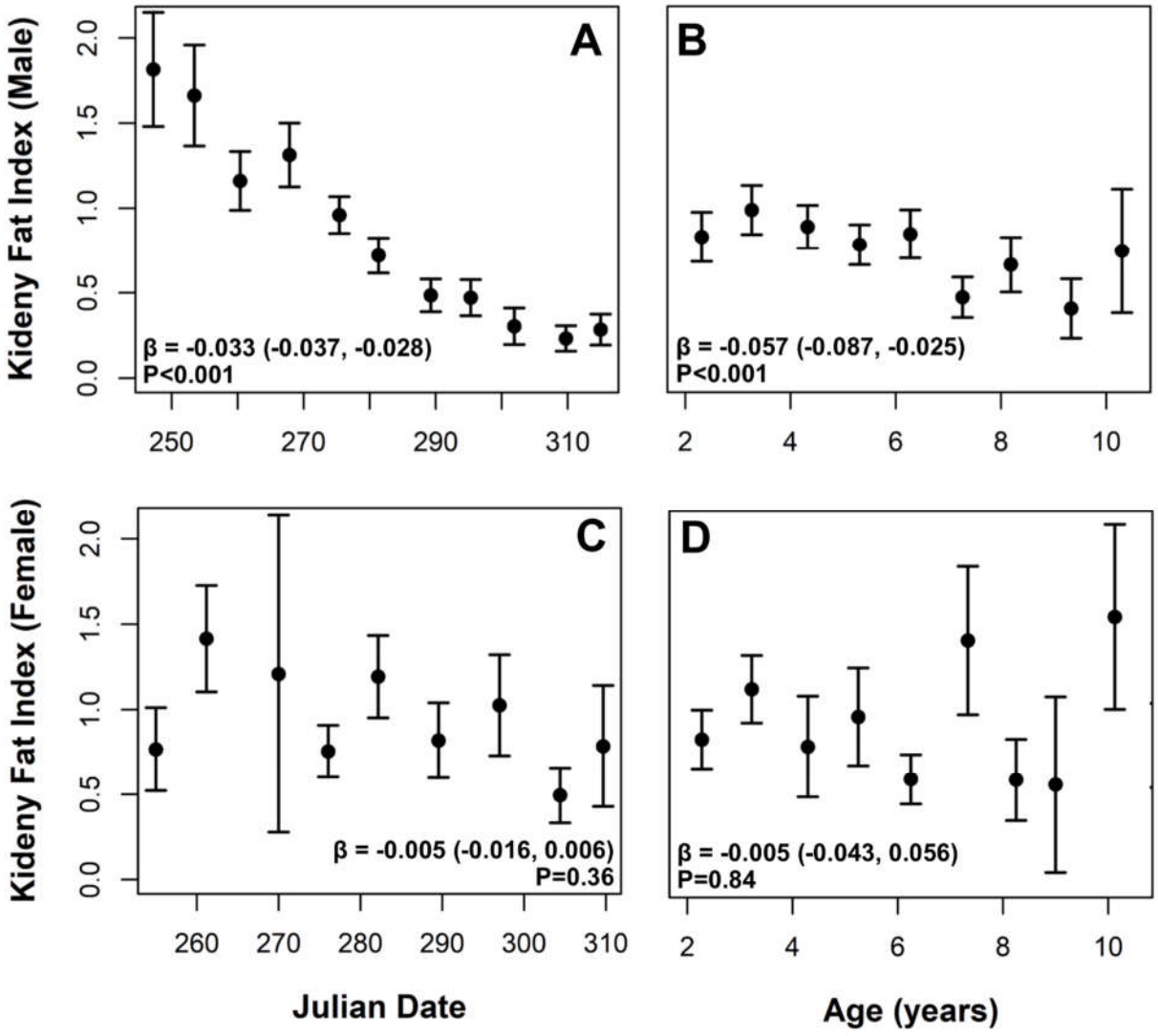


Fig 7. Relationship between (A) fecal progestagens and pregnancy, (B) nutritional condition of females and pregnancy, (C) pregnancy status and nutritional condition, and (D) nutritional condition and population growth rate. (A) Red dashed line represents the CART-based threshold in fecal progestagens (2291.3 ng/g) for determining pregnancy. The grey polygon is the Monte Carlo-based 95% confidence interval (1340.9 ng/g to 3344.9 ng/g) for the threshold. By excluding samples whose fecal progestagen values fell within the bounds of the grey polygon, 93% accuracy was achieved because false negative and false positives were reduced. (B) Red dashed line represents a threshold in nutritional condition (5.3% ingesta-free body fat) beyond which probability of pregnancy is great. (D) Red dashed lines indicate the population-level nutritional condition at which population growth is stable (i.e., nutritional carrying capacity) for mule deer (*Odocoileus hemionus*) in the central Sierra Nevada of California, USA (Monteith et al. 2014b). Note that panel D should be used as a heuristic for moose rather than an empirical example. The threshold at which stable population growth is achieved falls within the 95% confidence interval (4.2% to 6.4% IFBFat) for the threshold in nutritional condition that females must reach to become pregnant (panel B). Thus, pregnancy estimates stemming from fecal progestagen can be linked directly to population growth rate.

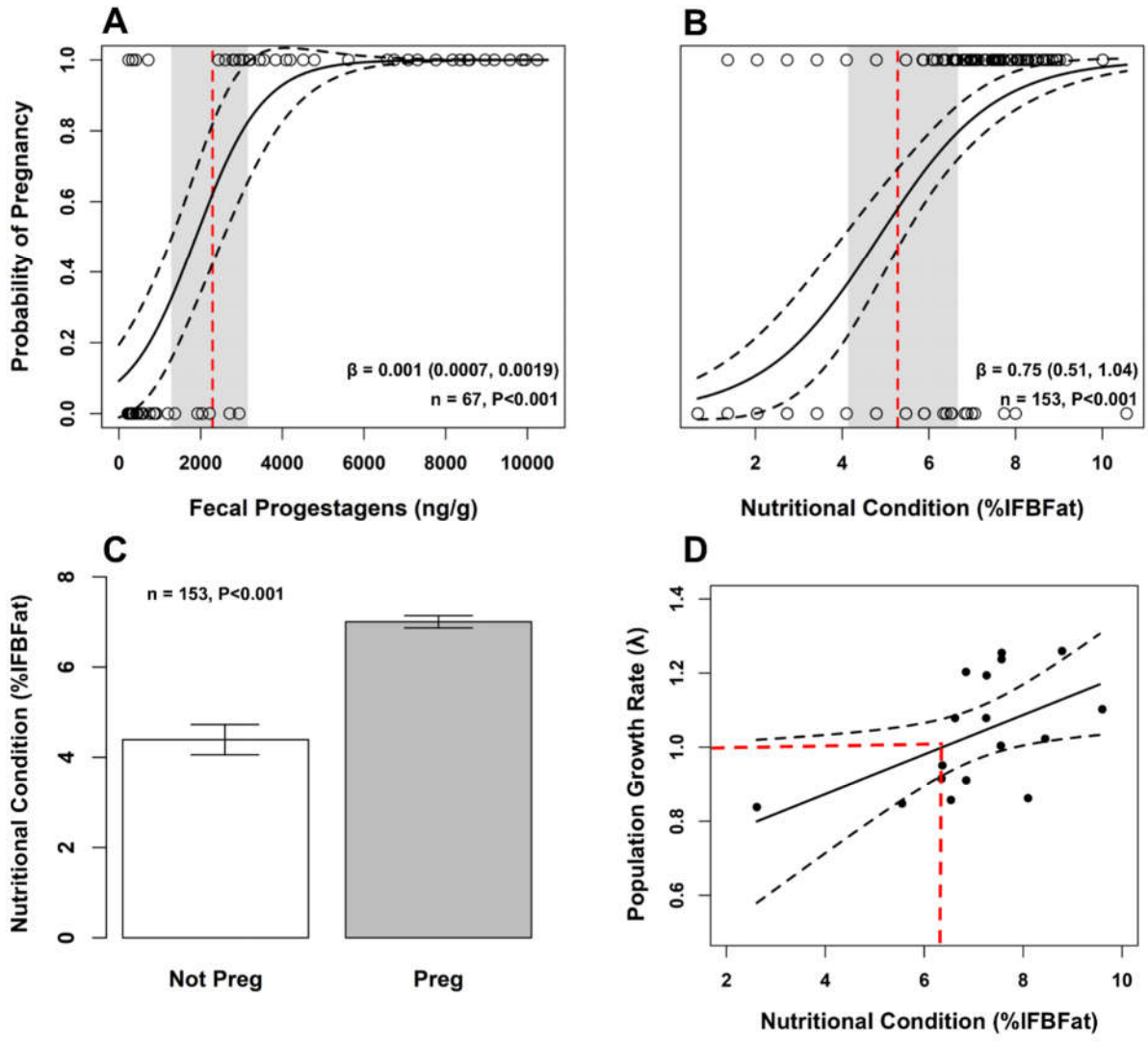


Fig. 8. Path diagram illustrating the nutritional ecology of moose. Arrow size depicts strength of relationship as estimated by standardized partial coefficients. Arrow color indicates statistical significance (black) or lack thereof (grey) at alpha=0.95. Solid boxes detail the pathway by which climate effects recruitment through pregnancy. In contrast, dashed-line boxes demonstrate the pathway by with climate influences recruitment by affecting energy and nutrients available for lactation. Time step t refers to the current year, whereas time steps t-1 and t-2 refer to one and two years prior to current year recruitment estimate. The SEM explained 69% of variation observed in annual recruitment, 43% of variation in annual pregnancy rates, and ~90% of variation in autumn nutrition (see table S2 for parameter estimates and goodness of fit measures).

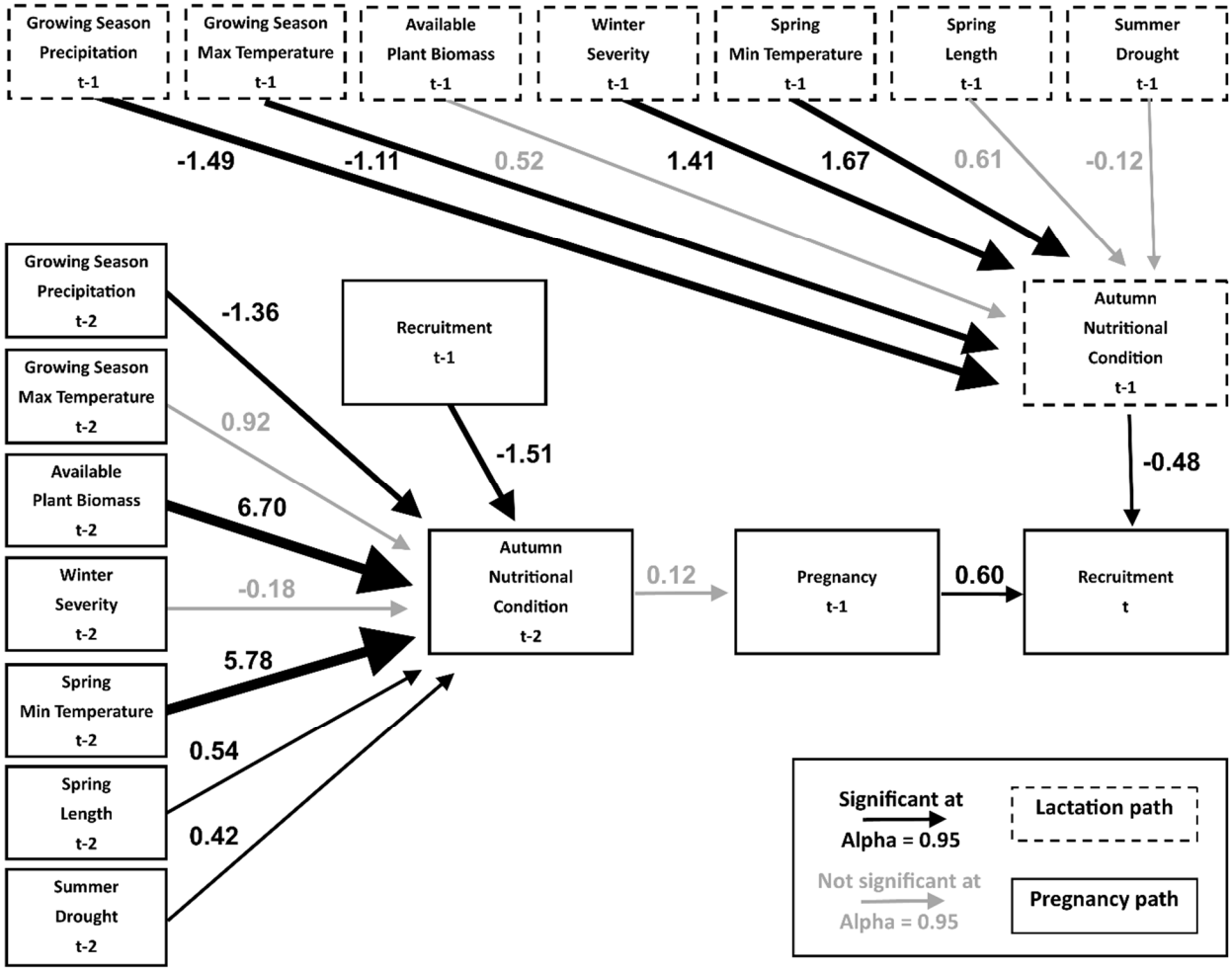


Fig 9. Path diagram illustrating the influence of weather on (A) summer diet quality (fecal nitrogen) of males, (B) winter diet quality of males, and (C) winter diet quality of females. Arrow size depicts strength of relationship as estimated by standardized partial coefficients. Arrow color indicates statistical significance (black) or lack thereof (grey) at alpha=0.95.

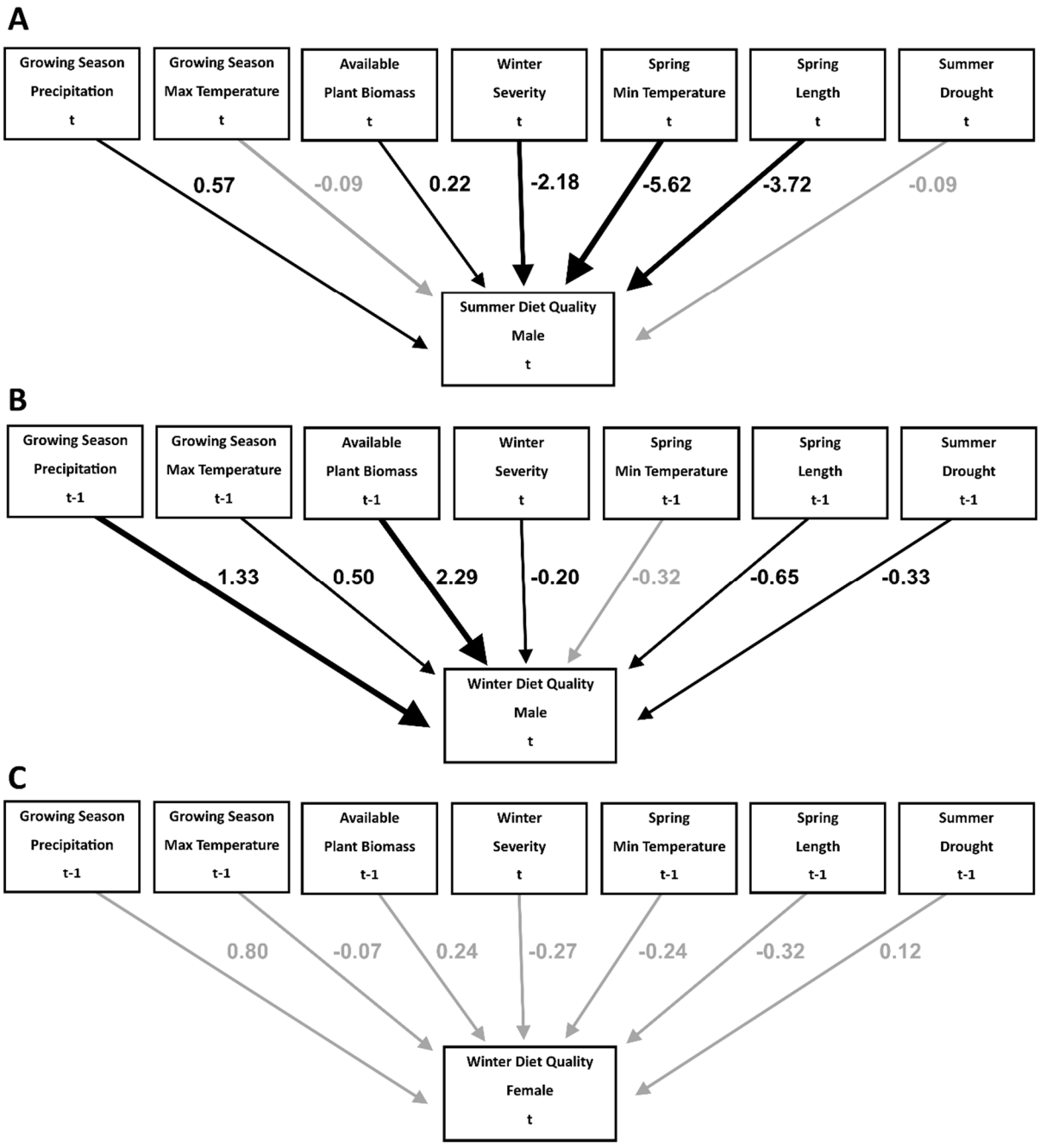


Fig 10. Relationship between summer diet quality (fecal nitrogen) of males and population-level (A) calf recruitment, (B) pregnancy, and (C) autumn nutritional condition of females. (D) The relationship between pregnancy and calf recruitment, and (E) browse condition (live-dead Index) and calf recruitment. Correlation coefficients (*r*) and permuted 80% confidence intervals and p-values. Solid lines and grey polygons represent predicted relationships and 80% confidence intervals stemming from ordinary regression. Together, these relationships provide a suite of tools that can be used to measure resource limitation and thus proximity to nutritional carrying capacity.

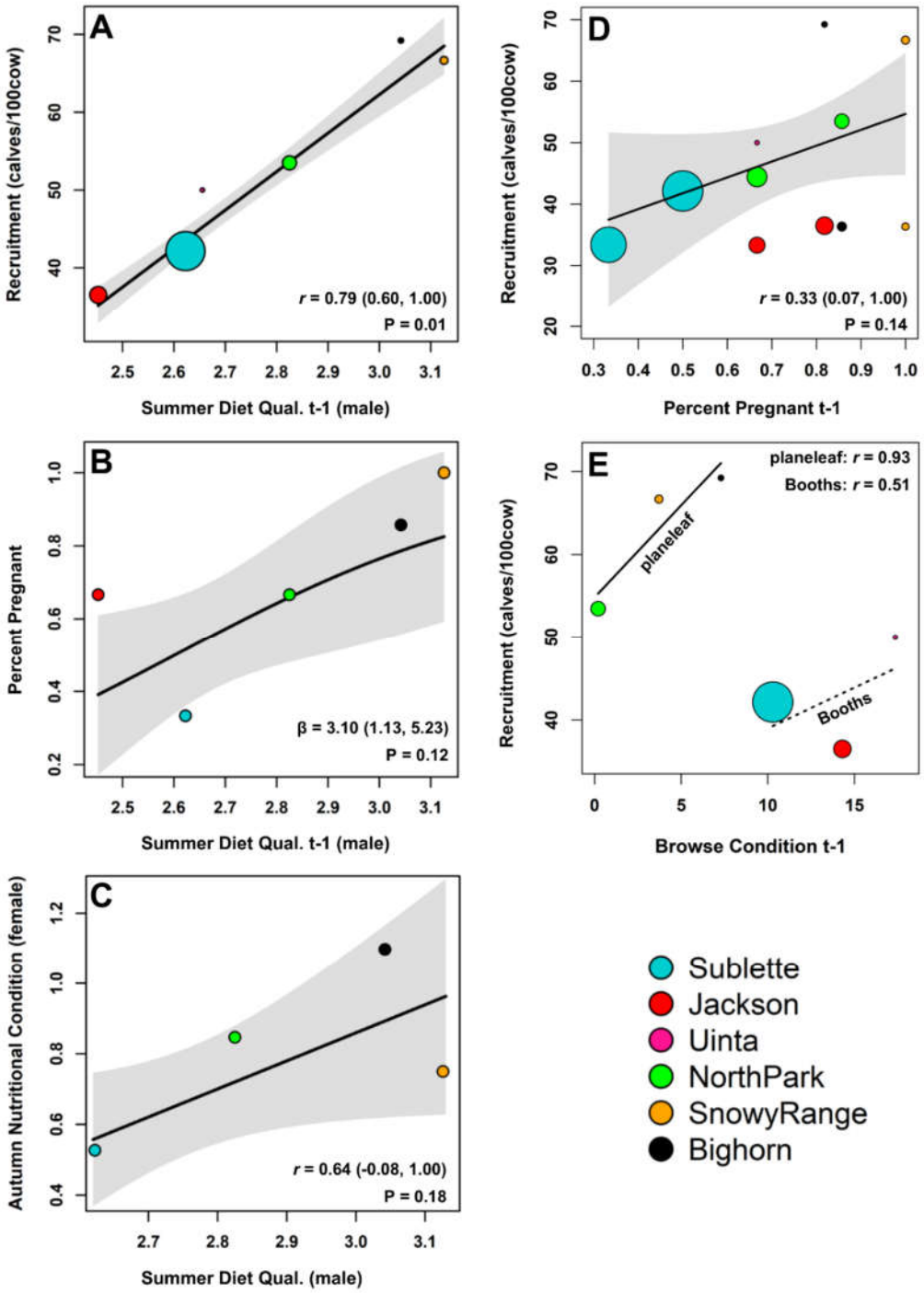
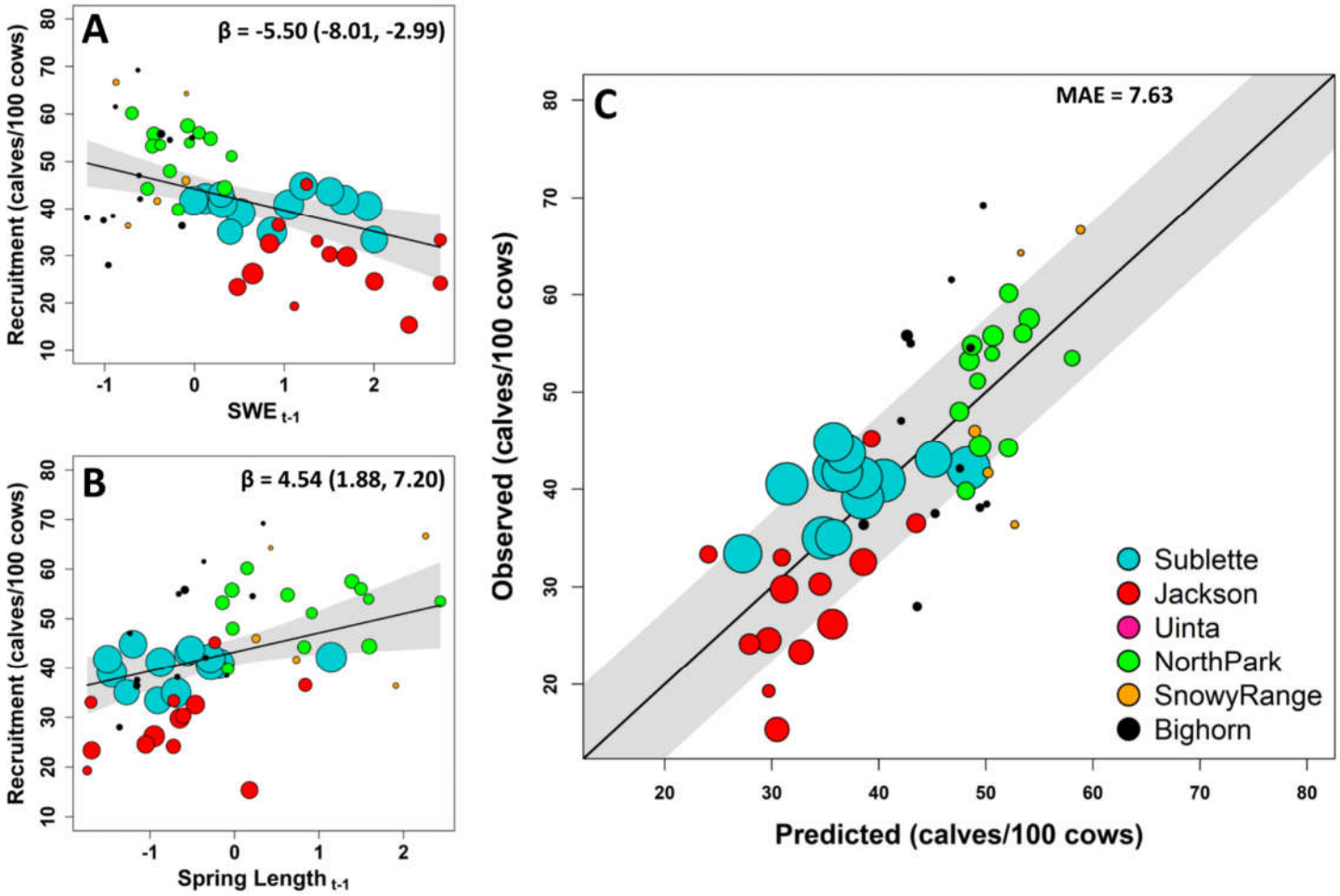


Fig 11. Effects sizes of (A) winter severity, and (B) plant phenology. Slope coefficients (β) and 95% confidence intervals are provided. Panel (C) illustrates the predictive power of model averaged equation (Table 1). Circle size reflects confidence (number of cows surveyed) in the observed estimates of calf recruitment (sample size used to estimate calf recruitment varied markedly). The solid line is a 1:1 line representing perfect predictability. Grey polygon depicts the mean absolute error (+\- 7.63 calves per 100 cows) of model predictions according to leave-one-out cross validation. The Recruitment within a population varied with inter-annual variation in weather and average recruitment varied with regional climate (i.e., long-term (10-20 yr) average weather conditions).



APPENDIX S1

Table S1. Multiplex PCR conditions used for microsatellite analysis of individual and sex identification of moose (*Alces alces*).

Regent (concentration)	**volume (µl)**
Water	0.700
Qiagen MM (2X)	4.500
Q_Sol (5X)	2.000
BM4513F (20µM)	0.075
BM4513R (20µM)	0.075
BM4208F (20µM)	0.075
BM4208R (20µM)	0.075
BL42F (20µM)	0.075
BL42R (20µM)	0.075
BM888F (20µM)	0.075
BM888R (20µM)	0.075
FCB193F (20µM)	0.075
FCB193R (20µM)	0.075
KY1 (20µM)	0.075
KY2 (20µM)	0.075
BM203F (20µM)	0.125
BM203R (20µM)	0.125
BM848F (20µM)	0.125
BM848R (20µM)	0.125
BM1225F (20µM)	0.150
BM1225R (20µM)	0.150
BM2830F (10µM)	0.050
BM2830R (10µM)	0.050
DNA	1.000
Total	**10.000**

Table S2. Partial coefficient estimates (~) and covariance (~~) between all variables in the structural equation model depicting the nutritional ecology of moose (Fig. 8). Standard errors, z-scores, p-values and confidence intervals are provided.

Dependent	op	Independent	est	se	z	pvalue	ci.lower	ci.upper
juv100fem	~	t1_preg	0.604	0.150	4.034	0.000	0.311	0.898
t1_preg	~	t2_fat_mean_f	0.118	0.100	1.182	0.237	-0.078	0.313
t2_fat_mean_f	~	t1_juv100fem	-1.513	0.380	-3.978	0.000	-2.259	-0.768
t2_fat_mean_f	~	s2_mean_spr_len	0.536	0.213	2.516	0.012	0.118	0.953
t2_fat_mean_f	~	s2_mean_spr_tmin	5.776	0.919	6.282	0.000	3.974	7.578
t2_fat_mean_f	~	s2_cum_wint_swe	-0.118	0.475	-0.247	0.805	-1.049	0.814
t2_fat_mean_f	~	s2_cum_summ_pdsi	0.418	0.209	1.997	0.046	0.008	0.829
t2_fat_mean_f	~	s2_mean_sumNDVI	6.697	1.323	5.062	0.000	4.104	9.290
t2_fat_mean_f	~	s2_mean_grow_tmax	0.916	0.494	1.852	0.064	-0.053	1.884
t2_fat_mean_f	~	s2_cum_grow_prcp	-1.363	0.659	-2.069	0.039	-2.654	-0.072
juv100fem	~	t1_fat_mean_f	-0.480	0.150	-3.208	0.001	-0.773	-0.187
t1_fat_mean_f	~	s1_mean_spr_len	0.611	0.354	1.725	0.085	-0.083	1.305
t1_fat_mean_f	~	s1_mean_spr_tmin	1.666	0.736	2.262	0.024	0.223	3.108
t1_fat_mean_f	~	s1_cum_wint_swe	1.407	0.460	3.062	0.002	0.506	2.308
t1_fat_mean_f	~	s1_cum_summ_pdsi	-0.122	0.208	-0.587	0.557	-0.528	0.285
t1_fat_mean_f	~	s1_mean_sumNDVI	0.518	0.656	0.789	0.430	-0.768	1.803
t1_fat_mean_f	~	s1_mean_grow_tmax	-1.109	0.449	-2.469	0.014	-1.990	-0.229
t1_fat_mean_f	~	s1_cum_grow_prcp	-1.487	0.615	-2.418	0.016	-2.692	-0.282
juv100fem	~~	juv100fem	0.417	0.207	2.012	0.044	0.011	0.823
t1_preg	~~	t1_preg	1.203	0.573	2.100	0.036	0.080	2.326
t2_fat_mean_f	~~	t2_fat_mean_f	0.125	0.054	2.328	0.020	0.020	0.229
t1_fat_mean_f	~~	t1_fat_mean_f	0.443	0.211	2.098	0.036	0.029	0.857
t1_juv100fem	~~	t1_juv100fem	1.286	0.311	4.132	0.000	0.676	1.896
t1_juv100fem	~~	s2_mean_spr_len	0.498	0.223	2.236	0.025	0.062	0.935
t1_juv100fem	~~	s2_mean_spr_tmin	-0.380	0.182	-2.092	0.037	-0.736	-0.024
t1_juv100fem	~~	s2_cum_wint_swe	-0.801	0.247	-3.241	0.001	-1.286	-0.317
t1_juv100fem	~~	s2_cum_summ_pdsi	-0.212	0.185	-1.142	0.254	-0.575	0.152
t1_juv100fem	~~	s2_mean_sumNDVI	0.403	0.202	1.994	0.046	0.007	0.799
t1_juv100fem	~~	s2_mean_grow_tmax	0.080	0.160	0.504	0.614	-0.232	0.393
t1_juv100fem	~~	s2_cum_grow_prcp	-0.300	0.180	-1.668	0.095	-0.653	0.053
t1_juv100fem	~~	s1_mean_spr_len	0.366	0.217	1.688	0.091	-0.059	0.791
t1_juv100fem	~~	s1_mean_spr_tmin	-0.311	0.165	-1.887	0.059	-0.635	0.012
t1_juv100fem	~~	s1_cum_wint_swe	-0.685	0.233	-2.944	0.003	-1.140	-0.229
t1_juv100fem	~~	s1_cum_summ_pdsi	-0.266	0.204	-1.302	0.193	-0.666	0.134
t1_juv100fem	~~	s1_mean_sumNDVI	0.306	0.208	1.469	0.142	-0.102	0.714
t1_juv100fem	~~	s1_mean_grow_tmax	0.029	0.156	0.188	0.851	-0.277	0.336
t1_juv100fem	~~	s1_cum_grow_prcp	-0.133	0.174	-0.762	0.446	-0.473	0.208
s2_mean_spr_len	~~	s2_mean_spr_len	1.107	0.248	4.472	0.000	0.622	1.592

s2_mean_spr_len	~~	s2_mean_spr_tmin	-0.776	0.187	-4.138	0.000	-1.143	-0.408
s2_mean_spr_len	~~	s2_cum_wint_swe	-0.506	0.205	-2.463	0.014	-0.908	-0.103
s2_mean_spr_len	~~	s2_cum_summ_pdsi	-0.401	0.179	-2.242	0.025	-0.751	-0.050
s2_mean_spr_len	~~	s2_mean_sumNDVI	0.104	0.158	0.660	0.509	-0.205	0.413
s2_mean_spr_len	~~	s2_mean_grow_tmax	-0.117	0.134	-0.874	0.382	-0.381	0.146
s2_mean_spr_len	~~	s2_cum_grow_prcp	0.005	0.146	0.035	0.972	-0.282	0.292
s2_mean_spr_len	~~	s1_mean_spr_len	0.546	0.195	2.797	0.005	0.164	0.929
s2_mean_spr_len	~~	s1_mean_spr_tmin	-0.269	0.142	-1.898	0.058	-0.547	0.009
s2_mean_spr_len	~~	s1_cum_wint_swe	-0.254	0.188	-1.348	0.178	-0.623	0.115
s2_mean_spr_len	~~	s1_cum_summ_pdsi	-0.122	0.182	-0.672	0.501	-0.479	0.234
s2_mean_spr_len	~~	s1_mean_sumNDVI	-0.296	0.170	-1.742	0.082	-0.628	0.037
s2_mean_spr_len	~~	s1_mean_grow_tmax	-0.048	0.136	-0.355	0.722	-0.314	0.218
s2_mean_spr_len	~~	s1_cum_grow_prcp	0.213	0.151	1.409	0.159	-0.083	0.510
s2_mean_spr_tmin	~~	s2_mean_spr_tmin	0.726	0.162	4.472	0.000	0.408	1.044
s2_mean_spr_tmin	~~	s2_cum_wint_swe	0.429	0.167	2.560	0.011	0.101	0.757
s2_mean_spr_tmin	~~	s2_cum_summ_pdsi	0.273	0.142	1.919	0.055	-0.006	0.551
s2_mean_spr_tmin	~~	s2_mean_sumNDVI	-0.100	0.128	-0.785	0.433	-0.351	0.150
s2_mean_spr_tmin	~~	s2_mean_grow_tmax	0.155	0.110	1.400	0.162	-0.062	0.371
s2_mean_spr_tmin	~~	s2_cum_grow_prcp	-0.018	0.119	-0.149	0.881	-0.250	0.215
s2_mean_spr_tmin	~~	s1_mean_spr_len	-0.430	0.157	-2.733	0.006	-0.738	-0.122
s2_mean_spr_tmin	~~	s1_mean_spr_tmin	0.217	0.115	1.887	0.059	-0.008	0.442
s2_mean_spr_tmin	~~	s1_cum_wint_swe	0.218	0.153	1.423	0.155	-0.082	0.518
s2_mean_spr_tmin	~~	s1_cum_summ_pdsi	0.215	0.150	1.428	0.153	-0.080	0.509
s2_mean_spr_tmin	~~	s1_mean_sumNDVI	0.296	0.140	2.110	0.035	0.021	0.571
s2_mean_spr_tmin	~~	s1_mean_grow_tmax	0.000	0.110	0.000	1.000	-0.215	0.215
s2_mean_spr_tmin	~~	s1_cum_grow_prcp	-0.171	0.123	-1.399	0.162	-0.411	0.069
s2_cum_wint_swe	~~	s2_cum_wint_swe	1.292	0.289	4.472	0.000	0.726	1.858
s2_cum_wint_swe	~~	s2_cum_summ_pdsi	0.067	0.181	0.370	0.712	-0.288	0.422
s2_cum_wint_swe	~~	s2_mean_sumNDVI	-0.235	0.173	-1.354	0.176	-0.575	0.105
s2_cum_wint_swe	~~	s2_mean_grow_tmax	0.092	0.144	0.637	0.524	-0.191	0.375
s2_cum_wint_swe	~~	s2_cum_grow_prcp	0.491	0.176	2.791	0.005	0.146	0.836
s2_cum_wint_swe	~~	s1_mean_spr_len	-0.589	0.211	-2.794	0.005	-1.002	-0.176
s2_cum_wint_swe	~~	s1_mean_spr_tmin	0.424	0.161	2.638	0.008	0.109	0.739
s2_cum_wint_swe	~~	s1_cum_wint_swe	0.946	0.249	3.803	0.000	0.458	1.434
s2_cum_wint_swe	~~	s1_cum_summ_pdsi	0.553	0.214	2.583	0.010	0.133	0.972
s2_cum_wint_swe	~~	s1_mean_sumNDVI	-0.237	0.180	-1.317	0.188	-0.591	0.116
s2_cum_wint_swe	~~	s1_mean_grow_tmax	-0.049	0.146	-0.332	0.740	-0.336	0.238
s2_cum_wint_swe	~~	s1_cum_grow_prcp	0.430	0.173	2.485	0.013	0.091	0.770
s2_cum_summ_pdsi	~~	s2_cum_summ_pdsi	1.010	0.226	4.472	0.000	0.567	1.453
s2_cum_summ_pdsi	~~	s2_mean_sumNDVI	-0.284	0.156	-1.816	0.069	-0.590	0.023
s2_cum_summ_pdsi	~~	s2_mean_grow_tmax	-0.180	0.130	-1.385	0.166	-0.436	0.075
s2_cum_summ_pdsi	~~	s2_cum_grow_prcp	0.058	0.140	0.411	0.681	-0.217	0.332

s2_cum_summ_pdsi	~~	s1_mean_spr_len	0.174	0.170	1.028	0.304	-0.158	0.507
s2_cum_summ_pdsi	~~	s1_mean_spr_tmin	-0.270	0.136	-1.984	0.047	-0.537	-0.003
s2_cum_summ_pdsi	~~	s1_cum_wint_swe	-0.005	0.176	-0.030	0.976	-0.350	0.339
s2_cum_summ_pdsi	~~	s1_cum_summ_pdsi	0.022	0.173	0.125	0.901	-0.317	0.360
s2_cum_summ_pdsi	~~	s1_mean_sumNDVI	-0.042	0.156	-0.268	0.789	-0.348	0.264
s2_cum_summ_pdsi	~~	s1_mean_grow_tmax	0.178	0.132	1.341	0.180	-0.082	0.437
s2_cum_summ_pdsi	~~	s1_cum_grow_prcp	-0.388	0.154	-2.525	0.012	-0.689	-0.087
s2_mean_sumNDVI	~~	s2_mean_sumNDVI	0.889	0.199	4.472	0.000	0.499	1.278
s2_mean_sumNDVI	~~	s2_mean_grow_tmax	0.254	0.126	2.023	0.043	0.008	0.501
s2_mean_sumNDVI	~~	s2_cum_grow_prcp	-0.379	0.144	-2.629	0.009	-0.661	-0.096
s2_mean_sumNDVI	~~	s1_mean_spr_len	-0.222	0.161	-1.383	0.167	-0.537	0.093
s2_mean_sumNDVI	~~	s1_mean_spr_tmin	0.267	0.128	2.078	0.038	0.015	0.518
s2_mean_sumNDVI	~~	s1_cum_wint_swe	-0.103	0.166	-0.622	0.534	-0.428	0.222
s2_mean_sumNDVI	~~	s1_cum_summ_pdsi	-0.141	0.164	-0.863	0.388	-0.461	0.179
s2_mean_sumNDVI	~~	s1_mean_sumNDVI	0.578	0.172	3.351	0.001	0.240	0.916
s2_mean_sumNDVI	~~	s1_mean_grow_tmax	0.371	0.135	2.754	0.006	0.107	0.635
s2_mean_sumNDVI	~~	s1_cum_grow_prcp	-0.226	0.137	-1.649	0.099	-0.494	0.043
s2_mean_grow_tmax	~~	s2_mean_grow_tmax	0.639	0.143	4.472	0.000	0.359	0.919
s2_mean_grow_tmax	~~	s2_cum_grow_prcp	-0.378	0.126	-2.995	0.003	-0.625	-0.131
s2_mean_grow_tmax	~~	s1_mean_spr_len	-0.109	0.134	-0.816	0.415	-0.372	0.154
s2_mean_grow_tmax	~~	s1_mean_spr_tmin	0.127	0.105	1.217	0.224	-0.078	0.333
s2_mean_grow_tmax	~~	s1_cum_wint_swe	0.062	0.140	0.445	0.656	-0.212	0.337
s2_mean_grow_tmax	~~	s1_cum_summ_pdsi	-0.077	0.138	-0.559	0.576	-0.347	0.193
s2_mean_grow_tmax	~~	s1_mean_sumNDVI	0.380	0.138	2.759	0.006	0.110	0.650
s2_mean_grow_tmax	~~	s1_mean_grow_tmax	0.353	0.117	3.019	0.003	0.124	0.583
s2_mean_grow_tmax	~~	s1_cum_grow_prcp	-0.118	0.114	-1.040	0.298	-0.341	0.105
s2_cum_grow_prcp	~~	s2_cum_grow_prcp	0.773	0.173	4.472	0.000	0.434	1.112
s2_cum_grow_prcp	~~	s1_mean_spr_len	0.066	0.147	0.449	0.654	-0.222	0.353
s2_cum_grow_prcp	~~	s1_mean_spr_tmin	-0.068	0.114	-0.598	0.550	-0.291	0.155
s2_cum_grow_prcp	~~	s1_cum_wint_swe	0.306	0.161	1.897	0.058	-0.010	0.622
s2_cum_grow_prcp	~~	s1_cum_summ_pdsi	0.352	0.161	2.186	0.029	0.036	0.667
s2_cum_grow_prcp	~~	s1_mean_sumNDVI	-0.325	0.146	-2.229	0.026	-0.611	-0.039
s2_cum_grow_prcp	~~	s1_mean_grow_tmax	-0.418	0.131	-3.190	0.001	-0.675	-0.161
s2_cum_grow_prcp	~~	s1_cum_grow_prcp	0.508	0.147	3.455	0.001	0.220	0.797
s1_mean_spr_len	~~	s1_mean_spr_len	1.108	0.248	4.472	0.000	0.622	1.594
s1_mean_spr_len	~~	s1_mean_spr_tmin	-0.740	0.179	-4.136	0.000	-1.091	-0.389
s1_mean_spr_len	~~	s1_cum_wint_swe	-0.425	0.196	-2.170	0.030	-0.810	-0.041
s1_mean_spr_len	~~	s1_cum_summ_pdsi	-0.424	0.193	-2.198	0.028	-0.802	-0.046
s1_mean_spr_len	~~	s1_mean_sumNDVI	0.003	0.163	0.019	0.985	-0.317	0.323
s1_mean_spr_len	~~	s1_mean_grow_tmax	-0.055	0.136	-0.402	0.688	-0.321	0.211
s1_mean_spr_len	~~	s1_cum_grow_prcp	-0.030	0.148	-0.200	0.841	-0.319	0.260
s1_mean_spr_tmin	~~	s1_mean_spr_tmin	0.661	0.148	4.472	0.000	0.372	0.951

s1_mean_spr_tmin	~~	s1_cum_wint_swe	0.310	0.151	2.059	0.040	0.015	0.605
s1_mean_spr_tmin	~~	s1_cum_summ_pdsi	0.281	0.147	1.914	0.056	-0.007	0.568
s1_mean_spr_tmin	~~	s1_mean_sumNDVI	-0.034	0.126	-0.265	0.791	-0.281	0.214
s1_mean_spr_tmin	~~	s1_mean_grow_tmax	0.071	0.105	0.675	0.500	-0.135	0.277
s1_mean_spr_tmin	~~	s1_cum_grow_prcp	0.030	0.114	0.262	0.793	-0.194	0.254
s1_cum_wint_swe	~~	s1_cum_wint_swe	1.224	0.274	4.472	0.000	0.688	1.761
s1_cum_wint_swe	~~	s1_cum_summ_pdsi	-0.042	0.190	-0.221	0.826	-0.415	0.331
s1_cum_wint_swe	~~	s1_mean_sumNDVI	-0.232	0.176	-1.324	0.186	-0.576	0.112
s1_cum_wint_swe	~~	s1_mean_grow_tmax	0.094	0.143	0.655	0.512	-0.187	0.374
s1_cum_wint_swe	~~	s1_cum_grow_prcp	0.422	0.169	2.497	0.013	0.091	0.752
s1_cum_summ_pdsi	~~	s1_cum_summ_pdsi	1.181	0.264	4.472	0.000	0.663	1.698
s1_cum_summ_pdsi	~~	s1_mean_sumNDVI	-0.188	0.171	-1.099	0.272	-0.524	0.147
s1_cum_summ_pdsi	~~	s1_mean_grow_tmax	-0.293	0.147	-1.987	0.047	-0.581	-0.004
s1_cum_summ_pdsi	~~	s1_cum_grow_prcp	0.205	0.156	1.317	0.188	-0.100	0.510
s1_mean_sumNDVI	~~	s1_mean_sumNDVI	0.962	0.215	4.472	0.000	0.541	1.384
s1_mean_sumNDVI	~~	s1_mean_grow_tmax	0.223	0.131	1.700	0.089	-0.034	0.480
s1_mean_sumNDVI	~~	s1_cum_grow_prcp	-0.281	0.145	-1.946	0.052	-0.564	0.002
s1_mean_grow_tmax	~~	s1_mean_grow_tmax	0.662	0.148	4.472	0.000	0.372	0.953
s1_mean_grow_tmax	~~	s1_cum_grow_prcp	-0.422	0.132	-3.194	0.001	-0.681	-0.163
s1_cum_grow_prcp	~~	s1_cum_grow_prcp	0.786	0.176	4.472	0.000	0.442	1.130
juv100fem	~1		0.138	0.181	0.761	0.446	-0.217	0.492
t1_preg	~1		0.260	0.308	0.844	0.399	-0.344	0.865
t2_fat_mean_f	~1		-1.180	0.288	-4.101	0.000	-1.744	-0.616
t1_fat_mean_f	~1		-0.970	0.441	-2.199	0.028	-1.835	-0.106
t1_juv100fem	~1		0.304	0.192	1.588	0.112	-0.071	0.680
s2_mean_spr_len	~1		0.158	0.166	0.951	0.342	-0.168	0.484
s2_mean_spr_tmin	~1		0.537	0.135	3.987	0.000	0.273	0.801
s2_cum_wint_swe	~1		0.165	0.180	0.918	0.359	-0.187	0.517
s2_cum_summ_pdsi	~1		0.228	0.159	1.435	0.151	-0.084	0.540
s2_mean_sumNDVI	~1		-0.402	0.149	-2.696	0.007	-0.694	-0.110
s2_mean_grow_tmax	~1		0.140	0.126	1.111	0.267	-0.107	0.388
s2_cum_grow_prcp	~1		-0.081	0.139	-0.585	0.559	-0.354	0.191
s1_mean_spr_len	~1		0.130	0.166	0.779	0.436	-0.197	0.456
s1_mean_spr_tmin	~1		0.519	0.129	4.035	0.000	0.267	0.771
s1_cum_wint_swe	~1		0.045	0.175	0.257	0.797	-0.298	0.388
s1_cum_summ_pdsi	~1		0.271	0.172	1.575	0.115	-0.066	0.607
s1_mean_sumNDVI	~1		-0.328	0.155	-2.111	0.035	-0.632	-0.023
s1_mean_grow_tmax	~1		0.138	0.129	1.069	0.285	-0.115	0.390
s1_cum_grow_prcp	~1		-0.045	0.140	-0.320	0.749	-0.320	0.230

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Table S3. Partial coefficient estimates (~) and covariance (~~) between all variables in the structural equation model illustrating the relationship between male diet quality and weather (Fig. 9). Standard errors, z-scores, p-values and confidence intervals are provided.

Dependent	op	Independent	est	se	z	pvalue	ci.lower	ci.upper
FN_mean_summ_M	~	s_mean_spr_len	-3.721	0.247	-15.051	0.000	-4.206	-3.236
FN_mean_summ_M	~	s_mean_spr_tmin	-5.617	0.224	-25.043	0.000	-6.057	-5.178
FN_mean_summ_M	~	s_cum_wint_swe	-2.175	0.104	-20.944	0.000	-2.379	-1.972
FN_mean_summ_M	~	s_cum_summ_pdsi	-0.092	0.063	-1.445	0.149	-0.216	0.033
FN_mean_summ_M	~	s_mean_sumNDVI	0.224	0.025	9.083	0.000	0.175	0.272
FN_mean_summ_M	~	s_mean_grow_tmax	-0.086	0.079	-1.088	0.277	-0.240	0.069
FN_mean_summ_M	~	s_cum_grow_prcp	0.573	0.065	8.849	0.000	0.446	0.700
FN_mean_summ_M	~~	FN_mean_summ_M	0.006	NA	NA	NA	NA	NA
s_mean_spr_len	~~	s_mean_spr_len	1.152	0.259	4.454	0.000	0.645	1.658
s_mean_spr_len	~~	s_mean_spr_tmin	-0.778	0.194	-4.019	0.000	-1.157	-0.399
s_mean_spr_len	~~	s_cum_wint_swe	-0.421	0.209	-2.011	0.044	-0.830	-0.011
s_mean_spr_len	~~	s_cum_summ_pdsi	-0.318	0.203	-1.567	0.117	-0.715	0.080
s_mean_spr_len	~~	s_mean_sumNDVI	-0.045	0.183	-0.247	0.805	-0.404	0.314
s_mean_spr_len	~~	s_mean_grow_tmax	-0.099	0.146	-0.677	0.499	-0.384	0.187
s_mean_spr_len	~~	s_cum_grow_prcp	-0.070	0.179	-0.394	0.694	-0.420	0.280
s_mean_spr_tmin	~~	s_mean_spr_tmin	0.739	0.169	4.372	0.000	0.408	1.070
s_mean_spr_tmin	~~	s_cum_wint_swe	0.243	0.165	1.471	0.141	-0.081	0.568
s_mean_spr_tmin	~~	s_cum_summ_pdsi	0.209	0.163	1.282	0.200	-0.110	0.528
s_mean_spr_tmin	~~	s_mean_sumNDVI	-0.023	0.148	-0.157	0.876	-0.313	0.266
s_mean_spr_tmin	~~	s_mean_grow_tmax	0.194	0.121	1.601	0.109	-0.044	0.432
s_mean_spr_tmin	~~	s_cum_grow_prcp	-0.079	0.145	-0.547	0.584	-0.364	0.205
s_cum_wint_swe	~~	s_cum_wint_swe	1.204	0.322	3.743	0.000	0.574	1.835
s_cum_wint_swe	~~	s_cum_summ_pdsi	-0.172	0.218	-0.788	0.431	-0.598	0.255
s_cum_wint_swe	~~	s_mean_sumNDVI	-0.176	0.207	-0.849	0.396	-0.581	0.230
s_cum_wint_swe	~~	s_mean_grow_tmax	0.168	0.163	1.034	0.301	-0.151	0.487
s_cum_wint_swe	~~	s_cum_grow_prcp	0.472	0.229	2.062	0.039	0.023	0.921
s_cum_summ_pdsi	~~	s_cum_summ_pdsi	1.272	0.300	4.234	0.000	0.683	1.860
s_cum_summ_pdsi	~~	s_mean_sumNDVI	-0.145	0.199	-0.727	0.467	-0.535	0.245
s_cum_summ_pdsi	~~	s_mean_grow_tmax	-0.362	0.167	-2.166	0.030	-0.690	-0.034
s_cum_summ_pdsi	~~	s_cum_grow_prcp	0.385	0.203	1.897	0.058	-0.013	0.784
s_mean_sumNDVI	~~	s_mean_sumNDVI	1.111	0.258	4.303	0.000	0.605	1.618
s_mean_sumNDVI	~~	s_mean_grow_tmax	0.173	0.148	1.163	0.245	-0.118	0.464
s_mean_sumNDVI	~~	s_cum_grow_prcp	-0.197	0.182	-1.082	0.279	-0.554	0.160
s_mean_grow_tmax	~~	s_mean_grow_tmax	0.694	0.161	4.312	0.000	0.379	1.010
s_mean_grow_tmax	~~	s_cum_grow_prcp	-0.471	0.162	-2.918	0.004	-0.788	-0.155
s_cum_grow_prcp	~~	s_cum_grow_prcp	1.080	0.246	4.389	0.000	0.598	1.563
FN_mean_summ_M	~1		1.987	0.184	10.812	0.000	1.627	2.347
s_mean_spr_len	~1		0.216	0.170	1.275	0.202	-0.116	0.549

s_mean_spr_tmin	~1		0.408	0.136	3.004	0.003	0.142	0.675
s_cum_wint_swe	~1		-0.046	0.190	-0.241	0.810	-0.418	0.327
s_cum_summ_pdsi	~1		0.246	0.178	1.381	0.167	-0.103	0.596
s_mean_sumNDVI	~1		-0.101	0.167	-0.608	0.543	-0.428	0.225
s_mean_grow_tmax	~1		0.052	0.132	0.391	0.696	-0.207	0.310
s_cum_grow_prcp	~1		0.177	0.164	1.076	0.282	-0.145	0.499
FN_mean_wint_M	~	w1_mean_spr_len	-0.651	0.187	-3.481	0.000	-1.017	-0.284
FN_mean_wint_M	~	w1_mean_spr_tmin	-0.322	0.374	-0.861	0.389	-1.054	0.411
FN_mean_wint_M	~	w_cum_wint_swe	-0.201	0.098	-2.065	0.039	-0.392	-0.010
FN_mean_wint_M	~	w1_cum_summ_pdsi	0.327	0.118	2.776	0.006	0.096	0.558
FN_mean_wint_M	~	w1_mean_sumNDVI	2.285	0.310	7.375	0.000	1.678	2.893
FN_mean_wint_M	~	w1_mean_grow_tmax	0.501	0.182	2.756	0.006	0.145	0.858
FN_mean_wint_M	~	w1_cum_grow_prcp	1.329	0.289	4.598	0.000	0.762	1.895
FN_mean_wint_M	~~	FN_mean_wint_M	0.063	0.026	2.434	0.015	0.012	0.113
w1_mean_spr_len	~~	w1_mean_spr_len	1.107	0.248	4.473	0.000	0.622	1.592
w1_mean_spr_len	~~	w1_mean_spr_tmin	-0.668	0.169	-3.962	0.000	-0.999	-0.338
w1_mean_spr_len	~~	w_cum_wint_swe	-0.141	0.182	-0.773	0.439	-0.498	0.216
w1_mean_spr_len	~~	w1_cum_summ_pdsi	-0.434	0.193	-2.246	0.025	-0.813	-0.055
w1_mean_spr_len	~~	w1_mean_sumNDVI	0.013	0.159	0.084	0.933	-0.299	0.326
w1_mean_spr_len	~~	w1_mean_grow_tmax	-0.063	0.141	-0.443	0.658	-0.339	0.214
w1_mean_spr_len	~~	w1_cum_grow_prcp	-0.059	0.148	-0.399	0.690	-0.349	0.231
w1_mean_spr_tmin	~~	w1_mean_spr_tmin	0.625	0.140	4.477	0.000	0.352	0.899
w1_mean_spr_tmin	~~	w_cum_wint_swe	0.156	0.141	1.104	0.270	-0.121	0.432
w1_mean_spr_tmin	~~	w1_cum_summ_pdsi	0.259	0.142	1.826	0.068	-0.019	0.537
w1_mean_spr_tmin	~~	w1_mean_sumNDVI	-0.096	0.121	-0.794	0.427	-0.333	0.141
w1_mean_spr_tmin	~~	w1_mean_grow_tmax	0.072	0.106	0.677	0.498	-0.137	0.281
w1_mean_spr_tmin	~~	w1_cum_grow_prcp	0.127	0.113	1.129	0.259	-0.094	0.348
w_cum_wint_swe	~~	w_cum_wint_swe	1.031	0.255	4.051	0.000	0.532	1.530
w_cum_wint_swe	~~	w1_cum_summ_pdsi	-0.118	0.206	-0.573	0.567	-0.521	0.285
w_cum_wint_swe	~~	w1_mean_sumNDVI	-0.107	0.178	-0.602	0.547	-0.455	0.241
w_cum_wint_swe	~~	w1_mean_grow_tmax	0.013	0.165	0.080	0.936	-0.311	0.338
w_cum_wint_swe	~~	w1_cum_grow_prcp	0.232	0.178	1.305	0.192	-0.116	0.580
w1_cum_summ_pdsi	~~	w1_cum_summ_pdsi	1.181	0.264	4.475	0.000	0.664	1.698
w1_cum_summ_pdsi	~~	w1_mean_sumNDVI	-0.175	0.167	-1.046	0.296	-0.502	0.153
w1_cum_summ_pdsi	~~	w1_mean_grow_tmax	-0.270	0.152	-1.780	0.075	-0.567	0.027
w1_cum_summ_pdsi	~~	w1_cum_grow_prcp	0.190	0.155	1.226	0.220	-0.114	0.495
w1_mean_sumNDVI	~~	w1_mean_sumNDVI	0.919	0.205	4.472	0.000	0.516	1.322
w1_mean_sumNDVI	~~	w1_mean_grow_tmax	0.299	0.137	2.189	0.029	0.031	0.567
w1_mean_sumNDVI	~~	w1_cum_grow_prcp	-0.286	0.142	-2.018	0.044	-0.564	-0.008
w1_mean_grow_tmax	~~	w1_mean_grow_tmax	0.717	0.160	4.472	0.000	0.403	1.031
w1_mean_grow_tmax	~~	w1_cum_grow_prcp	-0.446	0.138	-3.229	0.001	-0.717	-0.175
w1_cum_grow_prcp	~~	w1_cum_grow_prcp	0.786	0.176	4.469	0.000	0.442	1.131
FN_mean_wint_M	~1		1.883	0.222	8.472	0.000	1.447	2.318

w1_mean_spr_len	~1		0.106	0.166	0.639	0.523	-0.220	0.432
w1_mean_spr_tmin	~1		0.493	0.125	3.944	0.000	0.248	0.738
w_cum_wint_swe	~1		-0.081	0.192	-0.424	0.672	-0.457	0.295
w1_cum_summ_pdsi	~1		0.288	0.172	1.674	0.094	-0.049	0.624
w1_mean_sumNDVI	~1		-0.320	0.152	-2.110	0.035	-0.617	-0.023
w1_mean_grow_tmax	~1		0.126	0.134	0.943	0.346	-0.136	0.389
w1_cum_grow_prcp	~1		-0.045	0.140	-0.323	0.747	-0.320	0.229
FN_mean_wint_F	~	w1_mean_spr_len	-0.317	0.551	-0.575	0.565	-1.398	0.763
FN_mean_wint_F	~	w1_mean_spr_tmin	-0.242	0.937	-0.258	0.796	-2.079	1.595
FN_mean_wint_F	~	w_cum_wint_swe	-0.268	0.291	-0.923	0.356	-0.838	0.302
FN_mean_wint_F	~	w1_cum_summ_pdsi	0.119	0.348	0.342	0.733	-0.563	0.801
FN_mean_wint_F	~	w1_mean_sumNDVI	0.243	0.540	0.450	0.653	-0.815	1.300
FN_mean_wint_F	~	w1_mean_grow_tmax	-0.072	0.497	-0.145	0.884	-1.045	0.901
FN_mean_wint_F	~	w1_cum_grow_prcp	0.800	0.688	1.163	0.245	-0.548	2.148
FN_mean_wint_F	~~	FN_mean_wint_F	0.551	0.218	2.531	0.011	0.124	0.978
w1_mean_spr_len	~~	w1_mean_spr_len	1.107	0.248	4.472	0.000	0.622	1.593
w1_mean_spr_len	~~	w1_mean_spr_tmin	-0.669	0.169	-3.960	0.000	-1.000	-0.338
w1_mean_spr_len	~~	w_cum_wint_swe	-0.131	0.183	-0.713	0.476	-0.489	0.228
w1_mean_spr_len	~~	w1_cum_summ_pdsi	-0.434	0.193	-2.245	0.025	-0.814	-0.055
w1_mean_spr_len	~~	w1_mean_sumNDVI	0.013	0.160	0.084	0.933	-0.299	0.326
w1_mean_spr_len	~~	w1_mean_grow_tmax	-0.063	0.141	-0.444	0.657	-0.339	0.214
w1_mean_spr_len	~~	w1_cum_grow_prcp	-0.059	0.148	-0.399	0.690	-0.349	0.231
w1_mean_spr_tmin	~~	w1_mean_spr_tmin	0.626	0.140	4.472	0.000	0.352	0.900
w1_mean_spr_tmin	~~	w_cum_wint_swe	0.152	0.142	1.071	0.284	-0.126	0.429
w1_mean_spr_tmin	~~	w1_cum_summ_pdsi	0.259	0.142	1.824	0.068	-0.019	0.537
w1_mean_spr_tmin	~~	w1_mean_sumNDVI	-0.096	0.121	-0.797	0.425	-0.333	0.141
w1_mean_spr_tmin	~~	w1_mean_grow_tmax	0.072	0.107	0.677	0.499	-0.137	0.281
w1_mean_spr_tmin	~~	w1_cum_grow_prcp	0.127	0.113	1.129	0.259	-0.094	0.348
w_cum_wint_swe	~~	w_cum_wint_swe	1.038	0.258	4.029	0.000	0.533	1.543
w_cum_wint_swe	~~	w1_cum_summ_pdsi	-0.101	0.208	-0.487	0.626	-0.508	0.306
w_cum_wint_swe	~~	w1_mean_sumNDVI	-0.109	0.179	-0.612	0.541	-0.459	0.241
w_cum_wint_swe	~~	w1_mean_grow_tmax	-0.007	0.168	-0.040	0.968	-0.336	0.322
w_cum_wint_swe	~~	w1_cum_grow_prcp	0.248	0.180	1.377	0.168	-0.105	0.601
w1_cum_summ_pdsi	~~	w1_cum_summ_pdsi	1.182	0.264	4.472	0.000	0.664	1.700
w1_cum_summ_pdsi	~~	w1_mean_sumNDVI	-0.174	0.167	-1.041	0.298	-0.501	0.153
w1_cum_summ_pdsi	~~	w1_mean_grow_tmax	-0.270	0.152	-1.779	0.075	-0.567	0.027
w1_cum_summ_pdsi	~~	w1_cum_grow_prcp	0.190	0.155	1.226	0.220	-0.114	0.495
w1_mean_sumNDVI	~~	w1_mean_sumNDVI	0.919	0.205	4.472	0.000	0.516	1.321
w1_mean_sumNDVI	~~	w1_mean_grow_tmax	0.299	0.137	2.187	0.029	0.031	0.567
w1_mean_sumNDVI	~~	w1_cum_grow_prcp	-0.286	0.142	-2.018	0.044	-0.564	-0.008
w1_mean_grow_tmax	~~	w1_mean_grow_tmax	0.717	0.160	4.472	0.000	0.403	1.031
w1_mean_grow_tmax	~~	w1_cum_grow_prcp	-0.446	0.138	-3.231	0.001	-0.717	-0.175
w1_cum_grow_prcp	~~	w1_cum_grow_prcp	0.786	0.176	4.472	0.000	0.441	1.130

FN_mean_wint_F	~1		0.751	0.594	1.263	0.206	-0.414	1.916
w1_mean_spr_len	~1		0.107	0.166	0.640	0.522	-0.220	0.433
w1_mean_spr_tmin	~1		0.494	0.125	3.946	0.000	0.248	0.739
w_cum_wint_swe	~1		-0.065	0.194	-0.333	0.739	-0.444	0.315
w1_cum_summ_pdsi	~1		0.287	0.172	1.672	0.094	-0.049	0.624
w1_mean_sumNDVI	~1		-0.320	0.152	-2.109	0.035	-0.617	-0.023
w1_mean_grow_tmax	~1		0.126	0.134	0.945	0.345	-0.136	0.389
w1_cum_grow_prcp	~1		-0.045	0.140	-0.320	0.749	-0.320	0.230

1039

Table S4. Parameter estimates for models of calf recruitment. Weather and plant phenology parameters measured one year prior to recruitment estimates are signified by t-1, whereas parameters measured two years prior are signified by t-2. Models treating population as a random intercept are illustrated by (1|pop), and models allowing for a random intercept and slope by population are indicated by ((1+var||pop). All variables were centered and scaled prior to model fitting, meaning parameter estimates (β coefficients) reflect relative effect sizes.

i

Int	Spring Length $_{t-1}$	Winter Severity $_{t-1}$	Summer Drought $_{t-1}$	Integrated NDVI $_{t-1}$	Integrated NDVI $_{t-2}$	Grow Season Max Temp $_{t-2}$	Winter Severity $_{t-2}$	Summer Drought $_{t-2}$
45.34	4.96	-5.54	1.91	-	-	-	-	-
45.39	4.15	-5.48	2.21	1.77	-	-	-	-
45.39	4.62	-5.74	-	-	-	-	-	-
45.52	3.84	-5.74	2.15	2.38	-1.71	-	-	-
45.00	5.09	-4.70	1.97	-	-	-	-	-
45.88	3.17	-6.51	2.23	2.53	-1.67	1.51	-	-
45.09	4.50	-5.06	-	-	-	-	-	-
45.12	4.37	-4.71	2.27	1.65	-	-	-	-
45.10	3.73	-4.59	2.03	2.21	-1.95	-	-	-
45.44	3.29	-5.34	2.21	2.40	-1.79	1.31	-	-
43.66	4.07	-	-	-	-	-	-	-
43.66	4.07	-	-	-	-	-	-	-
45.55	4.51	-5.37	-	-	-	-	-	-
45.12	-	-7.05	-	-	-	-	-	-
45.03	5.06	-4.77	1.58	-	-	-	-	-
45.48	4.13	-3.57	2.26	-	-	-	-2.48	-
46.13	2.70	-4.44	2.93	-	-	2.50	-4.10	-
42.63	-	-	-	-	-	-	-	-
46.31	1.61	-4.22	2.39	-	-	3.24	-4.78	1.85

ii

(1|herd)	(1+var||herd)	df	logLik	AICc	delta	weight	R^2 marginal	R^2 conditional
-	-	5	-	406.15	0.00	0.22	0.52	-
-	-	6	-	406.80	0.65	0.16	0.53	-
-	-	4	-	406.95	0.80	0.15	0.49	-
-	-	7	-	407.22	1.07	0.13	0.56	-
+	-	6	-	407.94	1.80	0.09	0.49	0.53
-	-	8	-	408.36	2.22	0.07	0.57	-
+	-	5	-	408.84	2.70	0.06	0.46	0.49
+	-	7	-	408.95	2.80	0.05	0.51	0.54
+	-	8	-	409.04	2.89	0.05	0.49	0.55
+	-	9	-	410.91	4.76	0.02	0.52	0.56
+	-	4	-	412.49	6.34	0.01	0.14	0.45
-	+	5	-	414.90	8.75	0.00	0.14	0.45
-	+	8	-	416.05	9.90	0.00	0.47	0.51
-	+	3	-	418.69	12.54	0.00	0.35	0.35
-	+	11	-	421.26	15.11	0.00	0.48	0.57
-	+	14	-	429.24	23.09	0.00	0.51	0.58
-	+	17	-	438.16	32.01	0.00	0.57	0.59
-	-	2	-	440.62	34.47	0.00	-	-
-	+	20	-	449.43	43.29	0.00	0.59	0.62

Fig S1. Relationship between temporal autocorrelation (ACF) of annual recruitment estimates (calves/100 cows) and temporal lag. Blue lines indicate statistically significant temporal autocorrelation. Residual autocorrelation was weak (panels A and D) and unimproved by autoregressive error structures (panels B and C).

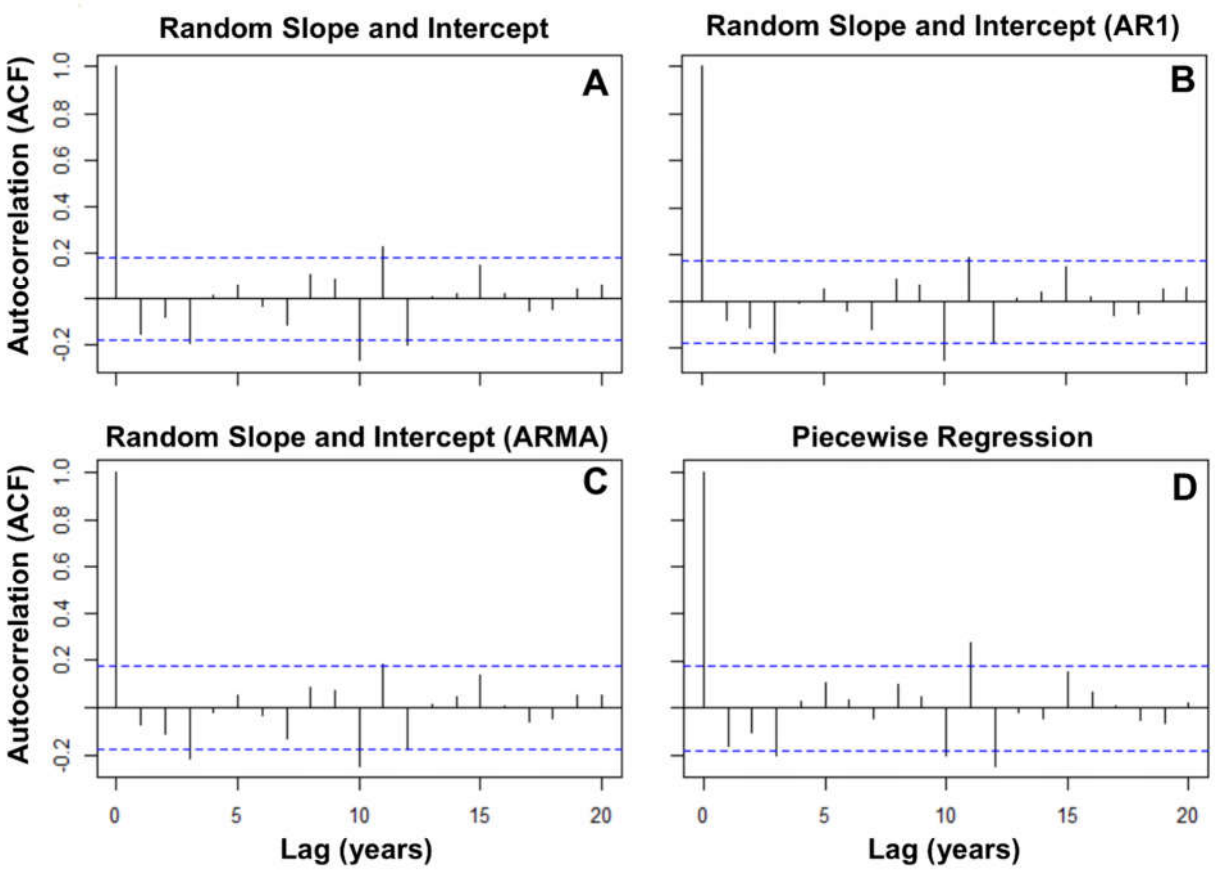
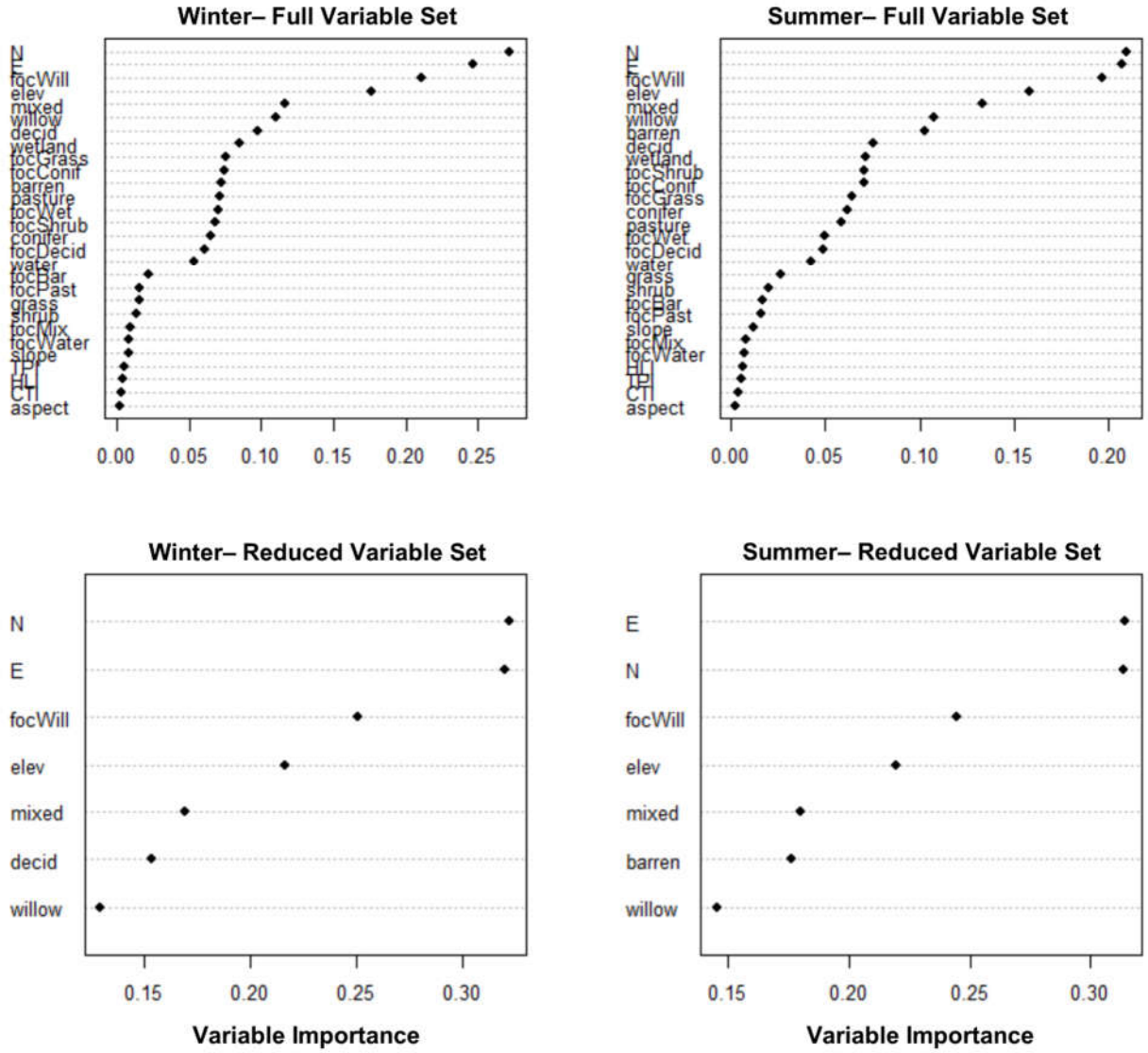


Fig S2. Importance factors of 28 topographic and habitat variables (top panels) thought to influence moose space-use. Reduce parameter set (n = 6, bottom panels) derived from the model selection function in the rfUtils package of Program R.



CHAPTER TWO

STATE-DEPENDENT BEHAVIOR ALTERS ENDOCRINE-ENERGY RELATIONSHIP: IMPLICATIONS FOR CONSERVATION AND MANAGEMENT

ABSTRACT

Glucocorticoids (GC) and triiodothyronine (T3) are two endocrine markers commonly used to quantify resource limitation, yet the relationships between these markers and the energetic state of animals has been studied primarily in small-bodied species in captivity. Free-ranging animals, however, adjust energy intake in accordance with their energy reserves, a behavior known as state-dependent foraging. Further, links between life-history strategies and metabolic allometries cause energy intake and energy reserves to be more strongly coupled in small animals relative to large animals. Because GC and T3 may reflect energy intake or energy reserves, state-dependent foraging and body size may cause endocrine-energy relationships to vary among taxa and environments. To extend the utility of endocrine markers to large-bodied, free-ranging animals, I evaluated how state-dependent foraging, energy reserves, and energy intake influenced fecal GC and fecal T3 concentrations in free-ranging moose (*Alces alces*). Compared with individuals possessing abundant energy reserves, individuals with few energy reserves had higher energy intake and high fecal T3 concentrations, thereby supporting state-dependent foraging. Although fecal GC did not vary strongly with energy reserves, individuals with higher fecal GC tended to have fewer energy reserves and substantially greater energy intake than those with low fecal GC. Consequently, individuals with greater energy intake had both high fecal T3 and high fecal GC

concentrations, a pattern inconsistent with previous documentation from captive animal studies. I posit that a positive relationship between GC and T3 may be expected in animals exhibiting state-dependent foraging if GC is associated with increased foraging and energy intake. Thus, I recommend that additional investigations of GC- and T3-energy relationships be conducted in free-ranging animals across a diversity of body size and life-history strategies before these endocrine markers are applied broadly to wildlife conservation and management.

INTRODUCTION

Resource consumption drives individual fitness and population dynamics across a diversity of vertebrates (O'Donoghue et al. 1997, Taylor et al. 2005, Falls et al. 2007, Parker et al. 2009, Cury et al. 2011, Monteith et al. 2014b). Endocrine markers such as glucocorticoids (GC) and triiodothyronine (T3) are closely tied to energy balance (Danforth and Burger 1989, McEwen and Wingfield 2003), and thus provide a measure of resource limitation in animal populations. Both energy reserves (fat stores) and energy intake (forage) influence GC and T3 profiles (Dallman et al. 1999, Kitaysky et al. 1999, Kitaysky et al. 2005, du Dot et al. 2009, Kitaysky et al. 2010), making endocrinology a useful lens for identifying the nutritional factors that affect population growth and a valuable tool for wildlife conservation and management (Wikelski and Cooke 2006).

The hypothalamic-pituitary-adrenal and hypothalamic-pituitary-thyroid axes are responsible for GC and T3 production. The conservation of these hormonal axes across vertebrate taxa (Denver 2009, Sower et al. 2009) suggests that GC and T3 might be interpreted as measures of energy balance – and thus resource limitation – across a multitude of taxonomic groups. When an animal experiences negative energy balance, declines in

1105 plasma glucose activate the hypothalamic-pituitary-adrenal axis and increase GC production
1106 (Dallman et al. 1999). Therefore, high levels of GC often indicate negative energy balance
1107 (i.e., low energy reserves or energy intake [Fig. 1A, B]; Kitaysky et al. 1999, du Dot et al.
1108 2009). When an animal experiences positive energy balance and plasma glucose is increased,
1109 the hypothalamic-pituitary-thyroid axis increases T3 production (Eales 1988). Consequently,
1110 high levels of T3 indicate positive energy balance (i.e., high energy reserves or energy intake
1111 [Fig. 1A, B]; Cherel et al. 1988b, Danforth and Burger 1989).
1112 There is reason for skepticism regarding the extent to which GC- and T3-energy
1113 relationships can be generalized across taxa (for review see Bonier et al. 2009). For example,
1114 endocrine response to environmental stress varies among disparate life-history strategies
1115 (Boonstra 2013, Sheriff and Love 2013). Further, metabolic allometries cause energy intake
1116 and energy reserves to be more strongly coupled in taxa exhibiting 'fast' life histories
1117 (typically small-bodied animals) compared to taxa exhibiting 'slow' life histories (typically
1118 large-bodied animals; Lindstedt and Boyce 1985, Stearns 1989, Ricklefs and Wikelski 2002).
1119 Relationships between GC, T3, energy intake, and energy reserves are well documented in
1120 species with 'fast' life histories, but usually only for one component of their energy budget
1121 (e.g., energy intake or energy reserves; Romero 2004, Dantzer et al. 2014), leading to
1122 uncertainty in whether GC and T3 reflect energy intake or energy reserves. Nevertheless, GC-
1123 and T3-energy relationships derived from small-bodied species are currently the only
1124 reference available for applying endocrine markers to large-bodied species (Wasser et al.
1125 2011, Gobush et al. 2014). Therefore, if GC- and T3-energy relationships are to be broadly
1126 informative, it is critical to quantify their relationships across an array of life-history strategies
1127 (Crespi et al. 2013).

Current understanding of GC- and T3-energy relationships is largely influenced by biomedical studies conducted in captivity (Eales 1988, Danforth and Burger 1989, Romero 2004, Dantzer et al. 2014). In captive studies of GC- and T3-energy relationships, researchers often control the quantity or quality of foods experimentally – and thus the amount of energy available for intake – which constrains an animal's ability to adjust foraging in accord with energetic needs. In contrast, free-ranging animals often increase energy intake in response to negative energy balance, a phenomenon known as state-dependent foraging (Houston and McNamara 1999). State-dependent foraging is expected according to theory and has been empirically demonstrated across taxa (e.g., Arnold and Birrell 1977, Pettersson and Brönmark 1993, Skutelsky 1996, Gils et al. 2006, Hamel and Cote 2008). State-dependent foraging may alter GC- and T3-energy relationships compared with those documented in captive animals, especially in large-bodied animals where metabolic allometries cause energy reserves to respond to changes in energy intake much slower than in small-bodied species (Lindstedt and Boyce 1985). For example, captive animals with low energy reserves generally have high GC and low T3 (Bahnak et al. 1981, Kitaysky et al. 1999, Douyon and Schteingart 2002, Daminet et al. 2003, du Dot et al. 2009), but if GC and T3 reflect energy intake, large-bodied state-dependent foragers may instead exhibit high T3 because they increase energy intake when energy reserves are low (Fig. 1C). Accordingly, GC levels may rise in concert with T3 (Gobush et al. 2014), because increased GC is associated with foraging activity and energy intake (Fig. 1C, D; Kitaysky et al. 2001, Wingfield and Kitaysky 2002).

To extend the utility of endocrine markers in wildlife ecology, I quantified energy-intake, energy-reserves, fecal GC, and fecal T3 in free-ranging moose (*Alces alces*). The large body size of moose (~300kg in my study area) should cause their energy reserves to respond

1151 weakly to changes in energy intake over short time periods, and like other large herbivores,
1152 moose are likely to exhibit state-dependent foraging (Hamel and Cote 2008, Monteith et al.
1153 2013). To evaluate moose endocrine-energy relationships I tested predictions stemming from
1154 three alternative hypotheses:
1155
1156 **State-Dependent Hypothesis:** If moose forage in a state-dependent manner, individuals with
1157 low energy reserves will have higher energy intake than individuals with greater energy
1158 reserves. Accordingly, GC and T3 will be greater in individuals with low energy reserves
1159 (Fig. 1C) because GC encourages energy intake and T3 production is expected to increase in
1160 response to increased energy intake (Fig. 1D).
1161
1162 **Energy Reserves Hypothesis:** Energy reserves determine GC and T3 profiles. This
1163 hypothesis predicts that T3 will be greater and GC to be lower in individuals with greater
1164 energy reserves (Fig. 1A).
1165
1166 **Energy Intake Hypothesis:** Current (past ~24 hr) energy intake determines GC and T3
1167 profiles. This hypothesis predicts T3 to be greater in animals with higher energy intake
1168 because increased energy intake should increase blood glucose. This hypothesis also predicts
1169 GC concentration to be lower in individuals with greater energy intake because individuals
1170 should rely less on catabolism of energy reserves to reach energy homeostasis (Fig. 1B).
1171

METHODS

Study area— I studied moose in the southern Greater Yellowstone Ecosystem of Wyoming, USA (42.8653˚N, 110.0708˚W) during mid-February in 2012 and 2013. The study area was characterized by deep snow (annual mean snowfall 160cm) and cold temperatures (mean December-March temperature -10˚C). Moose used riparian shrublands along the Green River and its primary tributaries: north and south Horse Creek, north and south Cottonwood Creek, and north and south Beaver Creek (~2200m in elevation). These riparian habitats were dominated by Booth's willow (*Salix boothii*), Geyer's willow (*Salix geyeriana*) and cottonwood (*Populus* spp.) adjacent to mixed coniferous (*Abies lasiocarpa*, *Picea engelmannii*, *Pinus contorta, Pseudotsuga menziesii*) forest, aspen (*Populus tremuloides*) forest, mixed conifer-aspen forest, and sagebrush (*Artemisia* spp.) steppe. Disturbance associated with human activity may represent a psychological stressor for wildlife and increase GC production (Creel et al. 2002). Although I did not monitor vehicle traffic or snowmobile activity in moose home-ranges, the riparian habitats inhabited by moose during winter were located primarily on private ranch lands away from human activity (Oates 2016). During the study, no wolves (*Canis lupis*) existed within or near the home-ranges of moose, bears (*Ursus americana* and *U. arctos*) were hibernating, and mountain lions (*Puma concolor*) were largely absent during my study (Oates 2016). The extremely low density of predators in the study area means that the potential influence of psychological stress caused by predation risk likely had little to no influence on GC levels (Creel et al. 2009).

Energy reserves, energy intake, and covariates— In February 2012 and February 2013, I assisted in the captured 143 adult (>1 yr old) female moose using a net gun fired from a

1195 helicopter (Barrett 1982, Krausman et al. 1985). To determine the energy reserves of each
1196 moose, Dr. Kevin L. Monteith and I used ultrasonography to determine the maximum depth
1197 of subcutaneous rump fat, and used a standardized protocol validated in other species to
1198 assign a body condition score (Stephenson et al. 1998, Cook et al. 2010). Whereas the depth
1199 of subcutaneous rump fat was used to estimate percent ingesta-free body fat (%IFBFat) for
1200 moose with measurable fat, body condition scores were used to estimate percent ingesta-free
1201 body fat for animals without subcutaneous fat based on the linear relationship between
1202 ingesta-free body fat and body condition score of moose with measurable rump fat (Cook et
1203 al. 2010; Monteith *et al*. unpublished). I collected fecal samples (10–12 pellets) via rectal
1204 palpation, which were immediately froze at -20˚C until assayed for fecal neutral detergent
1205 fiber (NDF), fecal nitrogen (N), fecal GC and fecal T3 metabolite concentrations. All capture
1206 and handling methodologies were approved by the Institutional Animal Care and Use
1207 Committee at the University of Wyoming (Permit # A-3216-01).
1208 For ruminants, dietary nitrogen (N) and its fecal proxy are measures of protein and
1209 energy intake (Van Soest 1994, Hodgman et al. 1996, Leslie et al. 2008). Further, neutral
1210 detergent fiber (NDF) of forage and its fecal proxy provide a measure of digestible energy and
1211 an additional measure of protein availability (Van Soest 1994, Brown et al. 1995, Hodgman et
1212 al. 1996). Under high protein–high energy diets, fecal NDF is reduced relative to low protein–
1213 high energy diets (Brown et al. 1995), likely because increased protein can increase gut
1214 microbe production and enhance fiber digestion. Therefore, the interaction between fecal
1215 NDF and fecal N may be a better measure of energy intake compared to either metric alone.
1216 Additionally, increased NDF increases digestion time, thereby reducing forage intake
1217 (Mubanga et al. 1985, Church 1988, Allen 1996, Meyer et al. 2010). Moreover, small changes

1218 in diet quality can lead to large changes in energy intake over both short and long time-scales
1219 (i.e., the "multiplier effect"; White 1983). Because increased NDF reduces both digestible
1220 energy and forage intake and this can lead to meaningful changes in energy intake, the inverse
1221 of fecal NDF (NDF^{-1}) was considered a proxy for energy intake.
1222
1223 *Lab analyses*— Fecal GC and fecal T3 analyses were conducted by the Center for
1224 Conservation Biology (University of Washington, Seattle, WA, USA). Six pellets from each
1225 fecal sample were chosen at random and freeze-dried for 24–48 hours in a Labconco Freeze-
1226 Dry system at -50˚C, then thoroughly homogenized into a fine powder. Approximately 0.1g
1227 dry weight from each sample was used to control for mass-induced bias in metabolite
1228 concentration, thereby reducing the potential effect of inter-sample variation in fecal bulk
1229 caused by dietary fiber (Millspaugh and Washburn 2003, Page and Underwood 2006,
1230 Goymann 2012). A pulse-vortex double extraction with 15mL 70% ethanol was performed,
1231 and extracts were stored at -20˚C until assayed. Radioimmunoassays were performed on
1232 ethanol extracts at previously validated dilutions for GC (Wasser et al. 2000) and T3 (Wasser
1233 et al. 2010) using MP Biomedicals' 125-I corticosterone kit and 125-I Total T3 kit,
1234 respectively. The cross-reactivity between cortiscosterone and progesterone is 0.02% for MP
1235 Biomedicals' 125-I kit. All hormone extractions were performed in duplicate for each assay,
1236 and only those with intra-assay variation (% CV) below 10% were accepted.
1237 Fecal NDF and fecal N analyses were performed by the Washington State Habitat Lab
1238 (Washington State University, Pullman, WA, USA). Fecal samples were oven-dried at 55˚C,
1239 ground in a Wiley Mill, passed through a 1.0mm screen and homogenized. Fecal NDF was
1240 analyzed with an Ankom Fiber Analyzer (Ankom Technology, Fairport, NY, USA) following

1241 standard preparation procedures (Van Soest et al. 1970, Komarek 1993). The Dumas method
1242 of combustion (Assoc. Official Analytical Chemists Etheridge et al. 1998, Marvier et al.
1243 2004) was used to determine fecal N using a Truspec CN analyzer (LECO corp., St. Joseph,
1244 MI, USA). I report fecal NDF and fecal N on a percent dry matter basis.
1245
1246 *Statistical analyses*— Percent ingesta-free body fat of the 143 individuals ranged from 0.7 to
1247 10.5%. I stratified individuals into one of ten 1% body-fat strata to ensure that I sampled the
1248 entire range of energy reserves. I then chose at random five individuals within each of the first
1249 nine strata and all three individuals present within the 9.5–10.5% body fat strata (n=48) to
1250 assess endocrine-energy relationships. I used linear regression and calculated Pearson's
1251 correlation coefficient (r) to examine the effects of energy reserves on energy intake, and the
1252 effects of energy reserves and energy intake on fecal GC and fecal T3 profiles. I assessed the
1253 potential confounding effects of dietary fiber, age, and pregnancy on endocrine-energy
1254 relationships derived from fecal samples prior to characterizing the effects of energy intake
1255 and energy reserves on fecal hormone concentrations (see appendix S2). Shapiro-Wilk tests of
1256 normality (Royston 1982) were performed on the distribution of residuals to ensure model
1257 assumptions were met. All analyses were performed using program R (R Core Team 2014).
1258
1259 **RESULTS**
1260 Fecal NDF^{-1} and fecal N were not strongly correlated (r=0.21), so I considered fecal NDF^{-1}
1261 and fecal N to be independent predictors of energy intake. Energy reserves were weakly and
1262 negatively correlated with energy intake as indexed by fecal NDF^{-1} (Fig. 2A; r= -0.22,
1263 P=0.13) and fecal N (Fig 2B; r= -0.35, P=0.09), but energy reserves were strongly and

1264 negatively correlated with an interaction between fecal NDF^{-1} and fecal N (Fig. 2C; r= -0.38,
1265 P<0.01), indicating that individuals with low energy reserves had greater energy intake (i.e.,
1266 foraged in a state-dependent manner).

1267 Fecal GC and fecal T3 were best described by a single measure of energy intake, fecal
1268 NDF^{-1} (see table S1), indicating that these endocrine markers are more responsive to energy
1269 intake than energy reserves (% IFBFat) in moose. Both fecal GC (Fig. 3B; r= 0.56, P<0.001)
1270 and fecal T3 (Fig. 3D; r= 0.36, P=0.01) were substantially higher in individuals with greater
1271 energy intake than those with low energy intake. Fecal T3 concentrations were related
1272 negatively to energy reserves (3C; r= -0.27, P=0.05), whereas fecal GC was related weakly to
1273 energy reserves (Fig. 3A, r= -0.13, P=0.25). Fecal GC and fecal T3 were strongly and
1274 positively related (Fig. 4; r= 0.55, P=<0.0001). In summary, all models possessed slope
1275 coefficients consistent with state-dependent foraging, with the slope coefficients of three out
1276 of four models in the opposite direction of those reported for captive, small-bodied animals
1277 (compare Fig. 1 and 3).

1278 Validation of the effects of dietary fiber, pregnancy, and age on fecal hormone
1279 concentrations indicate that pregnancy and age (Table S1), but not dietary fiber (fecal NDF;
1280 Fig. S1), influenced fecal hormone concentrations (see appendix S1). Controlling for the
1281 effects of dietary fiber on fecal hormone concentration did not change either the slope or the
1282 intercept of endocrine-energy relationships (Fig. S1; ANCOVA, all P>0.5). Age was included
1283 in top models (i.e., within 2 AIC_C) for fecal T3, but explained only 1% additional variation
1284 beyond the effects of energy intake and energy reserves (%IFBFat; Table S1). Both age and
1285 pregnancy were included in top models for fecal GC and explained an additional 6%

variation. Neither age nor pregnancy weakened or altered the directional effect of energy intake and energy reserves on fecal T3 and fecal GC concentrations.

DISCUSSION

Endocrine markers are an attractive tool for assessing resource limitation and informing conservation and management decisions because they offer a method for quantifying energetic state and can be non-invasively obtained. Moose exhibited endocrine-energy relationships that contrast with those of studies on captive and small-bodied animals (Fig. 1, 3, 4). In extrapolating from studies on captive animals, researchers often have made two assumptions about free-ranging animals: GC is related negatively to both energy reserves and energy intake, and T3 is related positively to both energy reserves and energy intake (Romero 2004, Welcker et al. 2009, Hayward et al. 2011, Wasser et al. 2011, Boonstra 2013, Gobush et al. 2014). These assumptions are upheld in some study systems, such as marine iguanas (*Amblyrhynchus cristatus*; Romero and Wikelski 2001) and black-legged kittiwakes (*Rissa tridactyla*; Kitaysky et al. 2010), but were not supported for a large-bodied, state-dependent forager (i.e., moose). Therefore, assumptions regarding endocrine-energy relationships deserve scrutiny when applied to taxa that exhibit state-dependent foraging and whose energy reserves do not respond quickly to changes in energy intake (e.g., large, free-ranging mammals).

Most research indicates that GC and T3 primarily reflect energy intake (Eales 1988, Kitaysky et al. 2007) because energy reserves quickly respond to changes in energy intake for species with high mass-specific metabolic rates (‘fast’ life histories), yet some studies, have related endocrine markers to energy reserves (Cherel et al. 1988b, Kitaysky et al. 1999,

1309 Daminet et al. 2003). The response of energy reserves to changes in energy intake of species
1310 possessing relatively low mass-specific metabolic rates (i.e., 'slow' life histories) are slow,
1311 which may allow for a clearer understanding of whether GC and T3 reflect energy intake or
1312 energy reserves. The relationship between fecal T3 and energy intake in moose was much
1313 stronger than the relationship between fecal T3 and energy reserves (Figs. 3C, 3D, Table S1),
1314 indicating that energy intake, and not energy reserves, more strongly controls expression of
1315 T3. These results support those of Hayden et al. (1993) who found that T3 levels in cattle (*Bos*
1316 *Taurus*) increase rapidly with increased energy intake. In contrast with previous reports, fecal
1317 T3 was negatively related to energy reserves (Fig. 3D; Danforth et al. 1979, Burger et al.
1318 1980, Danforth 1984, Cherel et al. 1988a, Cherel et al. 1988b, Eales 1988, Danforth and
1319 Burger 1989), which I suggest occurred because moose with few energy reserves had higher
1320 energy intake than moose with high energy reserves (Fig. 2). Although fecal GC was not
1321 related strongly to energy reserves (Fig. 3A), individuals with high energy intake possessed
1322 higher levels of fecal GC than those with low energy intake (Fig. 3B)—a pattern also in
1323 contradiction with previous reports (e.g., Kitaysky et al. 1999, Kitaysky et al. 2007, du Dot et
1324 al. 2009). I suggest that state-dependent foraging is the most likely explanation for these
1325 conflicting patterns (Figs. 1-3). Since state-dependent foraging is common among free-
1326 ranging animals, I recommend considering this behavior in future interpretations and
1327 applications of GC- and T3-energy relationships.

1328 Glucocorticoid (GC) production has been suggested to influence behavior and has
1329 been linked to state-dependent foraging through the idea of an "emergency life-history stage"
1330 (Wingfield et al. 1998). Animals experiencing an energy crisis (i.e., negative energy balance)
1331 enter an emergency life-history stage wherein behavior (foraging) and physiology (hormone

1332 production) are altered to regain energy balance. Glucocorticoids (GC) have been proposed to
1333 act as an anti-stress hormone rather than a stress hormone because the emergency life-history
1334 stage is adaptive (Wingfield and Kitaysky 2002, Boonstra 2013). In line with this notion,
1335 evidence indicates that increased GC resulting from reduced energy reserves or energy intake
1336 influences behaviors such as locomotor activity (Breuner et al. 1998, Lynn et al. 2003) and
1337 foraging rate (Kitaysky et al. 2001, Angelier et al. 2008). Although the relationship between
1338 energy reserves and fecal GC was not statistically significant, moose with low energy reserves
1339 generally exhibited higher levels of fecal GC than those with high energy reserves (Fig. 3A),
1340 and individuals with high fecal GC had higher energy intake than those with low fecal GC
1341 (Fig. 3B), which supports the State-Dependent Hypothesis and the notion that GC response in
1342 wild vertebrates is adaptive rather than pathological.
1343 Triiodothyronine (T3) profiles also may reflect foraging effort, and may therefore be
1344 useful in understanding state-dependent foraging. When energy reserves are depleted and
1345 energy intake is insufficient during fasting (e.g., breeding or molting in the wild, starvation in
1346 captivity), animals fall into negative energy balance and T3 declines to reduce energy
1347 consumption (Danforth 1984, Cherel et al. 1988a, Cherel et al. 1988b). Most free-ranging
1348 animals, however, are expected to be state-dependent foragers and alter foraging behavior
1349 when energetic reserves diminish (Houston and McNamara 1999). Increased foraging and
1350 locomotor activity increases field metabolic rate, which can be highly correlated with basal
1351 metabolic rate (Birt-Friesen et al. 1989). Although not confirmatory evidence, basal metabolic
1352 rate and the metabolic rate of many specific tissues is highly correlated with T3 production
1353 (Zheng et al. 2014). Thus, T3 may increase in concert with GC because GC encourages
1354 foraging activity and energy intake (Kitaysky et al. 2001). Supporting this notion, fecal GC

1355 was related positively with fecal T3 in moose (Fig. 4), a relationship also reported in free-
1356 ranging Hawaiian monk seals (*Monachus schauinslandi*; Gobush et al. 2014). Therefore, a
1357 positive relationship between GC and T3 may be expected in free-ranging animals if GC is
1358 associated with increased foraging and animals increase foraging when energy reserves are
1359 low (i.e., forage in a state-dependent manner).

1360 I assessed the effect of dietary fiber on fecal hormone concentrations because dietary
1361 fiber can both dilute or concentrate levels of fecal hormones relative to serum hormones
1362 (Goymann 2012). Further, I characterized the effects of age and pregnancy in moose before
1363 evaluating energy-endocrine relationships based on fecal hormones because these factors
1364 influence fecal GC independent of energy intake and energy reserves in red squirrels
1365 (*Tamiasciurus hundsoniscus*; Dantzer et al. 2010) and elk (*Cervus elaphus*; Creel et al. 2002;
1366 see appendix S2 for further discussion). Age and pregnancy influenced fecal GC and fecal T3
1367 concentrations in a similar fashion as reported for red squirrels and elk; the endocrine
1368 response of younger individuals was more sensitive to low levels of energy intake and energy
1369 reserves than the endocrine response of older individuals (Table S1). Similar to a previous
1370 report in another large herbivore (cattle; Rabiee et al. 2002), dietary fiber had no measurable
1371 effect on fecal hormone concentration in moose (see appendix S2). I suspect that my findings,
1372 and those previously reported for large herbivores, differ from the dilutive effects of dietary
1373 fiber discussed by Goymann (2012) for monogastric organisms, such as European stonechats
1374 (*Saxicola torquatus*) and chimpanzees (*Pan troglodytes*), because the digestive physiology of
1375 the rumen differs markedly from monogastric guts. For example, increased dietary fiber
1376 should reduce intake, reduce rate of digesta flow from rumen, and reduce fecal output,
1377 resulting in increased digesta transit time for ruminants (Gregory et al. 1985, Mertens 1987,

1378 Van Soest 1994, Allen 1996, Morrow et al. 2002). In contrast, increased fiber decreases
1379 digesta transit time in monograstric fermenters (Wasser et al. 1993, Goymann 2005). I suggest
1380 that the effects of fiber on fecal-based endocrine-energy relationships may differ across taxa,
1381 especially monogastric and ruminant fermenters (Millspaugh and Washburn 2004). I do
1382 acknowledge, however, that future experimental approaches to validating the relationship
1383 between fecal GC, fecal T3, and potentially confounding covariates are warranted.
1384 Accounting for such confounds in fecal assays and other non-invasive techniques is critical to
1385 ensure accurate application of endocrine markers.

1386 Understanding how energy intake and energy reserves influence endocrine markers is
1387 critical if these markers are to be used to identify factors limiting population growth and make
1388 conservation and management decisions regarding wild populations. Had I assumed GC- and
1389 T3-energy relationships derived from captive animals translated well to free-ranging moose, I
1390 would have mischaracterized the nutritional condition of moose in this study. This result
1391 carries important implications for the management and conservation of both harvestable
1392 species and species of conservation concern. The nutritional condition (energy reserves) of
1393 large herbivores underpins individual life-history characteristics, which in turn determine
1394 population dynamics, especially in the absence of strong top-down forcing (Eberhardt 2002,
1395 Monteith et al. 2014b). Hence, harvest quotas for large herbivores are often set to maintain
1396 populations near nutritional carrying capacity (i.e., the number of animals the landscape can
1397 energetically and nutritionally support). For species of conservation need, which tend to be
1398 cryptic or rare, endocrine markers often represent one of few approaches available to
1399 managers and scientists for assessing resource limitation (Millspaugh and Washburn 2004,
1400 Wikelski and Cooke 2006). Therefore, it is critical that endocrine-energy relationships are

broadly understood, and not simply assumed, so that endocrine markers can be implemented across taxa and environments without misleading inference regarding conservation and management. By demonstrating how endocrine-energy relationships can be altered from previous expectations through the foraging behavior and physiology of a free-ranging, large-bodied species, this study represents an important step towards a broader understanding of endocrine-energy relationships, and thus more accurate application of endocrine makers.

Fig. 1. Graphical comparison of predictions of associated with 'classical' endocrine-energy relationships (panels A and B) versus predictions of endocrine-energy relationships stemming from the State Dependent Hypothesis (panels C and D). Although predictions of GC and T3 profiles by themselves are common to multiple hypotheses, each hypothesis is defined by a unique combination of predicted GC and T3 profiles.

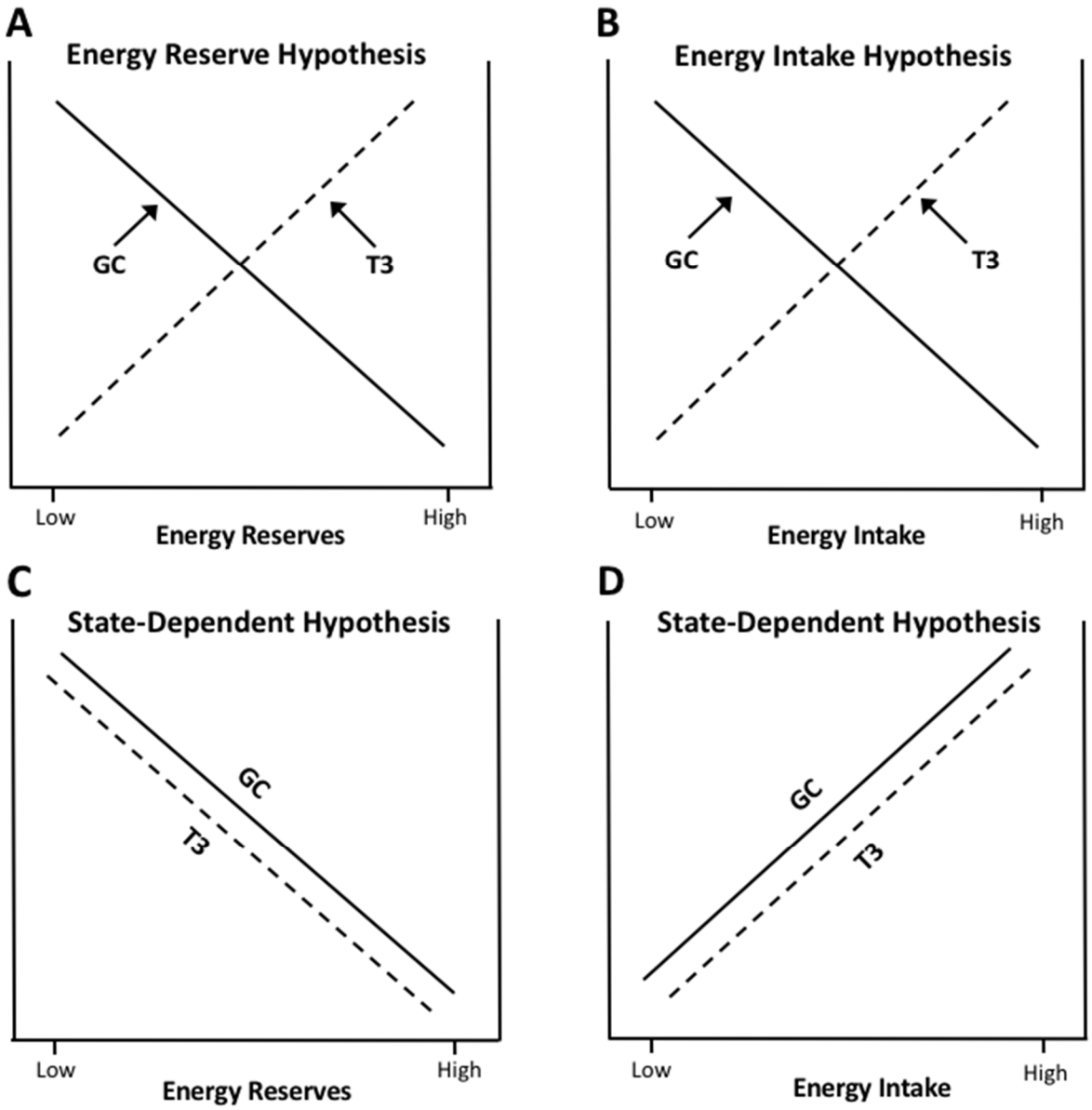


Fig. 2. Relationship between energy reserves (% IFBFat) and three metrics of energy intake for free-ranging moose in the southern Greater Yellowstone Ecosystem, WY, USA during winter: A) fecal NDF^{-1} ($FNDF^{-1}$), B) fecal N (FN), and C) $FNDF^{-1} \times FN$ (solid lines illustrate fitted regression line). Negative correlation coefficients indicate state-dependent foraging.

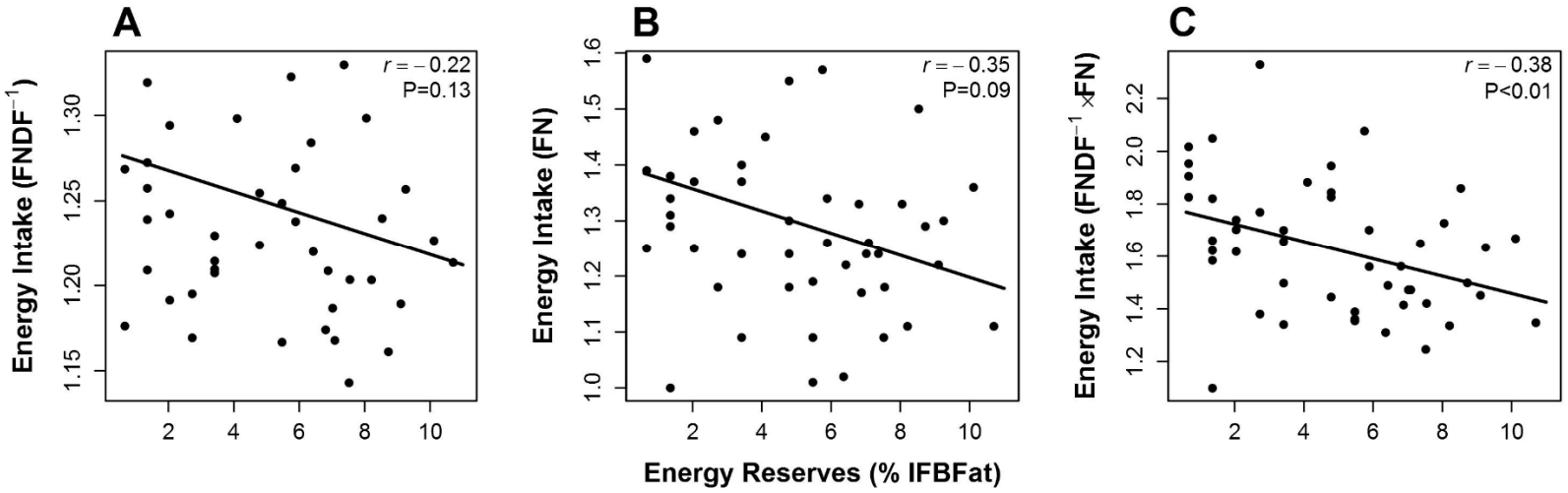


Fig. 3. The relationships between fecal glucocorticoid (GC) and fecal triiodothyronine (T3) metabolites and varying levels of energy reserves (% IFBFat) and energy intake ($FNDF^{-1}$) in free-ranging moose during winter in the southern Greater Yellowstone Ecosystem, WY, USA (solid lines illustrate fitted regression line). Correlation coefficients support the State-Dependent Hypothesis (Fig. 1C, 1D).

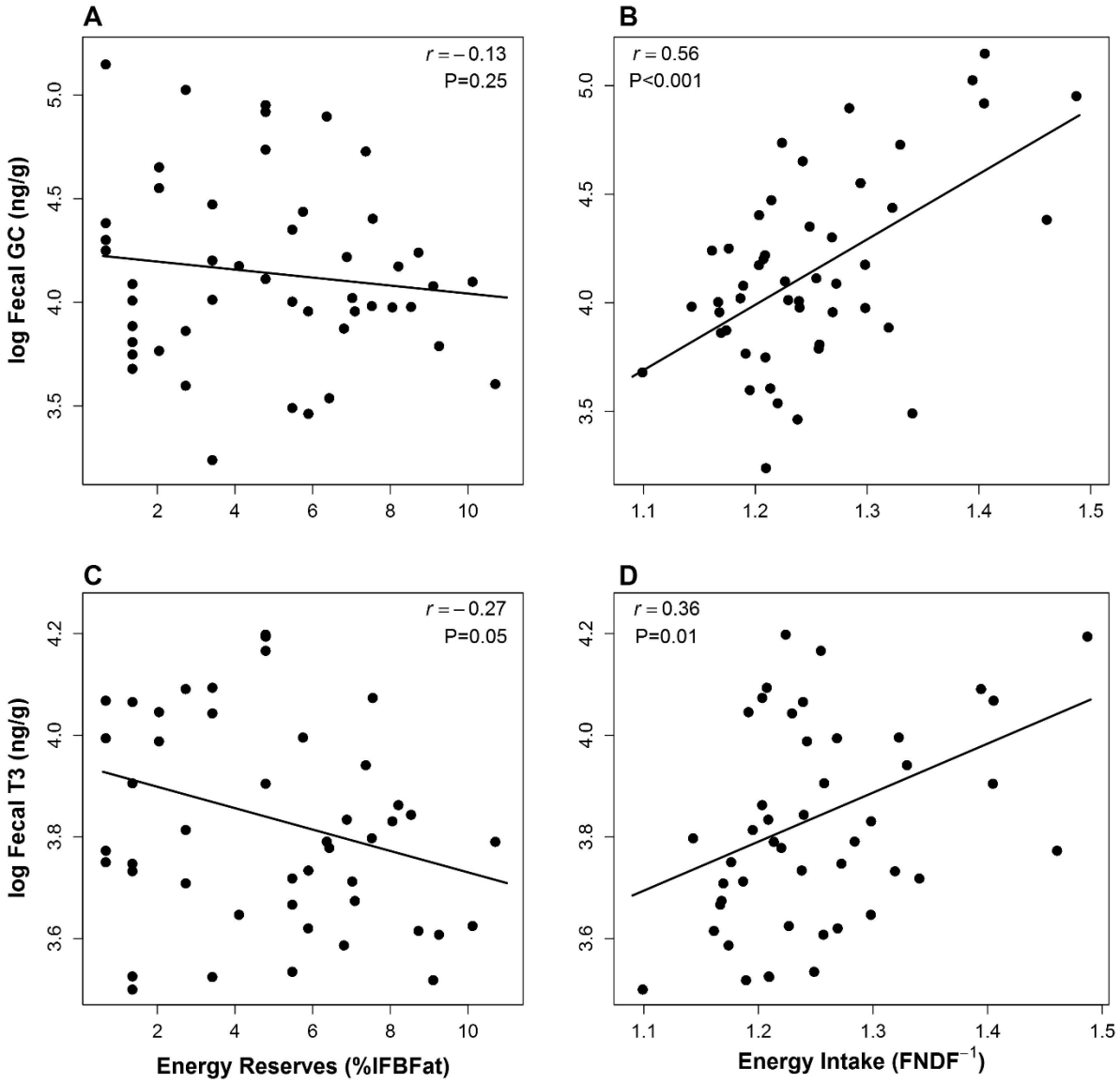
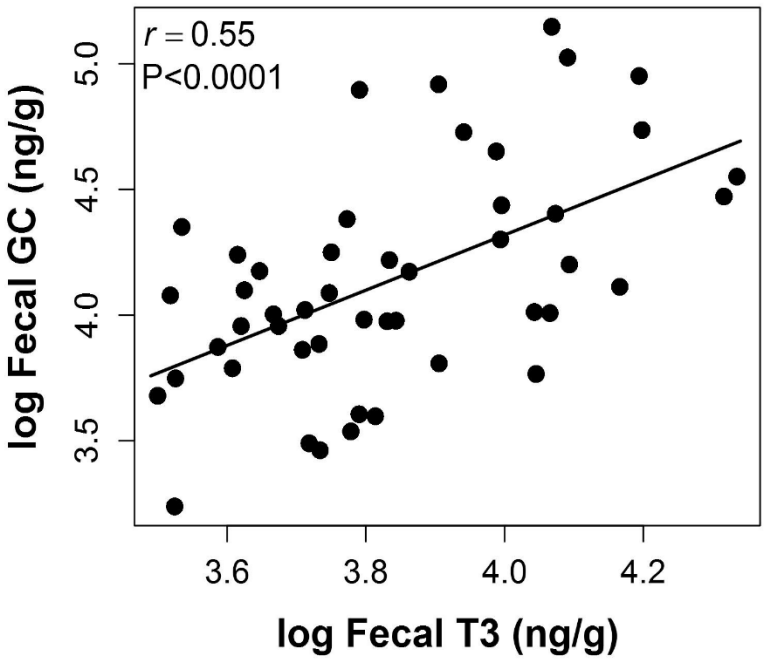


Fig. 4. The relationship between fecal glucocorticoid (GC) and triiodothyronine (T3) in free-ranging moose during winter in the southern Greater Yellowstone Ecosystem, WY, USA (solid lines illustrate fitted regression line). A positive correlation between high stress levels (GC) and high energy intake (T3) indicates state-dependent foraging.



APPENDIX S2

Advantages and potential confounding factors of fecal-based hormone profiles— Over the past decade, fecal-based analysis of endocrine markers has become increasingly popular because it offers a cost-effective, non-invasive method to quantify the endocrine status of free-ranging animals (Millspaugh and Washburn 2004, Palme 2005, Goymann 2012). Hormone metabolites pool in digesta over time, making fecal-based assessments advantageous because they provide 'smoothed' endocrine profiles (Millspaugh and Washburn 2004, Goymann 2005, Sheriff et al. 2011). Further, capture-related stress generally causes serum GC to spike within minutes (Creel et al. 1997, Romero and Reed 2005, Romero et al. 2008), whereas increased GC caused by capture stress in large ruminants is not expected to appear in feces for approximately 12–24 hours post-capture (Palme et al. 1996, Palme and Möstl 1997, Millspaugh et al. 2002, Morrow et al. 2002, Palme et al. 2003, Palme et al. 2005). Therefore, measuring fecal hormones eliminates the need to sample serum within minutes of capture (an impossibility given my study species and capture methods).

Diet may confound interpretation of energy-endocrine relationships because dietary fiber affects digesta passage rate and fecal mass, thereby influencing hormone metabolite pooling and fecal hormone concentrations (Goymann 2012). Dietary fiber has inconsistent effects on fecal hormone concentrations: Increased dietary fiber can increase fecal hormone concentrations relative to serum levels (Goldin et al. 1981, Goldin et al. 1982, Gorbach and Goldin 1987, Pusateri et al. 1990, Dantzer et al. 2011), but increased dietary fiber can also reduce fecal hormone concentrations relative to serum levels in monogastric organisms (Wasser et al. 1993, Goymann 2005). There has been little validation of the effect of dietary fiber on the relationship between serum and fecal hormone concentrations in ruminants, which process fiber differently

than monogastric animals (Millspaugh and Washburn 2004). I found a single report on the effect of dietary fiber on fecal hormone concentrations in a ruminant, the domestic cow (*Bos taurus*), which suggested that increased dietary fiber leads to increased fecal hormone concentrations relative to blood plasma (Morrow et al. 2002). In accordance with the findings of Morrow et al. (2002), ruminant physiology dictates that increased dietary fiber should reduce intake, reduce rate of rumen digesta flow, and reduce fecal output, resulting in increased digesta transit time (Gregory et al. 1985, Mertens 1987, Van Soest 1994, Allen 1996, Morrow et al. 2002). In response to variability in the effect of dietary fiber on fecal hormone concentration (Goymann 2012, pg. 759-760) I aimed to validate, and therefore control for, the effect of dietary fiber in the present study of fecal-based endocrine-energy relationships.

Age and pregnancy may also confound endocrine-energy relationships. For example, the reproductive state of females may influence GC profiles because gestation affects energy balance and may act as a stressor (Dantzer et al. 2010). Additionally, the responsiveness of the hypothalamic-pituitary-adrenal axis may change with age (for review, see Dantzer et al. 2014), and controlling for age may reveal important endocrine responses to stressors (Creel et al. 2002). Potential confounds for the interpretation of fecal T3 have not been addressed, likely because fecal T3 has a relatively short history in the fields of ecophysiology, conservation biology, and nutritional ecology compared to fecal GC. Therefore, age and pregnancy were considered potentially confounding covariates when assessing both fecal GC and fecal T3-energy relationships.

Fecal-based measures of energy intake— Dietary nitrogen (N) and its fecal proxy are measures of protein and energy intake in ruminants (Van Soest 1994, Hodgman et al. 1996, Leslie et al.

2008). Although debate exists (e.g., see Leslie and Starkey 1985, Hobbs 1987, Leslie and Starkey 1987), fecal N accurately characterizes forage quality within species, sex, and reproductive (lactation) categories (Leslie et al. 2008, Monteith et al. 2014a). The potential binding of plant nitrogen by secondary metabolites can inflate fecal N values as demonstrated by feeding herbivores high-tannin diets in captivity (e.g., diets consisting of >40% oak leaves or acorns, 100% maple leaves, 100% fireweed; Mould and Robbins 1981, Robbins et al. 1987, Osborn and Ginnett 2001, Verheyden et al. 2011). Free-ranging herbivores, however, rarely ingest such high levels of secondary metabolites, thereby minimizing the confounding effect of tannins on fecal N values (Hodgman et al. 1996, Leslie et al. 2008). I assumed a minimal effect of secondary metabolites on inter-individual measures of fecal N because all individuals were non-lactating females with similar forage composition. Thus, fecal N was considered a reliable measure of dietary protein.

For ruminants, forage neutral detergent fiber (NDF) and its fecal proxy provide a measure of digestible energy and an additional measure of protein availability (Van Soest 1994, Brown et al. 1995, Hodgman et al. 1996). Under high protein–high energy diets, fecal NDF is reduced relative to low protein–high energy diets (Brown et al. 1995). This likely is because increased protein can increase gut microbe production and thus fiber digestion. Therefore, the interaction between fecal NDF and fecal N may be a better measure of energy intake compared to either metric alone. Additionally, increased NDF increases digestion time, thus reducing forage intake (Mubanga et al. 1985, Church 1988, Allen 1996, Meyer et al. 2010). Further, small changes in diet quality can lead to large changes in energy intake over both short and long time scales (i.e., the "multiplier effect"; White 1983). Because increased NDF reduces both digestible energy and

forage intake and this can lead to meaningful changes in energy intake, the inverse of fecal NDF (NDF^{-1}) was considered a proxy for energy intake.

Field and lab methods for measuring potential confounding covariates— I captured and handled moose per the methodology presented in the main document. To assess the age of each individual, I extracted a incisiform canine (Swift et al. 2002) and counted cementum annuli (Matson Laboratory, Milltown, MT, USA). I collected a blood sample (20ml) via jugular venipuncture, and the resulting serum from centrifugation was pipetted into 5ml cryovials and stored at -20˚C until analyzed for pregnancy-specific protein B. All methodology was approved by the Institutional Animal Care and Use Committee at the University of Wyoming (Permit # A-3216-01).

The commercially available BioPRYN wild assay was used to determine pregnancy-specific protein B concentrations and was completed by BioTracking LLC (Moscow, ID, USA). BioPRYN wild is a typical sandwich enzyme-linked immunosorbent assay for determination of pregnancy-specific protein B levels in serum samples (Green et al. 2005). The presence of color development was determined by a plate reader with a filter wavelength of 450 nm (VersaMax, Molecular Devices, Inc). The assay included 4 standards run in duplicate on each plate. The standards were halving dilutions from 1 ng/ml to 0.125 ng/ml. Simple linear regression was then used to fit an equation to the standards for each plate. The resulting equation was used to calculate a quantitative measure of pregnancy-specific protein B concentration in each serum sample (non-pregnant $\bar{X} = 0.005$ ng/ml, range 0—0.09 ng/ml; pregnant $\bar{X} = 17.7$ ng/ml, range 5.3—35.4 ng/ml).

Quantifying the effect of potential confounding covariates— To characterize the possible confounding nature of dietary fiber, age, and pregnancy, I used a two-stage approach. First, to quantify the effects of dietary fiber on fecal hormone concentrations, I regressed fecal GC and fecal T3 on fecal NDF and extracted residual values. The residual values from the regressions represent fecal hormone concentrations after controlling for the effect of fiber. I then asked if the relationship between residual fecal hormone values and energy reserves (% IFBFat) were similar to the relationship between raw fecal hormone values and % IFBFat. If the relationship between raw hormone values and %IFBFat and residual hormone values and %IFBFat were similar, this would indicate that the effect of energy reserves on hormone concentrations are independent of dietary fiber and thereby provide evidence that dietary fiber does not strongly influence endocrine-energy relationships in my study. Alternatively, if the relationship between raw hormone values, residual hormone values, and %IFBFat differed, I would consider dietary fiber to affect my interpretation of endocrine-energy relationships. I compared the regression coefficients and intercepts with analysis of covariance (ANCOVA) after standardizing fecal GC, fecal T3, residual GC, and residual T3 values.

To address the effect of age and pregnancy on fecal GC and fecal T3 concentrations I used an information-theoretic approach (Burnham and Anderson 2002). I used Akaike's information criterion adjusted for small sample size (AIC_c) to assess the influence of age and pregnancy on the relationship between energy reserves, energy intake and fecal hormone concentrations. I examined correlation between explanatory variables using the Pearson correlation coefficient and excluded highly correlated explanatory variables ($r > 0.5$) from simultaneously entering the same model. I conducted a Shapiro-Wilk test of normality (Royston

1982) on the distribution of residuals to ensure model assumptions were met. All analyses were performed using program R (R Core Team 2014).

Fecal NDF did not alter the relationship between fecal hormone concentration and %IFBFat (Fig S1; A) GC [slope P=0.59, intercept P=1.0], B) T3 [slope P=0.76, intercept P=1.0]). Pregnancy was strongly related to energy reserves (logistic regression, P<0.01) and was not considered simultaneously with energy reserves in fecal GC or fecal T3 models. Neither age nor pregnancy were included in top models for fecal GC or fecal T3, however, they were included in top model sets (i.e., models within 2 AIC_c; Table S1). Including age or pregnancy explained only one percent additional variation in fecal T3; however, age and pregnancy explained an additional six percent of variation in fecal GC (Table S1). Nevertheless, neither age nor pregnancy changed the slope coefficients for %IFBFat, fecal NDF, or fecal N in direction or strength (Table S1), indicating that controlling for the effects of age and pregnancy were not critical in the interpretation of the relationships between energy reserves or energy intake and hormone concentrations.

Fig S1. Relationships between A) fecal GC, residual fecal GC and % IFBFat, B) fecal T3, residual fecal T3 and % IFBFat. Solid lines and grey polygons illustrate fitted regression equations and their 95% confidence interval for the relationship between fecal T3, fecal GC, and % IFBFat. Dashed lines and dotted lines illustrate fitted regression equations and their 95% confidence interval for the relationship between residual fecal T3, residual fecal GC, and % IFBFat. ANCOVA revealed no difference in intercept or slope between relationships (all P>0.5). All hormone values were standardized for direct comparison.

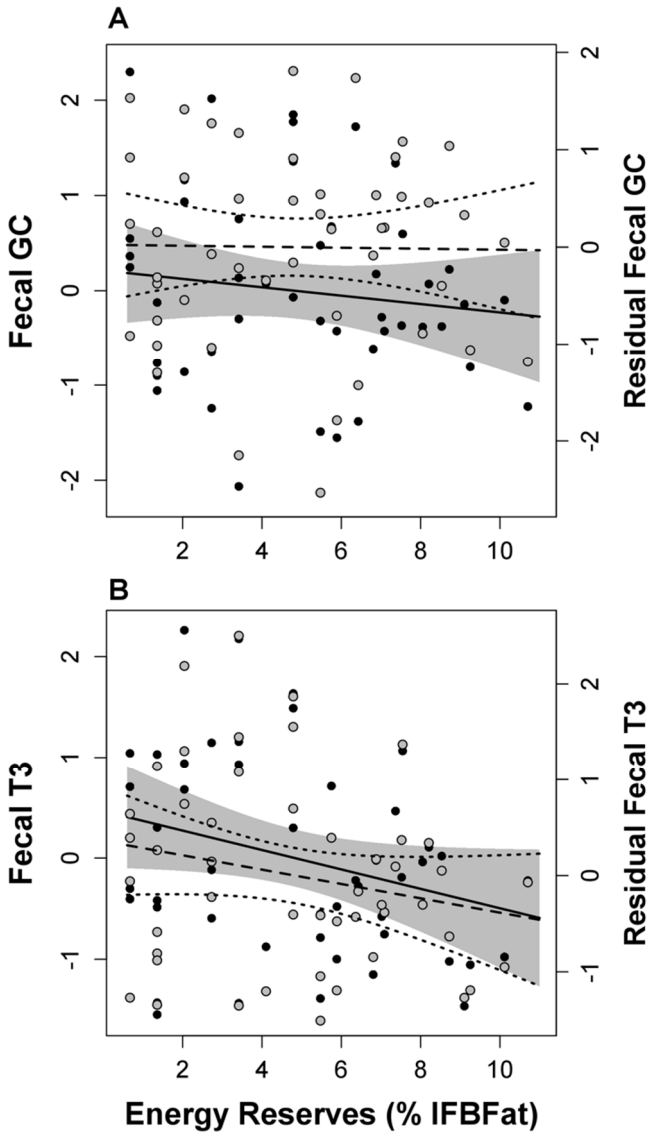


Table S1. Model covariates, fit statistics, and P-values. Considering age and pregnancy covariates do not have a sizable effect on the relationship between energy reserves, energy intake and fecal hormone concentrations. Energy reserves (% IFBFat) and energy intake (fecal NDF and fecal N) produce the most parsimonious models of fecal GC and fecal T3.

GC

IFBFat	FNDF	FN	FNDF * FN	age	preg	AICc	delta	weight	R^2	P
	0.56					44.70	0.00	0.27	0.31	<0.001
	0.62			-0.16	+	45.44	0.74	0.19	0.37	<0.001
	-1.03	-3.16	3.84			46.69	1.99	0.10	0.35	<0.001
	-0.94	-3.07	3.72		+	46.94	2.25	0.09	0.38	<0.001
0.00	0.56					47.08	2.38	0.08	0.31	<0.001
	0.59	0.01			+	47.14	2.45	0.08	0.34	<0.001
	-1.06	-3.34	4.07	-0.18	+	47.29	2.59	0.07	0.41	<0.001
-0.01	0.58			-0.17		47.49	2.80	0.07	0.34	<0.001
0.01	-1.15	-3.45	4.21	-0.20		49.21	4.51	0.03	0.39	<0.001
0.01	-1.03	-3.16	3.85			49.30	4.60	0.03	0.35	<0.001
		0.14				61.58	16.88	0.00	0.02	0.36
-0.13						61.71	17.02	0.00	0.02	0.39
					+	62.32	17.63	0.00	0.00	0.70
-0.09		0.11				63.62	18.92	0.00	0.03	0.56
-0.13				-0.08		63.79	19.09	0.00	0.02	0.60
		0.14			+	63.80	19.10	0.00	0.02	0.61
				-0.07	+	64.51	19.81	0.00	0.01	0.85
-0.09		0.11		-0.09		65.73	21.03	0.00	0.03	0.68
		0.15		-0.08	+	65.99	21.29	0.00	0.03	0.73

T3

IFBFat	FNDF	FN	FNDF * FN	age	preg	AICc	delta	weight	R^2	P
	0.36					-10.39	0.00	0.25	0.13	0.01
-0.21	0.31					-10.30	0.09	0.24	0.17	0.02
-0.21	0.33			-0.11		-8.54	1.85	0.10	0.18	0.03
	0.34				+	-8.21	2.19	0.08	0.13	0.04
-0.27						-7.68	2.72	0.06	0.08	0.05
	0.18	-0.15	0.35			-6.68	3.71	0.04	0.15	0.07
	0.36			-0.12	+	-6.46	3.93	0.04	0.14	0.08
		0.21				-6.17	4.22	0.03	0.05	0.14
-0.23		0.14				-6.14	4.25	0.03	0.09	0.11
-0.18	0.20	-0.10	0.24			-5.61	4.79	0.02	0.17	0.08
-0.28				-0.06		-5.48	4.91	0.02	0.08	0.16
					+	-4.82	5.58	0.02	0.02	0.35
		0.21			+	-4.70	5.69	0.01	0.06	0.22
	0.15	-0.18	0.40		+	-4.30	6.09	0.01	0.15	0.12
-0.23		0.14		-0.07		-3.93	6.47	0.01	0.10	0.21
-0.18	0.13	-0.28	0.46	-0.12		-3.70	6.69	0.01	0.19	0.11
				-0.07	+	-2.64	7.75	0.01	0.02	0.59
		0.22		-0.09	+	-2.61	7.79	0.01	0.07	0.34
	0.06	-0.38	0.65	-0.13	+	-2.52	7.87	0.00	0.17	0.15

CHAPTER THREE

ARE HERITABLE FORAGING TRAITS REQUIRED FOR INDIVIDUAL SPECIALIZATION? A TEST OF THE NICHE VARIATION HYPOTHESIS IN A RUMINANT HERBIVORE

ABSTRACT

Individual variation in resource use plays a central role in the ecology and evolution of species and communities. Nevertheless, context-dependent differences in how individual resource-use responds to resource limitation has led to uncertainty in the 'rules' that govern foraging behavior. While both the Niche Variation Hypothesis (NVH) and Optimal Foraging Theory (OFT) posit that total niche width increases with increased resource limitation, the NVH posits that individuals specialize on subsets of resources to reduce intraspecific competition, whereas OFT predicts that individuals use resources similarly and broaden their dietary niche to reduce competition for preferred resources. When behavioral and morphological phenotypes associated with foraging (i.e., dietary phenotypes) are inherited, individuals tend to specialize on subsets of resources. Using DNA microsatellites and DNA metabarcoding of trnL (plant) and 16S (bacteria and archea), I quantified the diet and rumen microbiome composition, and pairwise relatedness of 198 individual moose (*Alces alces*) across six populations that varied in degree of resource limitation. As resource limitation intensified, total niche width increased as a result of increased individual diet breadth rather than individual specialization. Neither diet nor microbiome was inherited from closely related conspecifics. I suggest coevolution of the rumen and toxic plant defenses promote flexible diet selection, reduce inheritance of diet, and thereby constrain the

ability of ruminants to specialize. Thus, one context under which OFT prevails over NVH is when the physiology and natural history of a species restrict heritability of dietary phenotypes.

INTRODUCTION

Recently, ecologists have come to appreciate that populations can be comprised of individuals that vary markedly in resource use, yet classical foraging theory (i.e., Optimal Foraging Theory; OFT) assumes that conspecifics exploit resources in a similar manner (Araujo et al. 2011). The Niche Variation Hypothesis (NVH; Van Valen 1965) posits that the breadth of resources used by a population (i.e., total niche width, sensu Roughgarden 1972) stems primarily from increases in among-individual diversity, wherein groups of individuals reduce intraspecific competition by specializing on subsets of resources available to the population (Fig. 1A; Roughgarden 1974, Bolnick et al. 2003, Tinker et al. 2008). In contrast to the NVH, OFT assumes that the total niche width of a population reflects an expansion of within-individual diversity in resource use (i.e., indvidual diet breadth; Fig. 1B; Krebs et al. 1977, Pyke 1984). Despite contrasting assumptions about how individuals use resources, both the NVH and OFT share an explicit prediction—total niche width expands as resources become limiting (Fig 1A, B; Roughgarden 1974, Krebs et al. 1977, Svanbäck and Bolnick 2007). Although there is increasing consensus that total niche width expands under resource limitation because of increased dietary specialization (i.e., low within-individual dietary diversity relative to total niche width; Bolnick et al. 2003, Bolnick et al. 2007), a recent meta-analysis demonstrated that niche expansion results from individuals increasing their diet breadth equally as often as from increased individual specialization (Fig. 1C; Araujo et al. 2011). Thus, although both the NVH and OFT clearly operate in the natural world, ecologists

lack a framework for understanding the context under which the predictions of the NVH and OFT should be upheld.

The context wherein the NVH and OFT explain consumer-resource interactions could be illuminated if the mechanisms by which individuals specialize on subsets of resources or broaden their diets were better understood (Araujo et al. 2011). Variation in phenotypic traits associated with foraging is one mechanism by which individuals might specialize on subsets of resources (Bolnick et al. 2007). For example, intraspecific variation in the size of gill-raker spines used to strain and retain prey allows three-spine sticklebacks (*Gasterosteus aculeatus*) to specialize on different-sized prey (Bolnick 2004, Matthews et al. 2010). The lengthening of the gastrointestinal track in Eurasian perch (*Perca fluviatilis*) permits them to specialize on prey that are otherwise difficult to digest (Svanback and Persson 2004, Olsson et al. 2007). And *Anolis* lizards (*Anolis marmoratus*) are capable of specializing on different-sized invertebrates because of variation in jaw size (Roughgarden 1974, Bolnick et al. 2007). Because these morphological traits are heritable, individual specialization is thought to be promoted and maintained by divergent selection (Bolnick 2004). Hence, when morphological variation is low and selection cannot promote individual specialization, increased diet breadth of individuals may underlie total niche width expansion.

Individual specialization may also be maintained through inheritance of behavioral phenotypes. For instance, diet selection may be genetically inherited or inherited via social learning (Ritchie 1991). Across the animal kingdom, foraging sites and behaviors that improve foraging efficiency are often socially learned (e.g., Weigl and Hanson 1980, Estes et al. 2003, Leadbeater and Chittka 2007, Slagsvold and Wiebe 2011, Aplin et al. 2015). Consequently, social learning of diet selection can be culturally transmitted across generations and maintain

individual specializations (Whiten 2005, Tinker et al. 2008, van de Waal et al. 2013, Kopps et al. 2014, Jesmer et al. 2018). In contrast, trial and error learning allows individuals to adjust diets in accord with resource availability (Freeland and Janzen 1974, Provenza and Balph 1987), resulting in increased individual diet breadth under resource limitation. Thus, whether the NVH or OFT explains taxa-specific foraging behavior may be mediated by whether diet selection is inherited and relatively rigid (i.e., giving rise to diet specialization and supporting the NVH) or flexible and capable of shifting with changing resource levels (i.e., giving rise to expanding individual diets and supporting OFT).

Decades of detailed experiments involving model organisms have provided a robust understanding of individual specialization and optimal foraging under resource limitation, yet such knowledge is lacking for many large-bodied species, including ruminant herbivores (Araujo et al. 2011). Optimal foraging in ruminant herbivores is dictated by a simple rule: maximize energy and nutrient intake while minimizing ingestion of plant toxins (Freeland and Janzen 1974, Belovsky 1978, Bryant and Kuropat 1980). The coevolution of plants and herbivores has resulted in virtually all plants possessing toxic chemical defenses (Bryant et al. 1983, Bryant et al. 1991, Karban and Agrawal 2002). Although ruminant herbivores counteract these defenses with proline rich saliva and symbiotic gut microbes capable of breaking down plant toxins (Hofmann 1989, Barboza et al. 2010), diets high in plant toxins nevertheless limit energy and nutrient assimilation (Barboza et al. 2009, McArt et al. 2009). As such, ruminant herbivores forage on a diverse array of plants to prevent over-ingestion of any single toxin (Provenza et al. 2003, Parikh et al. 2017). Further, phenological changes in the quality and quantity of plants cause herbivores and their gut microbiome to boast flexible diet preferences (Barboza et al. 2010, Lawrence et al. 2013). Hence, specializing on a small number of plants may be difficult for ruminant herbivores

1665 because their digestive physiology has evolved to be flexible, and ingestion of a small subset of
1666 toxins in large quantities is physiologically costly.

1667 Despite the constraints an herbivorous lifestyle may place on dietary specialization, many
1668 foraging behaviors of ruminant herbivores are indeed inherited (Edwards 1976, Provenza and
1669 Balph 1987, Sweanor and Sandegren 1989, Jesmer et al. 2018), suggesting that diet
1670 specialization may be maintained via either genetic inheritance or social learning. Additionally,
1671 the gut microbiome of herbivores may also be inherited via social transmission between mother
1672 and offspring during parturition, and post-parturition via contact with maternal feces, milk, skin,
1673 other social conspecifics, and the environment (Ducluzeau 1983, Barboza et al. 2010, Tung et al.
1674 2015). Thus, if diet composition is constrained by the gut microbiome (Kohl et al. 2014), then
1675 inheritance of the gut microbiome may help maintain diet specializations. Understanding the
1676 mechanisms that dictate diet preference in ruminant herbivores will therefore not only help
1677 illuminate the contexts within which the rules of the NVH and OFT determine niche breadth, but
1678 will also provide a greater appreciation for the natural history of this taxonomic guild.

1679 To evaluate the mechanisms by which herbivores alter their diet when resources become
1680 limited, I tested predictions stemming from four hypotheses. First, I evaluated whether the total
1681 niche width of moose (*Alces alces*), a generalist ruminant herbivore, expanded under resource
1682 limitation according to (1) the Niche Variation Hypothesis, in which the expansion of total niche
1683 width stems primarily from groups of individuals specializing on subsets of dietary resources
1684 (i.e., increase among-individual diversity; Fig. 1A), or (2) Optimal Foraging Theory, which
1685 posits that total niche width largely reflects individual diet breadth (i.e., within-individual
1686 diversity; Fig. 1B). I then assessed if individual diets, and by extension, total niche widths were
1687 shaped by inheritance of diet selection, a notion I refer to as the (3) Diet Inheritance Hypothesis

(Fig. 2). I also tested the (4) Gut Microbiome Inheritance Hypothesis, which posits that the gut microbiome is inherited and constrains diet selection (Fig. 2).

METHODS

Study Area—I studied six populations of moose in Wyoming, northern Colorado, and northern Utah, USA, where habitats were characterized by riparian shrublands dominated by Booth's willow (*Salix boothii*), Geyer's willow (*Salix geyeriana*), and planeleaf willow (*Salix planifolia*). Within riparian shublands, several other willow species, deciduous shrubs (e.g., *Betula glandulosa*, Rosaceae spp.), cottonwoods (*Populus* spp.), and a number of grasses (Poaceae spp.), sedges (*Carex* spp.) and forbs (e.g., Asteraceae, Onagraceae) also were common. Moose also used upland habitats that interspersed riparian habitats (hereafter "uplands"; Baigas 2008, Becker 2008, Oates 2016) characterized by mixed conifers (*Abies lasiocarpa*, *Picea engelmannii*, *Pinus contorta, Pseudotsuga menziesii*), aspen (*Populus tremuloides*), sagebrush (*Artemisia* spp.), mountain mahogany (*Cercocarpus* spp.), and bitterbrush (*Purshia tridentata*). All populations were exposed to high seasonality, with winters characterized by deep snow (mean February snow depth 78±15 cm) and cold temperatures (mean February low temperature -15±1˚C), while summers were characterized by low precipitation (mean July rainfall 4±1cm) and mild temperatures (mean July high temperature 23±2˚C; Western Regional Climate Center).

Study Design and Sampling— Rates of calf recruitment are a sensitive measure of resource limitation for ruminant herbivores (Gaillard et al. 1998, Eberhardt 2002). I therefore worked with the Wyoming Game and Fish Department and the Colorado Division of Parks and Wildlife to

obtain population-level calf recruitment estimates for each of my six study populations. To estimate calf recruitment, biologists counted and classified age (adult, yearling or juvenile) and sex (male or female for yearlings and adults) of individual moose from helicopters during winter (i.e., December to February). Calf recruitment is measured as the number of calves observed per 100 cows. From 1947-1987, moose were translocated from historical (native) populations in western Wyoming and northern Utah to mountain ranges in eastern Wyoming and northern Colorado possessing abundant moose habitat (Brimeyer and Thomas 2004). Combined with variation in climate and plant productivity, these translocations created a threefold difference in resource limitation (as indexed by calf recruitment) among the six populations (Fig. S1).

To quantify diet and microbiome composition of individuals in each population, I collected fecal samples via stratified random sampling along transects within two strata: riparian shrublands and uplands. I constrained my sampling to areas where moose were likely to be found foraging and defecating (hereafter "core habitat"), which I modeled using random forests (Evans et al. 2011; see S3 for detailed modeling procedure) and locations derived from GPS-collared individuals (n=1,523,829 locations) representing three populations and 174 individual moose (Baigas et al. 2010, Oates et al. 2018). I then used the National Land Cover Database (Homer et al. 2015) to further constrain my sampling within core habitat to riparian shrubland and upland habitat strata. Within each stratum, I identified 20 locations for each population using a spatially-balanced stratified random design (Stevens and Olsen 2004, Kincaid et al. 2012). At each location, I randomly selected a direction that would allow us to remain within the habitat strata for the entire 2-km sampling transect. I used detection dogs to find fecal samples along transects during summer when fecal samples scattered across vast areas, were hidden by thick vegetation, and were required to be recently defecated (<48 hr old) for DNA analysis (Dahlgren et al. 2012).

During winter, however, visual detection of fecal samples was feasible because feces were concentrated on winter ranges, readily detected in snow, and were frozen shortly after defecation by the cold winter conditions in my study area. All samples were collected according to a sterile protocol and placed frozen within 8 hr at -20^{o}C.

Genetic Analyses—To identify individual moose and their sex, I developed multi-locus genotypes from fecal samples using nine microsatellite loci and a sex marker (Table 1). I extracted DNA from fecal samples using a sterile protocol and the QIAamp DNA Stool Mini Kit (Qiagen, Inc.; Adams et al. 2011, Woodruff et al. 2014). Through an iterative trial-and-error process, I optimized multiplex PCR conditions such that all nine microsatellites and the sex marker were amplified in a single PCR reaction (Table S1). Fecal DNA is often highly degraded and fecal contamination may interfere with microsatellite amplification, resulting in genotyping errors (Pompanon et al. 2005). I therefore employed a multiple tubes approach, wherein a minimum of three PCR reactions were conducted for each fecal sample (Taberlet et al. 1996). Microsatellite fragment lengths were then quantified by Cornell University's Biotechnology Resource Center using an ABI 3730xl DNA Analyzer (Applied Biosystems). Each fragment analysis was genotyped by two independent observers using GeneMarker® (SoftGenetics, LLC). If fewer than five microsatellites amplified during the first three PCR attempts, the sample was discarded. If five or more microsatellites amplified during the first three PCR, I used program Reliotype (Miller et al. 2002) to estimate the number of additional genotypes needed to identify a reliable genotype for a given fecal sample. This process was iterated until a reliable genotype was identified or a sample was genotyped nine times, after which the sample was discarded. Because genotypic data derived from fecal DNA are prone to genotyping error, I used program

GIMLET (Valière 2002) to estimate genotyping error rates (Table 1) and create a final consensus genotypes from the genotypes developed for each PCR. I then used the genotypic data and the package AlleleMatch in Program R to identify individual moose (Galpern et al. 2012). I used the probability that two genotypes were indeed unique individuals and not simply siblings with similar genotypes (i.e., Psibs<0.05) as a conservative measure of individual identification (Waits et al. 2001). To facilitate assessment of the Diet Selection and Gut Microbiome Inheritance Hypotheses, I used the genotypic data to estimate pairwise relatedness coefficients in GeneAlEx 6.5 (Lynch and Ritland 1999, Peakall and Smouse 2012)

I used DNA metabarcoding techniques to quantify diet and microbiome composition of individual moose identified via multilocus genotyping. If multiple fecal samples belonged to the same individual, I randomly selected a single fecal sample to represent the diet and microbiome of that individual. DNA was extracted from fecal samples using the MoBio PowerSoil htp-96 well Isolation Kit (Qiagen, Inc.) according to the manufacturer's protocol. Diet composition was determined by sequencing the P6 loop of the chloroplast trnL(UAA) intron using c and h trnL primers (Taberlet et al. 2007; Table S1), whereas microbiome composition was quantified by sequencing the 16sRNA region of bacteria and archea using 515F and 806R primers (Caporaso et al. 2010b; Table 1, Bergmann et al. 2015). Both primer sets contained a 5' adaptor sequence to allow for subsequent indexing and Illumina sequencing. Amplicons were then cleaned using the UltraClean-htp 96 well PCR Clean-up kit (Qiagen, Inc.) according to standard protocol and stored at 4°C. A second round of PCR was performed to give each sample a unique 12-nucleotide index sequence. Final indexed amplicons from each sample were cleaned and normalized using SequalPrep Normalization Plates (Life Technologies) prior to being pooled together for sequencing on an Illumina MiSeq (Illumina Inc.) in the CU Boulder BioFrontiers

1780 Sequencing Center using the v2 300-cycle kit (cat# MS-102-2002). Plant trnL amplicons were
1781 then processed via the UPARSE pipeline (Edgar 2013) and assigned taxonomy via the UTAX
1782 protocol available in usearch (v8.1.1861), and 16S amplicons were processed via a joint QIIME
1783 (Caporaso et al. 2010a) and UPARSE pipeline similar to the protocol of Andrei et al. (2015; see
1784 S3 for detailed PCR and bioinformatics protocol).
1785
1786 *Statistical Analyses*— Distinct metabolic demands of male and female moose (and other
1787 ruminants) interact with seasonality to shape diet selection (Barboza and Bowyer 2000). I
1788 therefore separately quantified components of the dietary niche (i.e., total niche widths, among
1789 and within-individual dietary diversity) by year, season, and sex using multivariate analysis of
1790 variance. DNA metabarcoding techniques recover both rare OTUs and highly digested foods
1791 (Taberlet et al. 2007), meaning diet and microbiome compositions may contain large numbers of
1792 OTUs that contribute little to overall composition (e.g., <0.01 percent). I therefore calculated
1793 cumulative read curves and omitted all plant and microbe OTUs that did not contribute to the top
1794 95 percent of cumulative reads (Bergmann et al. 2015).
1795 I used package RInSp in Program R (Zaccarelli et al. 2013, R Core Team 2018) to
1796 estimate total niche widths, and among and within-individual dietary diversity (Roughgarden
1797 1974, Bolnick et al. 2002). I converted the number of plant OTU reads into proportions for each
1798 individual (argument pop.diet="average") so that individuals (i.e., fecal samples) with greater
1799 total OTU reads would not have undue influence on estimates of niche components (i.e., total
1800 niche widths, among and within-individual dietary diversity). I tested the null hypothesis that
1801 differences in diet selection among populations did not simply reflect differences in resource
1802 availability. I tested this hypothesis by simulating diets composed of 1000 random draws from

1803 available foods (i.e., food items observed identified in fecal samples) for each population. Hence,
1804 this resampling approach generated populations comprised of individuals that selected forage at
1805 random from the observed distribution of resources used by the entire population. Thus, any
1806 differences between observed and simulated foragers provides a measure of specialization after
1807 controlling for differences in availability (Bolnick et al. 2002, Zaccarelli et al. 2013).

1808 Across the six populations, the number of fecal samples collected within each of the six
1809 moose populations varied considerably (likely because of differences in moose density). Total
1810 niche width may expand because of increased resource limitation, but total niche width may also
1811 expand simply because additional food items are likely to be added as more individuals are
1812 sampled. Hence, sample size alone may account for differences in total niche width, among-
1813 individual dietary diversity, within-individual dietary diversity, and individual specialization. I
1814 assessed how sensitive the aforementioned niche components were to sample size by
1815 bootstrapping randomly sampled diets (n = 2-10; without replacement) from each population 500
1816 times and re-estimating niche components for each bootstrapped sample size. To quantify the
1817 effect of sample size on estimates of each niche component, I calculated the difference between
1818 the observed niche components and niche components computed for each of the 500 bootstrap
1819 replicates.

1820 I tested the predictions of the Individual Specialization and Individual Diet Breadth
1821 Hypotheses by assessing the strength and direction of correlations between resource limitation
1822 (as indexed by calf recruitment) and total niche widths, among and within-individual dietary
1823 diversity (Fig. 1). Predictions stemming from the Food Preference and Gut Microbiome
1824 Inheritance Hypotheses were evaluated by fitting spatially-explicit structural equation models
1825 (Lamb et al. 2014) to pairwise relatedness and Jaccard dissimilarity measures for diet and

microbiome. Spatially explicit structural equation models apply non-spatial structural equation models (SEM; Grace 2008) to subsets of data within distance bins, thereby incorporating spatial autocorrelation into the structural equation model and testing the null hypothesis that diets are more similar among close relatives simply because relatedness and food resources are spatially autocorrelated. I developed a simple SEM to test predictions stemming from both the Food Preference and Gut Microbiome Inheritance Hypotheses (Fig. 2) and fit the SEM within lag distances corresponding to twice the diameter of a moose home-range (7km; i.e., the distance at which two individuals were unlikely to have overlapping home ranges; Baigas 2008, Becker 2008, Oates 2016). Although my hypotheses regarding inheritance of dietary phenotypes (Fig. 2) are not mutually exclusive, structural equation models are ideally suited for multiple hypothesis testing when independent variables may be correlated (Grace 2008).

RESULTS

Sampling and Genetic Analyses— I obtained genotypes for 709 of 1,176 (60%) fecal samples across seasons and populations, representing 216 individuals (Table 2). Microsatellite polymorphism was variable across loci (range = 3-6). Genotyping error was low (Table 2) and consisted primarily of allelic dropout and false alleles. Metabarcoding of trnL and 16S amplicons identified 143 OTUs of plants (107 orders, 4 families, 32 genera) and 4,411 OTUs of bacteria and archea, representing 33 phyla and 66 classes. Analysis of cumulative read curves resulted in winter diets characterized by 37 OTUs, summer diets characterized by 24 OTUs, and the microbiome characterized by 400 OTUs (Fig. S2).

Resource Limitation, diet, microbiome, and relatedness—Diet composition varied considerably across seasons (PERMANOVA, $P < 0.01 – 0.05$) and slightly among years ($P < 0.01 – 0.35$), but was similar among males and females ($P = 0.07 – 0.79$; Table S3). Hence, data from each population was subset by season and year, but not sex. Population-level niche components stabilized when population-level datasets included six or more diet samples (Fig. S3). Therefore, I excluded any dataset with fewer than six samples (see Table 1).

Simulated foragers that selected foods at random from all available resources exhibited nearly identical diet selection across all populations, indicating that any differences in observed diet selection and dietary niche components were not simply a function of contrasting resource availability (Fig. S4). During summer, resource limitation was strongly correlated with total niche width ($r = -0.96$, $P <0.01$) and individual diet breadth (i.e., within-individual dietary diversity; $r = -0.99$, $P <0.01$), but only weakly with individual specialization (i.e., among-individual diversity; $r = -0.52$, $P = 0.37$; Fig 3). During winter, however, resource limitation was not correlated with total niche width, individual diet breadth, or individual specialization (all $r < 0.06$, $P >0.8$; Fig 3). Total niche width primarily reflected individual diet breadth ($r = 0.95$, $P<0.01$; Fig. 4), thereby supporting OFT. Neither the strength or directionality of relationships between resource limitation, total niche width, individual specialization and individual diet breadth were altered by subsetting each population's dataset to six samples (see bootstrapping methods in S3; Fig. S3). Together, these results support OFT (Fig. 1B).

Unstandardized path coefficients (i.e., effect sizes) from the spatially explicit structural equation model were small (<0.04) and not statistically significant ($P>0.05$) regardless of distance lag (Fig. 5), offering no evidence for inheritance of dietary phenotypes. Likewise, diet and microbiome similarity were not strongly correlated at any distance lag (Fig. 5A, B),

suggesting that large herbivore diets are not strongly constrained by microbiome composition. Although fecal samples from closely related individuals in close proximity had more similar diets in summer (i.e., a negative path coefficient), the effect of genetic relatedness on diet similarity was very small (<0.02; Fig. 5C). In winter, the effect of relatedness on diet similarity was consistently small across all distance lags (Fig. 5D). Similar to the relationship between diet similarity and genetic relatedness, fecal samples from closely related individuals found in closer proximity to each other had more similar microbiomes in summer (i.e., a negative path coefficient), but the effect of genetic relatedness on microbiome similarity was minuscule (<0.005; Fig. 5E). The effect of genetic relatedness on microbiome similarity was similarly minuscule in winter, yet related individuals tended to have even more dissimilar microbiomes at further lag distances (Fig. 5F). In accord with the results of the spatially explicit structural equation model, the non-spatial structural equation model also indicated weak relationships between diet similarity, microbiome similarity, and genetic relatedness (all unstandardized path coefficients <0.012). Hence, my results do not offer support for either the Diet Inheritance Hypothesis or the Gut Microbiome Inheritance Hypothesis (Fig. 2).

DISCUSSION

Despite the shared prediction that total niche width should expand as resources becoming limiting, the Niche Variation Hypothesis (NVH; Van Valen 1965) and Optimal Foraging Theory (OFT; Krebs et al. 1977) offer contrasting views about how animals should alter diet selection when intraspecific competition intensifies (Fig. 1). Many examples of increased total niche width stemming from increased individual specialization suggest that dietary specialization, and thus the NVH, arise from inheritance of morphological and behavioral traits that facilitate variation in

resource-use among individuals (Bolnick et al. 2007). In populations of moose in the Intermountain West, total niche width broadened as resources became increasingly limited (Fig. 3), and in accord with OFT, this stemmed primarily from increases in individual diet breadth (Fig. 3, 4). My results indicate that weak inheritance of traits associated with foraging in moose, such as diet selection and rumen microbiome (Fig. 5), facilitate flexibility in diet selection and constrain the ability of moose to develop specialized diets. Thus, a lack of phenotypic inheritance led to moose foraging in accordance with OFT rather than the NVH.

Diet similarity in moose across the Intermountain West of North America was weakly correlated with relatedness across distance lags (Fig. 5C, D), indicating that even if transmission of diet selection occurred early in life, such similarities dwindled as individuals foraged outside their natal ranges and as environmental conditions shifted over time. Social learning of dietary preferences represents an important avenue of phenotypic inheritance by which individual specialization is promoted and maintained (Estes et al. 2003, Tinker et al. 2008, Jaeggi et al. 2010, van de Waal et al. 2013). Nevertheless, while social learning early in life is important for the survival of juveniles (Thornton and Clutton-Brock 2011), such learned behavior may erode overtime in long-lived vertebrates as they experience variable environmental conditions (Teitelbaum et al. 2018). Indeed, individual fitness should be maximized when both social and asocial learning mechanisms are engaged (Galef and Laland 2005). Ruminant herbivores are long-lived vertebrates that spend extended periods of time within their natal range (e.g., Halls 1984, Franzmann and Schwartz 1997). As such, juvenile ruminants may adopt maternal diets during their first year of life via flavor cues in milk or through copying maternal foraging behavior, thereby reducing the cost of trial and error learning, which is likely substantial for naïve young individuals (Edwards 1976, Galef and Giraldeau 2001, Galef and Laland 2005).

Nevertheless, rigid adherence to socially learned diet selection may prove maladaptive in changing environments (Laland and Williams 1998, Keith and Bull 2017) and cause trial and error learning to be more adaptive for ruminant herbivores once they have disperse outside their natal range and encounter different environmental conditions (Provenza and Balph 1987, Galef and Whiskin 2001, Stephens et al. 2007). Because diet selection was either not inherited or adherence to inherited diet selection waned over time, individual specialization in moose did not occur (Fig. 3, 4). Instead, flexibility in diet selection promoted by consumption of plant toxins and the rumen microbiome likely caused the individual diet breadth of moose to expand as resources became limiting.

The rumen microbiome may facilitate flexibility in diet selection and constrain the ability of ruminants to specialize on subsets of resources. The core microbiome of ruminants across the globe is comprised of orders Bacteroidales (phylum *Bacteroidetes*), Clostridiales (phylum *Firmicutes*), and Methanobacteriales (phylum Euryarchaeota) despite different diets within and among species (Sundset et al. 2009, Henderson et al. 2015). Accordingly, I found weak association between diet and microbiome similarity (Fig. 5A; see also Bergmann et al. 2015). The lack of strong association between microbiome and diet was nevertheless surprising because, as with desert woodrats (*Neotoma lepida*) and domestic goats (*Capra aegagrus hircus*), 'secondary' (non-core) microbial groups play a large role in promoting ingestion of novel foods and foods high in plant toxins (Jones and Lowry 1984, Sundset et al. 2007, Kohl et al. 2014). Further, the gut microbiome itself is shaped by diet, so diet and microbiome composition typically are coupled (Lawrence et al. 2013, Salgado-Flores et al. 2016). As individual moose diversified their diets when resources became limiting, more diverse microbiomes were therefore expected. I demonstrate, however, that changes in moose diet do not require concomitant

changes in the microbiome, suggesting that the cellulolytic and detoxifying capacities of a diverse microbiome facilitate the dietary flexibility required to expand or contract diets with changing resource levels.

An emergent notion in ecology and evolutionary biology is that inheritance of dietary phenotypes underlie diet specialization and thus the Niche Variation Hypothesis (Bolnick 2004, Araujo et al. 2011). Nevertheless, the complementary notion that lack of phenotypic inheritance constrains diet specialization and gives rise to the predictions of OFT has not been evaluated. The flexible diets of ruminant herbivores represent one context under which predictions of the NVH are not met (Fig. 1A) and instead are better explained by OFT (Fig. 1B). As the preferred habitats of ruminant herbivores become limiting and individuals 'spill over' into secondary habitats (Fretwell and Lucas 1969, Darimont et al. 2007, van Beest et al. 2014a, van Beest et al. 2014b), concomitant shifts in diet were not observed (Fig. 3, 4). The natural history and ecophysiology of ruminants has resulted in a foraging strategy that promotes continuous sampling of foraging patches so that individuals can adjust to ever-changing plant quantity and quality (Provenza 1995, Stephens et al. 2007). Hence, specializing on a subset of plants is challenging for ruminants, meaning inheritance of dietary phenotypes has likely been selected against. Instead, reliance on increased diet breadth as a mechanism through which intraspecific competition can be reduced when resources become limiting may represent a more adaptive strategy (Provenza and Balph 1987, Provenza et al. 2003). Thus, lack of phenotypic inheritance provides a broad contextual understanding of when the predictions of OFT and the NVH are met.

1960 **Table 1.** Names of microsatellite (ms), sex identification (sex ID), plant (trnL), and bacteria and archea (16S) markers, their primer
1961 sequences, GenBank accession number, and the references from which marker information was derived.
1962

Marker	**Type**	**Forward** 5'-3'	**Reverse** 5'-3'	**GenBank Accession #**	**Reference**
BL42	ms	CAAGGTCAAGTCCAAATGCC	GCATTTTTGTGTTAATTTCATGC	DQ136013	Bishop et al. (1994)
BM1225	ms	TTTCTCAACAGAGGTGTCCAC	ACCCCTATCACCATGCTCTG	DQ136013	Bishop et al. (1994)
BM203	ms	GGGTGTGACATTTTGTTCCC	CTGCTCGCCACTAGTCCTTC	DQ136013	Bishop et al. (1994)
BM2830	ms	AATGGGCGTATAAACACAGATG	TGAGTCCTGTCACCATCAGC	DQ136013	Bishop et al. (1994)
BM4513	ms	GCGCAAGTTTCCTCATGC	TCAGCAATTCAGTACATCACCC	DQ136013	Bishop et al. (1994)
BM848	ms	TGGTTGGAAGGAAAACTTGG	CCTCTGCTCCTCAAGACAC	DQ136013	Bishop et al. (1994)
BM888	ms	AGGCCATATAGGAGGCAAGCTT	CTCGGTGAGCTCAAAACGAG	DQ136013	Bishop et al. (1994)
BM4208	ms	TCAGTACACTGGCCACCATG	CACTGCATGCTTTTCCAAAC	DQ136013	Bishop et al. (1994)
FCB193	ms	TTCATCTCAGACTGGGATTCAGAAAGGC	GCTTGGAAATAACCCTCCTGCATCCC	LO1533	Buchanan and Crawford (1993)
KY1/KY2	sex ID	GCCCAGCAGCCCTTCCAG	TGGCCAAGCTTCCAGAGGCA	FJ434496, FJ434497	Brinkman and Hundertmark (2008)
c/h	trnL	CGAAATCGGTAGACGCTACG	CCATTGAGTCTCTGCACCTATC	-	Taberlet et al. (2007)
515F/806R	16S	GTGYCAGCMGCCGCGGTAA	GGACTACNVGGGTWTCTAAT	-	Walters et al. (2016)

1963

Table 2. Number of individual moose identified per herd, per season via fecal DNA.

Herd	Summer		Winter		Total
	M	F	M	F	
Jackson	2	1	11	13	27
Sublette	3	8	5	5	21
Bighorn	11	15	19	5	50
Snowy Range	9	9	1	4	23
Uinta	15	14	7	7	43
North Park	8	9	8	8	33

Table 3. Type and frequency of genotyping error rates for multilocus genotypes established from moose feces. Allelic dropout indicates when an animal that is heterozygous at a given locus is genotyped as a homozygote (i.e., one allele 'drops out'). False alleles indicate individuals that a truly homozygous individual is genotyped as a heterozygote. Homozygous allele shifts signify base pair additions that occur during the PCR process.

Population	Locus	Dropout	False Allele	Homozygote Allele Shift	Population	Locus	Dropout	False Allele	Homozygote Allele Shift
Bighorn	KY	0.059	0.000	0.000	*Snowy Range*	KY	0.000	0.000	0.000
	BM2830	0.125	0.440	0.000		BM2830	0.093	0.022	0.000
	BL42	0.000	0.080	0.000		BL42	0.010	0.045	0.000
	FCB193	0.000	0.000	0.000		FCB193	0.000	0.014	0.000
	BM4208	0.000	0.000	0.000		BM4208	0.024	0.000	0.000
	BM848	0.000	0.077	0.000		BM848	0.018	0.000	0.000
	BM4513	0.017	0.000	0.000		BM4513	0.010	0.000	0.000
	BM203	0.000	0.000	0.000		BM203	0.000	0.000	0.000
	BM888	0.000	0.000	0.000		BM888	0.015	0.000	0.000
	BM1225	0.000	0.000	0.000		BM1225	0.000	0.038	0.013
Jackson	KY	0.027	0.000	0.000	*Sublette*	KY	0.000	0.000	0.000
	BM2830	0.026	0.021	0.000		BM2830	0.192	0.006	0.000
	BL42	0.005	0.083	0.000		BL42	0.000	0.000	0.000
	FCB193	0.000	0.014	0.000		FCB193	0.000	0.000	0.000
	BM4208	0.000	0.000	0.000		BM4208	0.060	0.023	0.000
	BM848	0.019	0.048	0.000		BM848	0.011	0.091	0.000
	BM4513	0.013	0.022	0.000		BM4513	0.000	0.000	0.000
	BM203	0.107	0.021	0.007		BM203	0.000	0.000	0.000
	BM888	0.026	0.000	0.000		BM888	0.000	0.014	0.000
	BM1225	0.041	0.028	0.000		BM1225	0.036	0.000	0.000
North Park	KY	0.017	0.022	0.000	*Uinta*	KY	0.000	0.000	0.000
	BM2830	0.000	0.018	0.011		BM2830	0.039	0.000	0.000
	BL42	0.021	0.000	0.000		BL42	0.000	0.063	0.000
	FCB193	0.077	0.000	0.000		FCB193	0.000	0.000	0.000
	BM4208	0.080	0.047	0.000		BM4208	0.000	0.000	0.000
	BM848	0.000	0.000	0.000		BM848	0.000	0.000	0.033
	BM4513	0.020	0.000	0.058		BM4513	0.000	0.000	0.000
	BM203	0.000	0.019	0.000		BM203	0.000	0.000	0.000
	BM888	0.400	0.000	0.000		BM888	0.000	0.000	0.019
	BM1225	0.000	0.000	0.000		BM1225	0.000	0.000	0.000

Fig 1. Heuristic illustration of individual dietary niches (black curves) under resource limitation according to (A) the Niche Variation Hypothesis, and (B) Optimal Foraging Theory. Blue dashed curves illustrate the total niche width (TNW) of a population when resources are abundant, whereas the red dashed curves represent the TNW of a population under resource limitation. The width of the black curves represents within-individual dietary diversity (WID) in resource use when resources are limiting, whereas the distance between the peaks of the black curves reflects the amount of among-individual diversity (AID) in resource use when resources are limiting. The Niche Variation Hypothesis predicts that groups of individuals specialize on subsets of resources (i.e., AID is large relative to TNW; panel A). In contrast, the Optimal Foraging Theory predicts that TNW is primarily a reflection of individual diet breadth (i.e., WID is large relative to TNW; panel B). (C) Evidence for the Individual Specialization Hypothesis (low WID/TNW ratio indicates dietary specialization) and the Individual Diet Breadth Hypothesis (i.e., high WID/TNW ratio indicates increased individual diet breadth). Figure adapted from Bolnick et al. (2003) and Araujo et al. (2011).

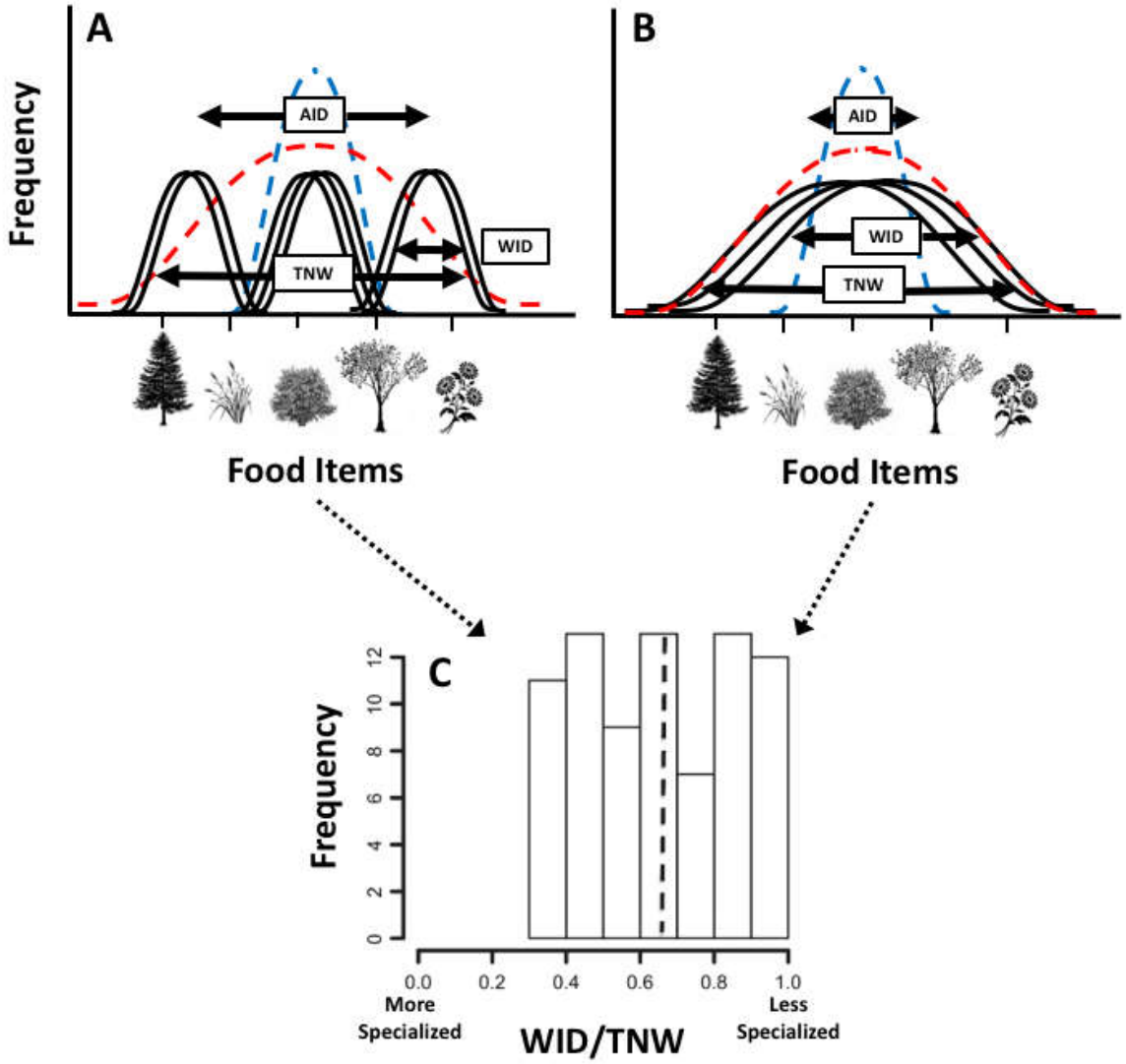


Fig 2. Path diagram illustrating the non-spatial structural equation model used to test the (i) Diet Selection Inheritance and (ii) Gut Microbiome Inheritance Hypotheses.

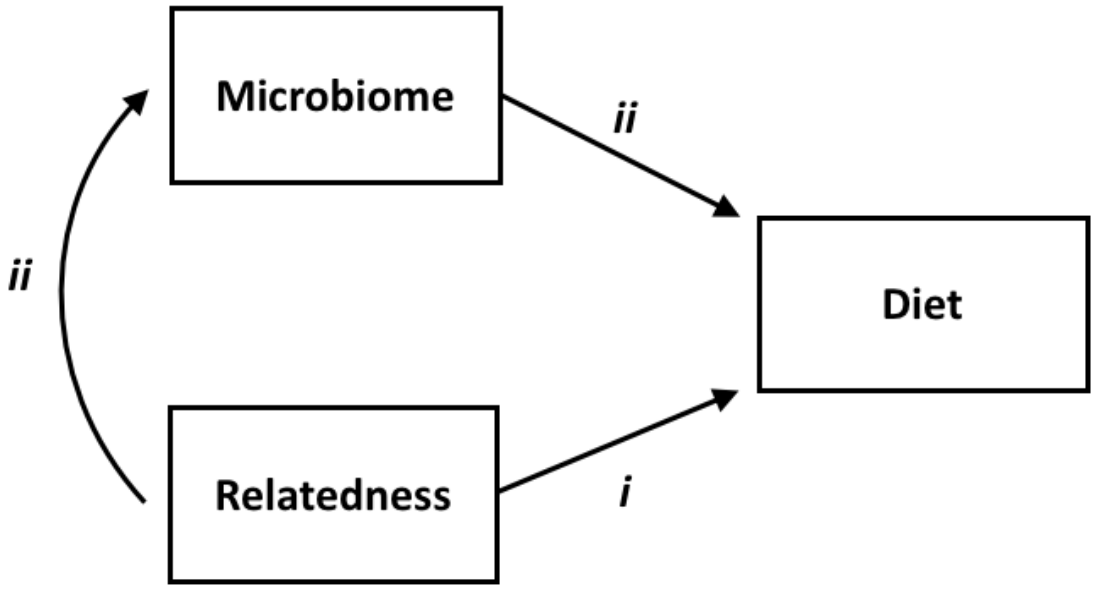


Fig 3. Correlation between resource limitation (number of calves per 100 cows; lower values represent resource limitation) and (A, D) total niche width (TNW), (B, E) Among-Individual Diversity (AID), and (C, F) Within-Individual Diversity (WID). Red circles (upper panels) represent niche components during summer, and black circles (lower panels) represent niche components during winter. Correlation coefficients (*r*) and p-values are presented. During summer, and in accordance with OFT, total niche width (panel A) and individual diet breadth (panel C) increased as resource limitation increased.

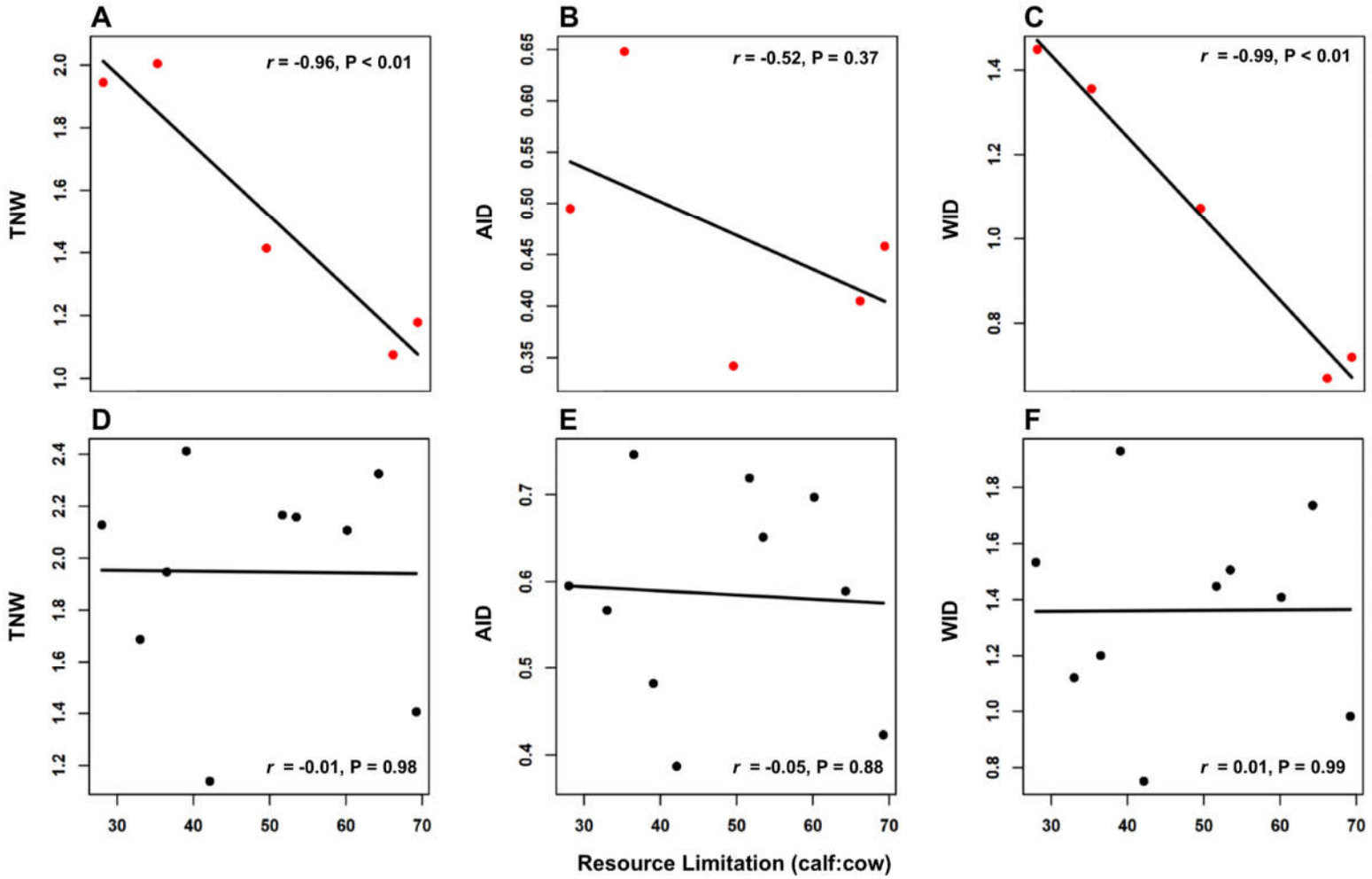


Fig 4. Relationship between total niche width (TNW) and Among-Individual Diversity (AID) and Within-Individual Diversity (WID). Although TNW is correlated with AID, WID explains 95% of variation in TNW, indicating that expansion of TNW stems from greater individual diet breadth (WID; see Figure 1).

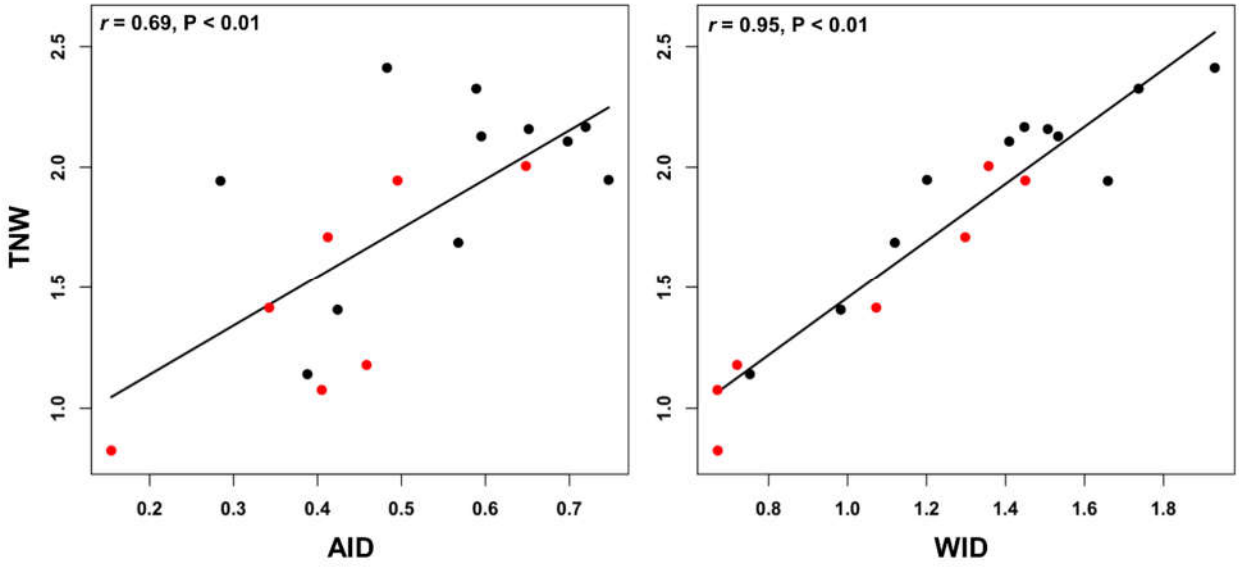
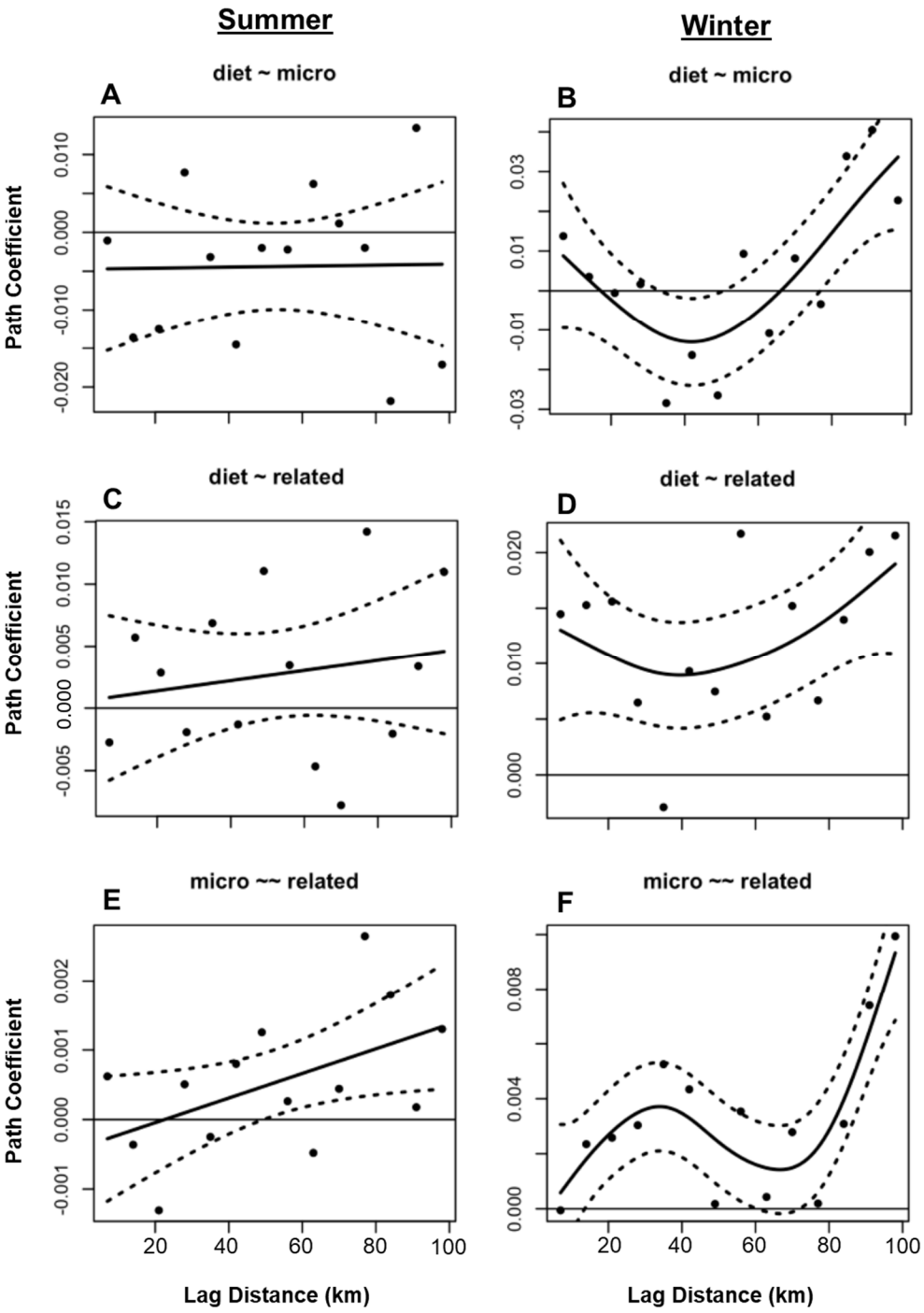


Fig 5. Path coefficients for the relationship between (A, B) diet dissimilarity and rumen microbiome dissimilarity, (C, D) diet dissimilarity and relatedness, and (E, F) microbiome dissimilarity and relatedness. Dissimilarity and relatedness measures are pairwise associations between individuals during summer (left panels) and winter (right panels). Note small effect sizes (partial (path) correlation coefficients).



APPENDIX S3

Site Selection

To model core habitat (i.e., high probability of use areas) in both winter and summer seasons, I divided GPS collar locations into two datasets representing winter and summer ranges. To identify the winter and summer ranges of migratory individuals, I used net-squared displacement to identify spring and fall migration (Bunnefeld et al. 2011, Jesmer et al. 2018). All points occurring between the end of spring migration and the start of fall migration were considered to occur on summer range (and vice versa for winter). To identify the winter and summer ranges of non-migratory individuals (i.e., individuals that had a single range throughout the year), I estimated the start of spring and start of winter for a given population's range using remotely-sensed phenological data (i.e., the Normalized Difference Vegetation Index; MODIS product MOD09Q1; 250-m spatial resolution, 8-day temporal resolution). I defined each population's range as the 95% minimum convex polygon around all GPS-collar data (Calenge 2006). I then extracted Normalized Difference Vegetation Index data from within the minimum convex polygon and quantified the start of spring and the start of winter by fitting a double logistic curve to the annual pattern of plant green-up (i.e., Normalized Difference Vegetation Index data). The Julian day at which spring and winter began were then estimated by calculating the first, second derivative (start of spring) and the second, second derivative (start of winter) of the double logistic curve (Bischof et al. 2012, Merkle et al. 2016). I then subset the GPS collar locations of non-migratory individuals into summer and winter locations according to my estimates of start of spring and start of winter.

Using random forests, I modeled second-order habitat selection (Johnson 1980, Evans et al. 2011) on summer and winter ranges and projected model predictions of probability of use

2042 across all six populations to inform the placement of transects along which I collected fecal
2043 samples. I parameterized random forest models with habitat covariates known to influence
2044 moose space-use in the study region (Becker 2008; see table S1 for list of model covariates ,
2045 Baigas et al. 2010). I used the National Land Cover Database (Homer et al. 2015) to define
2046 spatially explicit habitat availability. Because moose strongly select for riparian shrublands in
2047 my study area and the spatial resolution (30m x 30m) of the National Land Cover Database often
2048 lumps narrow (<30m wide) riparian shrublands with surrounding cover classes (e.g., deciduous
2049 or conifer forest; Homer et al. 2015), I also included topographic proxies of riparian shrublands
2050 (i.e., the compound topographic index and the topographic position index (i.e., ridge, midslope,
2051 valley bottom; Evans et al. 2014, Evans 2017). Like other classification and regression tree
2052 methods, random forest models are sensitive to unbalanced sample sizes among classes (in this
2053 case presence and psuedoabsence; Breiman 1984, Evans et al. 2011). Therefore, I randomly
2054 selected GPS-collar locations from the two more location-rich databases to standardize presence
2055 (collar locations, n = 51,515 per population in winter, n = 53,898 per population in summer). I
2056 then created and equal number of psuedoabsences by plotting random points across the entire
2057 study region (i.e., the bounding box illustrated in Fig. 2A). Overfitting is common with random
2058 forest models, so I used the model selection function in the rfUtilities package (Evans and
2059 Murphy 2018) to reduce the parameter set to include only highly informative parameters. I then
2060 fit random forest models using either winter or summer locations to estimate and map seasonal
2061 core habitat across the entire study area (Liaw and Wiener 2002, Hijmans 2017) to constrain the
2062 search area in which I collected fecal samples. Model performance was evaluated using a cross
2063 validation approach (i.e., ‘out of bag error’; Evans et al. 2011).

Using the habitat selection model, I then identified all areas of high-probability use by reclassifying the probability of use surface to only include the top quartile. Using the National Land Cover Database, I then masked the top quartile of the probability surface to only include willow riparian habitat and upland habitat (e.g., forests, xeric shrublands, grasslands) strata so that I could sample moose that may be diversifying their diets to include, or specializing on, a variety of resources. I identified 20 locations within each stratum for each population using a spatially-balanced stratified random (Stevens and Olsen 2004, Kincaid et al. 2012). At each location, I randomly selected a direction that would allow us to remain within the habitat strata for the entire 2km sampling transect. Within each strata, I identified 20 locations within each stratum for each population using a spatially-balanced stratified random design (Stevens and Olsen 2004, Kincaid et al. 2012). At each location, I randomly selected a direction that would allow us to remain within the habitat strata for the entire 2km sampling transect. I used detection dogs to find fecal samples along transects during summer when fecal samples scattered across vast summer ranges, were hidden by thick vegetation, and were required to be very fresh (<48 hr old) for DNA analysis (Dahlgren et al. 2012). During winter, however, visual detection of fecal samples was feasible because feces were concentrated on winter ranges, easy to detect in snow, and were frozen shortly after deposition by the cold winter conditions in my study area. All samples were collected according to a sterile protocol and placed frozen within 8 hr at -20^{o}C.

PCR parameters

Microsatellite analysis— Each 10µL PCR reaction (Table S2) was mixed according to the parameters specified in using Qiagen PCR Master Mix (Qiagen Inc.). DNA was PCR amplified using the following conditions: initial denaturation at 95°C for 15 min, followed by 50 cycles of

30 sec at 94°C, 90 sec at 54°C, 90 sec at 72°C and a final elongation at 60°C for 10 minutes. Microsatellite amplicons were then sent to Cornell University's Biotechnology Resource Center where fragment lengths were quantified using an ABI 3730xl DNA Analyzer (Applied Biosystems).

Plant trnL analysis—Each 40µL PCR reaction was mixed according to the Promega PCR Master Mix specifications (catalog # M5133, Promega Inc.) which included 0.4µM of primers *c* and *h* 3.2 µl of gDNA. DNA was PCR amplified using the following conditions: initial denaturation at 94°C for 1 minute, followed by 36 cycles of 1 minute at 94°C, 30 seconds at 55°C, and 30 seconds at 72°C, and a final elongation at 72°C for 1 minute. Amplicons were then cleaned using the UltraClean-htp 96 well PCR Clean-up kit (Qiagen Inc.) according to manufacturer's specifications and stored at 4°C. A second round of PCR was performed to give each sample a unique 12-nucleotide index sequence. The indexing PCR included Promega Master mix (Promega Inc.), 0.5µM of each primer and 4µL of template DNA (cleaned amplicon from the first PCR reaction) and consisted of an initial denaturation of 95°C for 3 minutes followed by 8 cycles of 95°C for 30 second, 55°C for 30 seconds and 72°C for 30 seconds. After trnL-specific and indexing PCR reaction, 5µl of PCR products of each sample were visualized on a 2% agarose gel.

Microbial 16sRNA analysis—Each 25µL PCR reaction was mixed according to the Promega PCR Master Mix specifications (catalog # M5133; Promega Inc.) which included 12.5µl Master Mix, 0.5µl of both 515F and 806R primers (Table 1), 1.0µl of gDNA, and 10.5µl DNase/RNase-free H2O. DNA was PCR amplified using the following conditions: initial denaturation at 95°C

for 5 minutes, followed by 35 cycles of 45 seconds at 95°C, 60 seconds at 50°C, and 90 seconds at 72°C, and a final elongation at 72°C for 10 minutes. PCR reaction was visually inspected and confirmed using a 2% agarose gel with 5µl of each sample as input. Amplicons were cleaned using the UltraClean 96 PCR Cleanup Kit (cat#12596-4; Qiagen Inc.). A second round of PCR was performed to give each sample a unique 12-nucleotide index sequence. The indexing PCR included Promega Master mix, 0.5µM of each primer and 2µl of template DNA (cleaned amplicon from the first PCR reaction) and consisted of an initial denaturation of 95°C for 3 minutes followed by 8 cycles of 95°C for 30 seconds, 55°C for 30 seconds and 72°C for 30 seconds. 5µl of indexing PCR product of each sample were visualized on a 2% agarose gel. Final indexed amplicons from each sample were cleaned and normalized using SequalPrep Normalization Plates (Life Technologies Inc.). 25µl of PCR amplicon is purified and normalize using the SequalPrep Normalization kit (cat#A10510-01; Life Technologies) according to the manufacturer's protocol. Samples are then pooled together by adding 5µl of each normalized sample to the pool.

Bioinformatics and metabarcoding

Plant trnL analysis— Sequences were demulitplexed in QIIME v1.9.1 (Caporaso et al. 2010a) using a python script available from: https://github.com/leffj/helper-code-for uparse/blob/master/prep_fastq_for_uparse_paired.py. Paired end reads were then merged using the -fastq_mergepairs option of usearch (Edgar 2010). Since merged reads often extended beyond the amplicon region of the sequencing construct (staggered merges; http://drive5.com/usearch/manual/cmd_fastq_mergepairs.html), usearch automatically trimmed overhangs, thereby removing the majority of primer and adapter regions. Any primer or adapter

regions that may have remained were removed using cutadapt (Martin 2011). Sequences were then trimmed to have a maximum expected number of errors per read of less than 0.5.

To assign taxonomy to each operational taxonomic unit (OTU; plant taxon), an 'in-house' UTAX trnL reference database was constructed by downloading all annotated GenBank (Benson et al. 2005) records that contained the trnL gene. The amplicon region bounded by the trnL c & h primers (Taberlet et al. 2007) was extracted from the GenBank records using the UTAX protocol. All extracted amplicon regions were dereplicated to 100% sequence identity and any identical sequence across lineages were collapsed to the lowest-common-ancestor. Closed-reference OTUs were generated by searching against the trnL reference database at 99% sequence similarity. To ensure increased specificity of trnL OTU assignment against the reference database the –maxaccepts and –maxrejects usearch options were increased 64 and 256 respectively.

Microbial 16sRNA analysis— Sequences were demultiplexed by using Golay barcodes (Caporaso et al. 2012) in QIIME v1.9.1. The following options were used to output raw unfiltered fastq files for both forward and reverse reads: split_libraries_fastq.py -q 0 --max_bad_run_length 250 --min_per_read_length_fraction 0.0001 --sequence_max_n 250 --store_demultiplexed_fastq. Paired-ends where then merged by the –fastq_mergepairs option of usearch v8 [7]. Primer sequences were then trimmed using cutadapt v1.8.1 (Martin 2011) to remove the primers 515F and 806R (Apprill et al. 2015, Parada et al. 2016, Walters et al. 2016). Sequences were discarded if either primer was not detected or the final merged sequence length was less than 100 base-pairs.

Quality control and OTU table construction was completed as per the UPARSE pipeline by clustering reads at 97% sequence similarity using de novo chimera detection defaults. The following alterations to the pipeline were implemented: the –minh option of -uchime_ref was set to 1.5 for reference-based chimera removal; to reduce the false positive detection of chimeras. The OTU table was generated by mapping quality filtered reads back to the closed reference OTUs by setting the following –usearch_global parameters: -maxaccepts 64 -maxrejects 1024. These parameters help to avoid over-inflation of specific OTU counts and ensure that individual reads are correctly mapped to their respective OTUs. Consensus taxonomy was assigned via the RDP classifier (Wang et al. 2007) on a custom-made SILVA v128 database (Pruesse et al. 2007).

Table S1. Multiplex PCR conditions used for microsatellite analysis of individuality and sex of moose (*Alces alces*).

Regent (concentration)	**volume (µl)**
Water	0.700
Qiagen MM (2X)	4.500
Q_Sol (5X)	2.000
BM4513F (20µM)	0.075
BM4513R (20µM)	0.075
BM4208F (20µM)	0.075
BM4208R (20µM)	0.075
BL42F (20µM)	0.075
BL42R (20µM)	0.075
BM888F (20µM)	0.075
BM888R (20µM)	0.075
FCB193F (20µM)	0.075
FCB193R (20µM)	0.075
KY1 (20µM)	0.075
KY2 (20µM)	0.075
BM203F (20µM)	0.125
BM203R (20µM)	0.125
BM848F (20µM)	0.125
BM848R (20µM)	0.125
BM1225F (20µM)	0.150
BM1225R (20µM)	0.150
BM2830F (10µM)	0.050
BM2830R (10µM)	0.050
DNA	1.000
Total	**10.000**

Table S2. Pairwise dietary dissimilarity (Jaccard's distance) among sexes, seasons, and years. Numbers in table represent p-values estimated via permutational multivariate analysis of variance (PERMANOVA) of distance matrices.

Population	Formula	Sex	Season	Year
Bighorn	dist~sex+seas+year	0.22	0.00	0.00
Jackson	dist~sex+seas+year	0.40	0.00	0.17
North Park	dist~sex+seas+year	0.69	0.00	0.25
Snowy Range	dist~sex+seas+year	0.07	0.00	0.04
Sublette	dist~sex+seas+year	1.00	0.05	0.08
Uinta	dist~sex+seas+year	0.79	0.00	0.35

Fig S1. Location of study areas in the Intermountain West, USA and trends in calf recruitment from 1990 to 2016. Note that during the study, recruitment ranged from 27 calves/ 100 cows to 70 calves/100 cows.

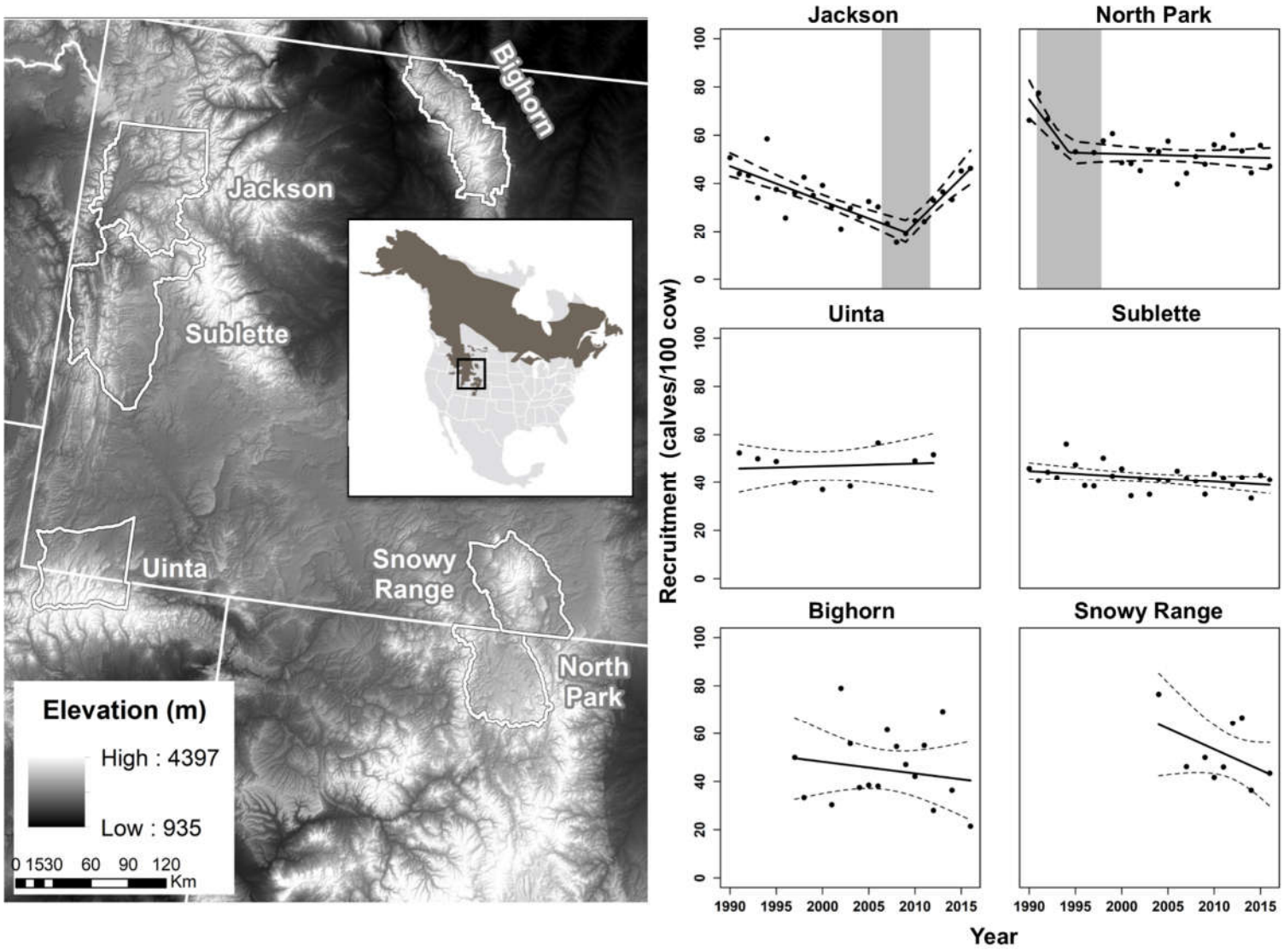


Fig S2. Relationship between cumulative number of trnL reads (top panels), the and the number of items observed in a the diets of 98 moose in summer (left panels) and 98 moose in winter (right panels). Percent reads (middle panels) represent the percent of trnL reads a given diet item contributed to the overall diet, and (bottom panels) represent cumulative percentage reads, wherein 24 diet items in summer and 37 diet items in winter comprised 95 percent of total diet composition.

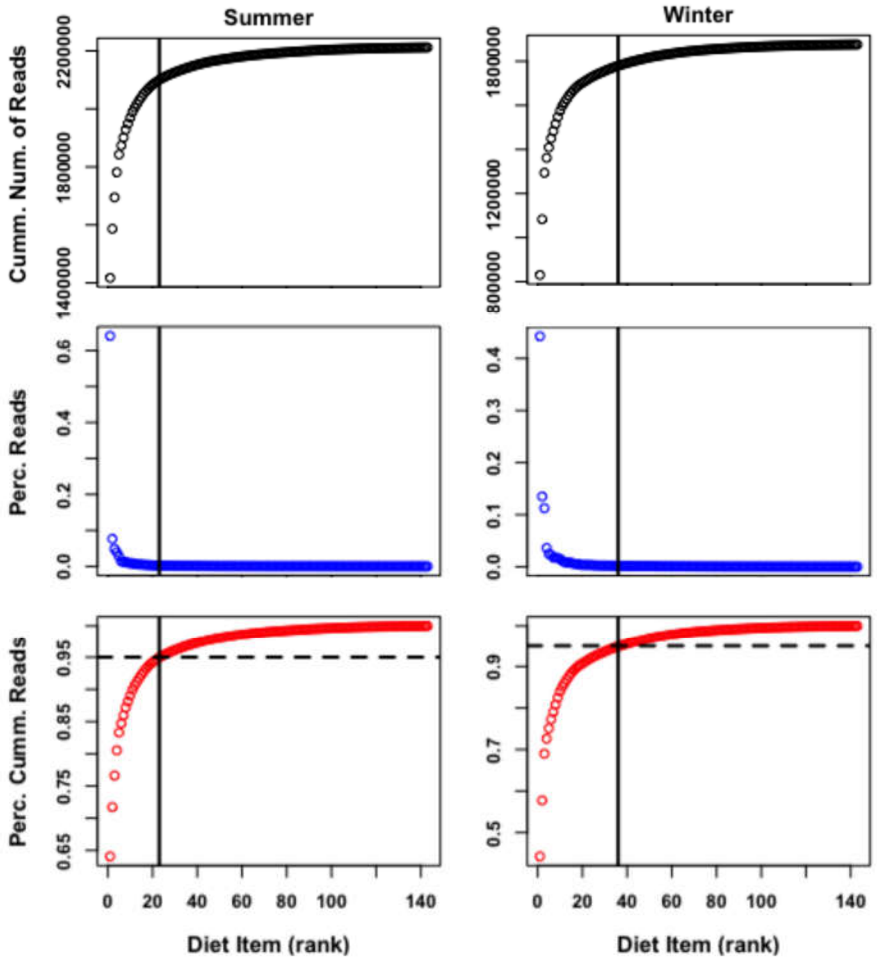


Fig S3. Difference ( ) between observed total niche width (TNW), Among-Individual Diversity (AID), Within-Individual Diversity (WID), ratio between WID and TNW (another measure of individual specialization [IS]) and the same niche components (TNW, AID, WID, IS) derived from random subsamples (n=2-10) of individual diets. Subsamples were iterated 500 times for each population and the median value for each population is represented by open circles. Trend lines (red) were estimated using generalized additive models.

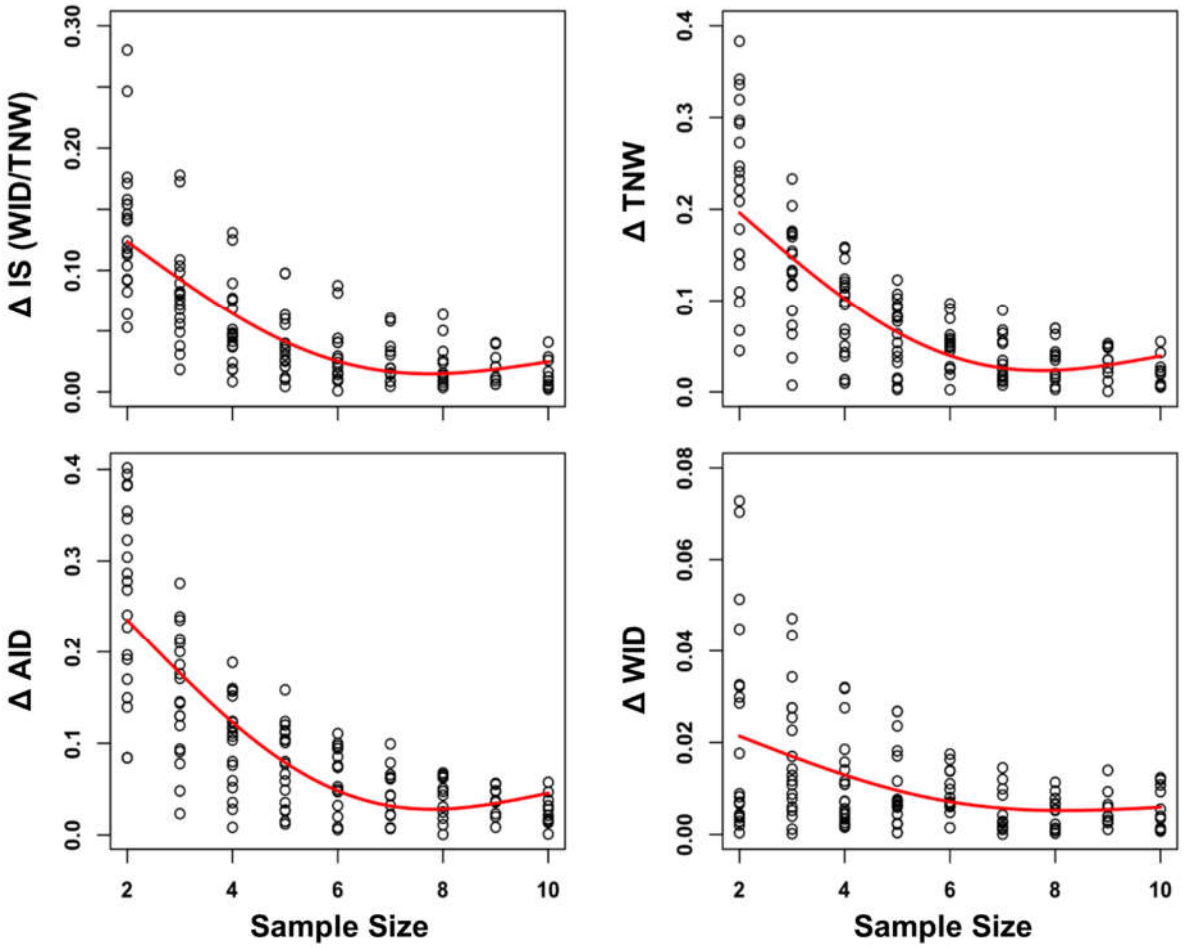
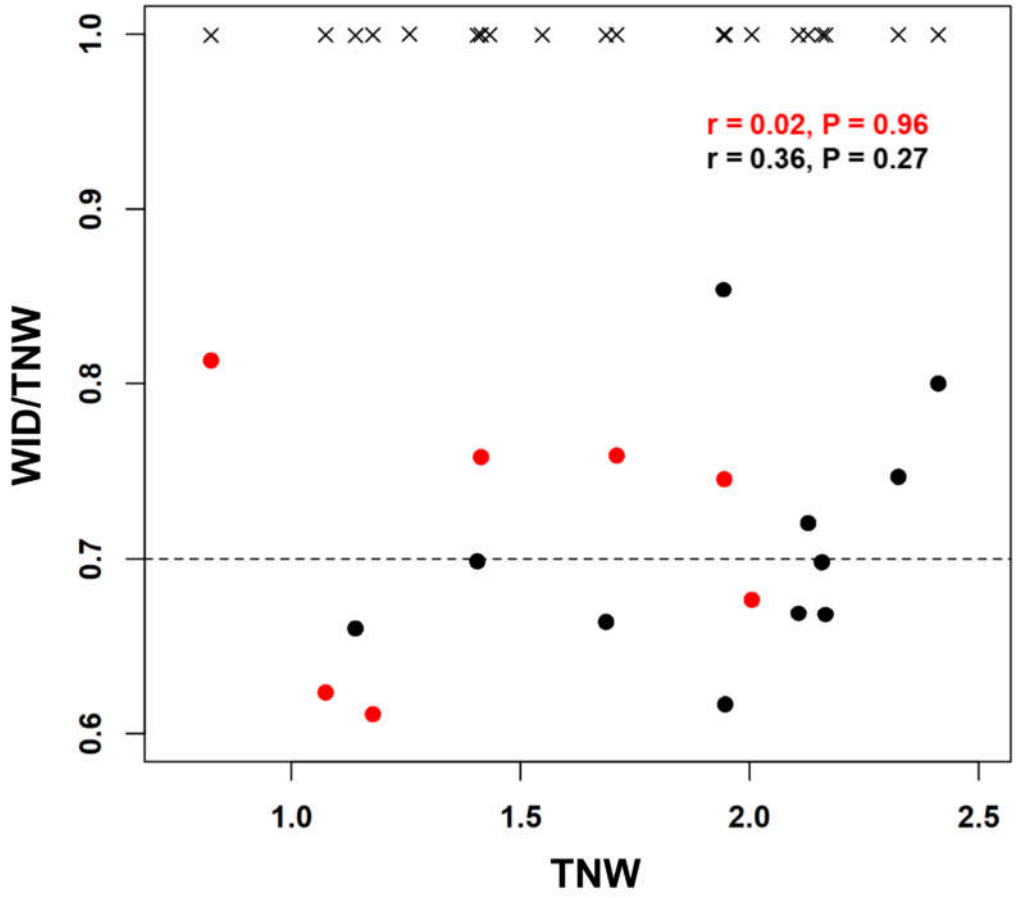


Fig S4. Relationship between total niche width (TNW) and individual specialization (as indexed by ratio of WID/TNW). Values of 1.0 for WID/TNW indicate individuals select diet items at random from all items available in their environment (i.e., are complete generalists). Black circles represent winter diet measures and red circles represent summer diet measures. Simulated diets composed of 1000 random draws from available foods (i.e., food items observed identified in fecal samples) for each population are represented by X's. Because all simulated values are 0.999, differences between observed and simulated foragers provide a measure of specialization after controlling for differences in availability. All populations are comprised of individuals that select diets with preference for certain items, yet there was no relationship between WID/TNW and TNW.



CHAPTER FOUR

IS UNGULATE MIGRATION CULTURALLY TRANSMITTED? EVIDENCE OF SOCIAL LEARNING FROM TRANSLOCATED ANIMALS

ABSTRACT

Ungulate migrations are assumed to stem from learning and cultural transmission of information regarding seasonal distribution of forage, but this hypothesis has not been tested empirically. I compared the migratory propensity of bighorn sheep and moose translocated into novel habitats with that of historical populations that had persisted for hundreds of years. While individuals from historical populations were largely migratory, translocated individuals initially were not. After multiple decades, however, translocated populations gained knowledge about surfing green waves of forage (tracking plant phenology) and increased their propensity to migrate. My findings indicate that learning and cultural transmission are the primary mechanisms by which ungulate migrations evolve. Loss of migration will therefore expunge generations of knowledge about the locations of high-quality forage and likely suppress population abundance.

MAIN TEXT

From tropical savannas to the Arctic tundra, the migrations of ungulates (hooved mammals) can span more than 1000 kilometers and are among the most awe-inspiring of natural phenomena. Migration allows ungulates to maximize energy intake by synchronizing their movements with the emergence of high-quality forage across vast landscapes (Merkle et al. 2016). Consequently, migration often bolsters fitness and results in migratory individuals greatly outnumbering residents (Fryxell et al. 1988, Rolandsen et al. 2016). Despite its critical importance, migrations

2232 are increasingly imperiled by human activities (Harris et al. 2009). Thus, understanding how
2233 migrations are developed and maintained is critical for the conservation of this global
2234 phenomena (Bolger et al. 2008). Ecologists have long speculated that memory and social
2235 learning underlie ungulate migration (Sweanor and Sandegren 1989, Nelson 1998, Boone et al.
2236 2006). Indeed, bison (*Bison bison*) remember the locations of high-quality forage and transmit
2237 such information to conspecifics (Merkle et al. 2015), while moose (*Alces alces*) and white-tailed
2238 deer (*Odocoileus virginianus*) adopt the movement strategies of their mothers (Sweanor and
2239 Sandegren 1989, Nelson 1998). Nevertheless, the hypothesis that social learning underlies the
2240 development and maintenance of ungulate migration has not been tested with empirical data.
2241 Animal migrations arise through a combination of learned behavior and genetically
2242 inherited neurological, morphological, physiological, and behavioral traits (Alerstam 2006,
2243 Bolger et al. 2008, Mueller et al. 2013). When behavior is primarily a consequence of social
2244 learning and persists across generations—a phenomenon known as culture—information is
2245 transmitted from generation to generation (Shettleworth 2010). Culture therefore is regarded as a
2246 "second inheritance system" analogous to the inheritance of genes that underlie innate behaviors
2247 (Whiten 2005, Tennie et al. 2009, Keith and Bull 2017). Thus, if social learning is the primary
2248 mechanism by which information regarding the seasonal distribution of high-quality forage is
2249 gained, cultural transmission may be the principal force by which ungulate migrations have
2250 evolved in landscapes conducive to migration.
2251 Ungulate migration is a strategy for exploiting altitudinal, longitudinal, and other
2252 topographic gradients of plant phenology that determine forage quality (Fryxell 1991,
2253 Hebblewhite et al. 2008). The ability of ungulates to synchronize their movements with
2254 phenological waves of nutritious, green plants—a behavior known as "green-wave surfing" (van

2255 der Graaf et al. 2006)—can result in migratory movements far beyond an individual's perceptual
2256 range (Bracis and Mueller 2017). Ungulates also can surf green waves of forage within year-
2257 round ranges, even in the absence of migration (*1*). Green-wave surfing may therefore represent
2258 a learned behavior that underlies migration, and such knowledge may accumulate over
2259 generations via cultural transmission (Tennie et al. 2009, Sasaki and Biro 2017).
2260 Across the American West, many bighorn sheep (*Ovis canadensis*) populations were
2261 extirpated in the late 1800s because of market hunting and transmission of disease from domestic
2262 sheep (*O. aries*; Fig. 1). To restore lost populations, wildlife managers translocated individuals
2263 from extant, migratory populations into vacant landscapes where extirpated populations once
2264 existed (Fig. 1). These individuals therefore had no knowledge about the landscapes (herein
2265 "novel landscapes") into which they were translocated. Thus, if migration does not stem
2266 primarily from a genetically inherited suite of traits, individuals should fail to migrate when first
2267 translocated into novel landscapes where migration would be a profitable strategy (Laland and
2268 Janik 2006).
2269 To test this prediction, I helped deploy global positioning system (GPS) collars on 181
2270 bighorn sheep sampled from four populations that had been extant for >200 years (herein
2271 "historical populations"; Fig. 1) and 131 bighorn sheep when first translocated into novel
2272 landscapes (Table S1). I defined migration as movement between distinct seasonal ranges and
2273 classified the movement of each collared individual as migratory or resident using net-squared
2274 displacement (Bunnefeld et al. 2011; S4). I then quantified how green waves of forage
2275 propagated across individual landscapes (1000–3600 km^2) by measuring the date each pixel in a
2276 rasterized time series of the Normalized Difference Vegetation Index (250-m spatial resolution,
2277 8-day temporal resolution) peaked in forage quality (S4; Aikens et al. 2017). Using this

rasterized measure of peak forage quality, I quantified the semivariance (magnitude of wave) in date of peak forage quality across a range of spatial lags (distance wave travelled; S4). Within historical populations, 65–100% of individuals migrated, whereas few (<7%; 9 of 131) individuals translocated into novel landscapes migrated (Fig. 2A). Migratory propensity of a population was not related to the magnitude of the green wave or the distance it traveled (Fig. S1), meaning landscape characteristics alone did not explain differences in migratory propensity among populations. The nine translocated individuals that migrated were translocated into existing populations of bighorn sheep (<200 individuals) reestablished three decades prior (S4), suggesting cultural transmission of migratory behavior among conspecifics (i.e., horizontal transmission). Because individuals from migratory populations failed to migrate when translocated into landscapes where they had no prior experience, genes are unlikely to be the primary agent underlying ungulate migration. Instead, migration may require extended periods of time for social learning and cultural transmission to occur.

To evaluate the hypothesis that green-wave surfing is a learned behavior, I first calculated the surfing ability of each GPS-collared individual as the absolute difference between the day an individual occupied a location and the day forage quality peaked at that location (Aikens et al. 2017). I then controlled for the influence that local differences in latitudinal, elevational, and topographical features may have on an individual's ability to surf the green wave (Aikens et al. 2017) by comparing observed green-wave surfing ability to that of a 'naïve forager' that moved at random and an 'omniscient forager' that had complete knowledge of phenological patterns (S4). By doing so, I was able to quantify how much knowledge individuals possessed about local patterns of phenology (Fig. S2). I found that the surfing knowledge of bighorn sheep from historical populations was approximately twice that of transplanted individuals (Fig. 2B),

2301 suggesting that knowledge about local green waves may improve over time as animals learn and
2302 culturally transmit information about the seasonal distribution of high-quality forage.
2303 The hypothesis that ungulate migration is established and maintained by cultural
2304 transmission predicts that green-wave surfing knowledge, and subsequently, the propensity to
2305 migrate should increase as animals learn how to exploit landscapes and transmit that foraging
2306 information across generations (i.e., vertical transmission of information). To evaluate the
2307 influence of vertical transmission on surfing knowledge and migratory propensity, I expanded
2308 my analysis to include individuals from four additional populations of bighorn sheep (an
2309 additional 108 individuals) and five populations of moose (*Alces alces*; 284 individuals) that
2310 were GPS collared ~10–110 years after either translocation or natural colonization (Fig. 1, Table
2311 S1, S4). I found that the surfing knowledge of both bighorn sheep and moose increased as time
2312 since population establishment increased (Fig. 3A). As time passed, and bighorn sheep and
2313 moose increased their surfing knowledge, their migratory propensity also increased (Fig. 3B,
2314 3C). Although population density and migratory propensity are sometimes correlated positively
2315 (Peters et al. 2017), migratory propensity did not change with dramatic decreases in population
2316 density caused by epizootics, habitat loss, and increased predation (Hnilicka et al. 2003, Oates
2317 2016). Together, these results demonstrate that ungulates accumulate knowledge of local
2318 phenological patterns over time via the 'ratcheting effect'—wherein each generation augments
2319 culturally transmitted information with information gained from their own experience—a process
2320 known as cumulative cultural evolution (Tennie et al. 2009, Sasaki and Biro 2017). Cultural
2321 transmission therefore acts as a second (non-genetic) inheritance system for ungulates, shaping
2322 their foraging and migratory behavior, and ultimately providing the primary mechanism by
2323 which their migrations have evolved.

Across the globe, anthropogenic barriers have disrupted ungulate migrations, triggered declines in population abundance, and even caused local extirpations (Harris et al. 2009). My results provide empirical evidence that learning and cultural transmission underlie the establishment and maintenance of ungulate migration. Because ungulate migrations stem from decades of social learning about spatial patterns of plant phenology, loss of migration will result in a dramatic decrease in the knowledge ungulates possess about how to optimally exploit their habitats. Hence, restoring migratory populations following extirpation or barriers to movement will be hindered by poor foraging efficiency, suppressed fitness and reduced population performance (Fryxell et al. 1988, Rolandsen et al. 2016). Thus, conservation of existing migration corridors, stopover sites, and seasonal ranges not only protect the landscapes that ungulates depend on (Sawyer and Kauffman 2011, Sawyer et al. 2013), but such efforts also maintain the traditional knowledge and culture that migratory animals use to bolster fitness and sustain abundant populations (Whitehead 2010, Keith and Bull 2017).

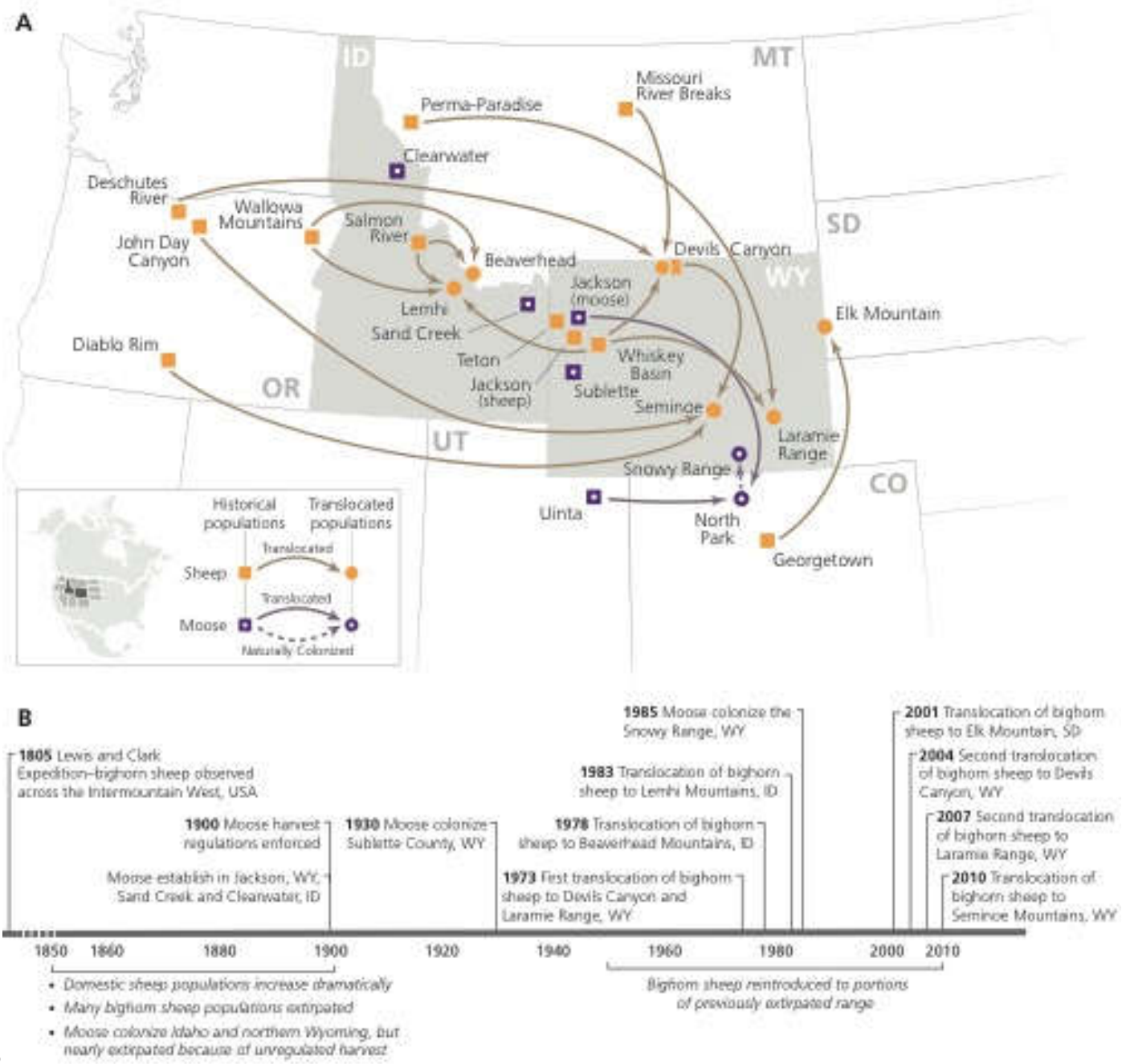


Fig. 1. Bighorn sheep and moose translocation history. (A) The subset of historical and translocated populations of bighorn sheep and moose used to assess the cultural basis of ungulate migration. (B) Timeline of bighorn sheep and moose translocations as well as other important events in the history of these species since settlement of western North America by European Americans. See S4 for further details about translocation history.

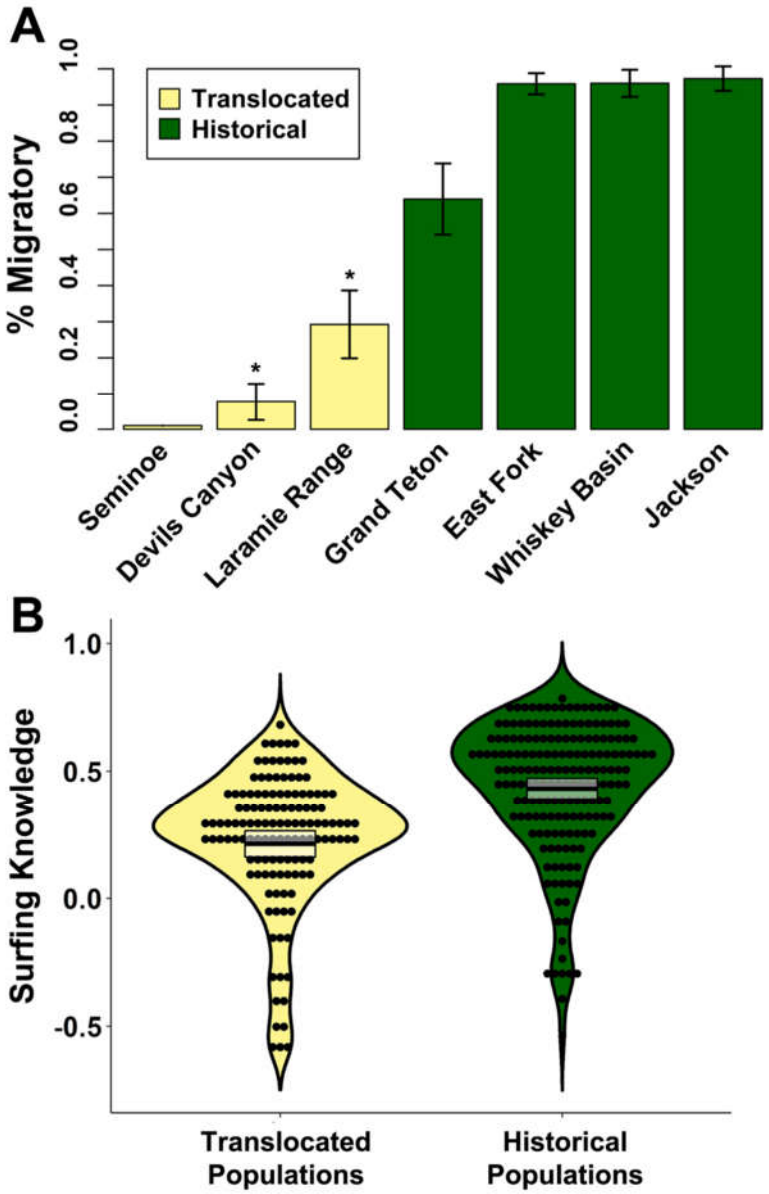
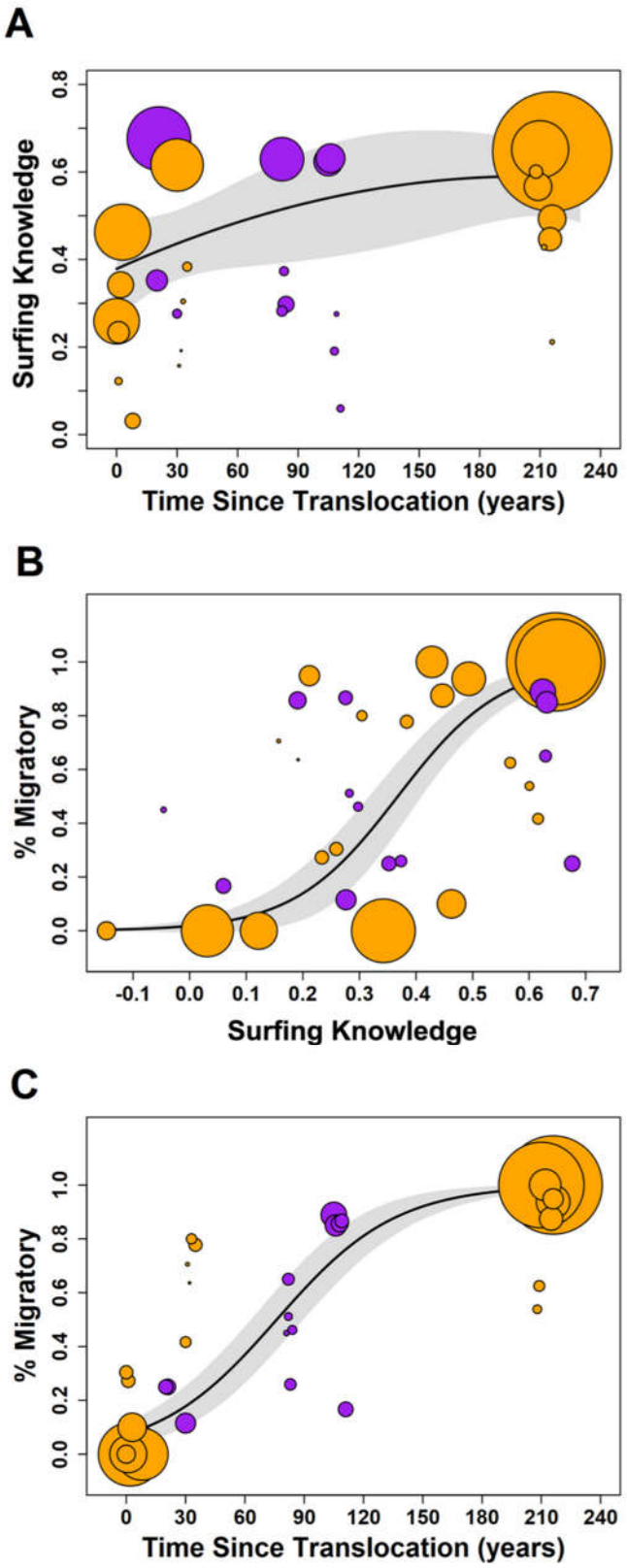


Fig 2. Migratory propensity and green-wave surfing knowledge of seven translocated and historical populations of bighorn sheep. (A) Migratory propensity (+/- SEM) of bighorn sheep translocated into novel landscapes (yellow bars) compared to historical (>200 years old) populations (green bars). Asterisks indicate landscapes where naïve individuals were translocated into populations previously established via translocation ~30 years prior. **(B)** Relative to omniscient and naïve foragers on the same landscape, surfing knowledge was lower for translocated (yellow) bighorn sheep compared to individuals from historical populations (green). Mean surfing knowledge (black horizontal bars) and associated 95% confidence intervals (white boxes) are presented. Surfing knowledge of individuals (black circles) in historical populations was significantly higher than that of translocated individuals (Mann-Whitney U Test, $W = 5863$, $P<0.001$).

Fig. 3. Green-wave surfing knowledge and migratory propensity over time. (A) Following translocation, populations of bighorn sheep (orange circles) and moose (purple circles) require decades to learn and culturally transmit information about how to best surf green waves, (B) eventually leading to the establishment of migration, which (C) takes many generations (generation time for bighorn sheep and moose is ~7 years). Circles represent estimates of surfing knowledge and migratory propensity for a given population in a given year (i.e., a migratory event). Circle size depicts the amount of confidence (inverse variance) in each estimate. Black lines and gray shaded areas illustrate fitted generalized linear model predictions and their 95% confidence intervals. All relationships are significant at $P<0.01$.



APPENDIX S4

Translocation History– Unregulated hunting and transmission of disease from domestic sheep (*Ovis aries*) to native bighorn sheep (*O. canadensis*) led to the extirpation of bighorn sheep from much of their historical range by the mid-twentieth century (Valdez and Krausman 1999; Fig. 1). To combat these extirpations, wildlife management and conservation agencies began translocating sheep from robust, extant populations into extirpated areas throughout the historical range of bighorn sheep (Singer et al. 2000). The genetics of all translocated individuals can be traced to one or more of seven migratory or partially migratory source populations (Sugden 1961, Hickey 2000, Beyer 2008, Kauffman et al. 2009, Clapp et al. 2014, Huwer 2015, Parr 2015): (i) Whiskey Basin, WY, USA, (ii) Georgetown, CO, USA, (iii) Missouri River Breaks, MT, USA (iv) Paradise-Perma, MT, USA, (v) Salmon River, ID, USA, (vi) Junction Sheep Range Provincial Park, BC, CA, and (vii) Jasper National Park, AB, CA. I studied eight bighorn sheep populations translocated in Wyoming, Idaho, and South Dakota, USA and four populations that have persisted since the time Europeans first occupied present-day Wyoming and Idaho (hereafter "historical populations"; Table S1).

The Devils Canyon population was initially established from individuals translocated from Whiskey Basin, WY in 1973. In 2005, individuals from Missouri River Breaks, MT (n=20), and Deschutes, OR (n=20) were added to bighorn sheep (n≈40) persisting from the original 1973 translocation (Kauffman et al. 2009). In 2009 and 2010, bighorn sheep were translocated from Devils Canyon, WY (n=12), Hart Mountain, OR (n=20), and John Day River Canyon, OR (n=20) into the Seminoe Mountains (Clapp et al. 2014). The Deschutes, OR and John Day Canyon, OR populations were established via translocation from Hart Mountain, OR, which itself was a translocated population stemming from individuals originating in Junction Sheep

Range Provincial Park, BC (Kornet 1978). The Laramie Range population was initially established in 1973 via translocated individuals from Whiskey Basin. In 2007, 30 individuals were translocated to Laramie Range from a population in the Perma-Paradise area of Montana (Sawyer et al. 2009b), which is a translocated, but partially migratory, population itself with an uncertain origin (Beyer 2008). Bighorn sheep in the Elk Mountain population of Wyoming and South Dakota were established via translocation of migratory individuals from the mountains surrounding Georgetown, CO (Parr 2015). Finally, the Lemhi and Beaverhead populations of Idaho were established via multiple translocations occurring from 1976–1989 using individuals from the Lostine River in the Wallowa Mountains of Oregon, which were themselves translocated from Jasper National Park, AB, as well as multiple populations from the Salmon River, ID region and the Whiskey Basin population of Wyoming (Idaho Fish and Game Department, Bighorn Sheep Management Plan; Table S1, Fig. 1).

Moose (*Alces alces*) were not present in the study region when Europeans first settled Jackson Hole, WY, in the mid-nineteenth century (Houston 1967). Southward expansion of moose from Montana in the late-nineteenth century, however, resulted in what is now considered the Jackson moose population (the greater Grand Teton National Park and Yellowstone National Park area of WY, USA), and the Clearwater and Sand Creek, ID populations by the turn of the twentieth century. By ca. 1930, moose had continued to expand their geographic range southward and began to occupy the area currently delineated as the Sublette population. In 1979, migratory moose from the Jackson population (n=12) and a population in the Uinta mountains of northern Utah (n=12) were translocated into the North Park region of the Medicine Bow mountain range of northern Colorado, USA. In 1987, the burgeoning population of moose in North Park were augmented by a second translocation of individuals (n=12) from Jackson. By

2425 ca. 1990, dispersing moose became established in the northern terminus of the Medicine Bow
2426 mountain range, and currently are managed as the Snowy Range moose population (Brimeyer
2427 and Thomas 2004; Table S1, Fig. 1).
2428
2429 **Materials and Methods:**
2430 *Animal capture and handling*– Detailed methods of capture, collar deployment, and translocation
2431 are reported elsewhere (Kauffman et al. 2009, Sawyer et al. 2009b, Clapp et al. 2014, Parr 2015)
2432 however, I briefly outline these methods here. Adult (>1 yo) bighorn sheep and moose were
2433 captured via either net fired from a helicopter (Barrett et al. 1982, Krausman et al. 1985), drop
2434 net (Kock et al. 1987), or dart containing a sedative fired from a truck or helicopter (Kreeger and
2435 Franzmann 1996). Translocated individuals were transported from source populations to release
2436 sites using a helicopter or a truck and livestock trailer. Each individual was equipped with a GPS
2437 collar (brand and model varied across study areas). All capture and handling methods were
2438 approved by the Oregon Department of Fish and Wildlife (Foster 2005), Idaho Department of
2439 Fish and Game Health Laboratory, South Dakota State University Animal Care and Use
2440 Committee (Approval Number 12-090A), or the Wyoming Game and Fish Department (Chapter
2441 10–1535 and Chapter 33–750 permits) and followed recommendations of the American Society
2442 of Mammalogists (Sikes et al. 2011).
2443
2444 *Assessment of Migratory Behavior*– I operationally defined migration as movement between
2445 distinct seasonal ranges (Bunnefeld et al. 2011, Singh et al. 2012) and considered multiple round
2446 trips between winter and summer ranges within a year as indicative of non-migratory behavior
2447 (Cagnacci et al. 2016). To distinguish migratory behavior from non-migratory behaviors (i.e.,

residency, nomadism, dispersal), I calculated the net squared displacement (NSD) in daily movements of individual bighorn sheep and moose from January 1 to December 31 (Seip and Bunnell 1985, Bunnefeld et al. 2011, Singh et al. 2012). I inspected the NSD plots for clear patterns of movement that mirrored a double logistic curve, which represent movement away from a winter range in spring followed by a movement back to winter range in fall (i.e., migration; Seip and Bunnell 1985, Bunnefeld et al. 2011, Singh et al. 2012). If an individual left its winter range in spring but did not return by December 31, I inspected the NSD plot for the following year and overlaid GPS collar locations onto topographic maps in ArcMap (Environmental Systems Research Institute, Redlands, CA) to determine if the individual returned to its winter range during mid-winter (e.g., January or February). As deep snow-adapted animals, moose often migrated back to their winter range in January or February, especially in years with below-average snow accumulation, making my multi-year assessment of NSD plots an important step in determining migratory status. A common migratory behavior observed in bighorn sheep is to winter on wind-blown ridges at mid or high-elevation, quickly move downhill in spring to forage on newly emergent vegetation at lower elevations, then track emerging high-quality forage up through mid or high-elevation winter ranges throughout the calendar months of summer (Whitten 1975, Seip and Bunnell 1985, Courtemanch et al. 2017). Therefore, I categorized this behavior as migratory even though it resulted in individuals returning to winter ranges at some point during the summer calendar months.

Measuring Forage Quality– For ungulates, forage quality is highest when plants are in an intermediate phenological state (i.e., when plants are midway through green-up) because this stage of growth offers an optimal balance between digestibility and biomass (Fryxell 1991,

Hebblewhite et al. 2008). In my study area, both bighorn sheep and moose select forage in an intermediate phenological state (Merkle et al. 2016). Therefore, I computed the date at which forage reached an intermediate phenological state across space and time by calculating the Instantaneous Rate of Green-up (IRG), a metric derived from a time series of the Normalized Difference Vegetation Index raster grids (NDVI; MODIS product MOD09Q1; 250-m spatial resolution, 8-day temporal resolution)(Bischof et al. 2012). Following the protocol of Merkle *et al.* (2016) and Bischof *et al.* (2013), I fit a double logistic function to the annual NDVI profile of each 250m x 250m pixel and estimated the date of peak IRG as the first derivative of the fitted double logistic function.

Accounting for Differences in Plant Phenological Gradients Among Landscapes—Genetics, learning, and local differences in patterns of plant phenology (i.e., environment) represent three, non-mutually exclusive, hypotheses as to why some populations are migratory and other populations are resident. To address the importance of local landscape characteristics on migratory propensity, I assessed patterns of plant phenology among the landscapes occupied by different populations (Mueller et al. 2011, Teitelbaum et al. 2015). I quantified gradients in plant phenology by calculating the semivariance in the date of peak IRG across distance lags within each landscape (Mueller et al. 2011, Teitelbaum et al. 2015). Landscapes in which patterns of phenology progress as a green wave (i.e. green-up which progresses sequentially across the landscape) should facilitate green-wave surfing and favor migration (van der Graaf et al. 2006, Armstrong et al. 2016). A perfect green wave, in which the date of peak IRG becomes later with greater distance lags (across the entire landscape), would result in a semi-variogram that continues to increase in semi-variance as the distance lag increases (Fig. S1 A). No change in

semivariance across distance lags would indicate the absence of a green wave (Fig. S1 B). An asymptotic curve in the semi-variogram represents a green wave that is continuous across only a portion of the landscape (Fig. S1 C). Thus, I used the maximum semivariance (excluding the last ¼ of each semi-variogram; Dale and Fortin 2014) to determine the duration of green-up across the landscape (i.e., magnitude of green wave), and the distance lag of the peak semivariance to represent the distance over which the green wave travelled (Fig S1).

To define each population-specific landscape, I first mapped population limit and calculated the size of each population's space-use by computing the 99% minimum convex polygon (MCP; Calenge 2006) surrounding each population's GPS locations. To standardize the delineation of each landscape, I created a circular buffer (defined as the radius of the maximum area of species-specific population ranges) around the centroid of each MCP (Teitelbaum et al. 2015). The area for each landscape was 828 km^2 for sheep populations and 3409 km^2 for moose populations. To ensure I measured the size and strength of the phenological gradients available to bighorn sheep and moose, I masked date of peak IRG by a species-specific habitat map (e.g., Fig. S1 D; see *Species-specific habitat delineation* below). Due to computational constraints, I resampled each landscape raster containing the date of peak IRG from a pixel size 250 m^2 to 500 m^2 before calculating the semi-variogram for each landscape and year in which I collar data existed. I found no relationship between migratory propensity of a population and the magnitude of green waves (Fig. S1 G) or the distance the green wave travelled (Fig. S1 H), indicating that landscape characteristics alone cannot explain the presence or absence of migration amongst these populations.

Evaluating Green-Wave Surfing Knowledge— The frequency with which collars recorded GPS locations was based on the objectives of each study and varied from 1–24h. Therefore, I standardized the fix rate of each GPS collar by subsampling to one location per day (the least-frequent fix rate in my data set). I determined the temporal window within which green-wave surfing (i.e., the ability to track green waves of plant phenology) would be assessed by first extracting the date of peak IRG for all collar locations within each population, then calculating the start of spring as the 2.5% quantile, and the end of spring as the 97.5% quantile of the Julian days that IRG peaked (sensu Aikens et al. 2017). The daily green-wave surfing ability of each individual was then computed as the absolute difference (in days) between the date individuals used a given IRG cell and the date peak IRG occurred in that same cell ("Days-From-Peak"; *23*). I then calculated a surfing ability score for each individual as the median Days-From-Peak the individual experienced between estimated start and end of spring.

Because the green waves of some landscapes may be easier to track than others (Aikens et al. 2017), directly comparing the surfing ability of individuals in different environments does not provide a robust estimate of knowledge possessed about local patterns of phenology. To quantify the amount of knowledge individuals and, by extension, populations possessed about local phenology, I assessed the degree to which observed green-wave surfing differed from two simulated foragers: (i) an omniscient forager with complete knowledge of local patterns in plant phenology, and (ii) a naïve forager with no knowledge of local patterns in plant phenology. Both naïve and omniscient foragers were forced to move within species-specific habitat (see *Species-Specific Habitat Delineation* below) and were limited by the distance (step length) they could move in a day. Daily step lengths were identified separately for bighorn sheep and moose by calculating the 99% quantile (to remove outliers) of daily step lengths occurring during the

spring period (moose=6049 m, bighorn sheep=6453 m). I simulated omniscient foraging by allowing simulated foragers to choose the IRG cell within its step-length radius that was closest to date in which its step occurred. If more than one cell possessed a peak IRG date that was equally close to the date in which the simulated forager's step occurred, the simulated forager chose the IRG cell closest to its current position. I simulated naïve foraging by allowing simulated foragers to make daily steps determined by randomly sampling (with replacement) from uniform distributions of turning angles and step lengths (i.e., a random walk). As with simulations of omniscient foragers, the movements of naïve foragers were constrained to occur within species-specific habitats and maximum daily step lengths. Because the simulated surfing ability of naïve foragers varied among iterations, I simulated 100 random walks per collared individual (sensu Fortin 2003). For each of the 706 collared bighorn sheep and moose (hereafter, "empirical foragers"), the distribution of surfing ability across all 100 simulated random walks was not normally distributed (Shapiro-Wilk test), so I considered the median surfing ability of all 100 random walks as the surfing ability for each naïve forager. Each simulated individual began foraging at the same location and date as its paired empirical forager (i.e., a collared sheep or moose). To measure the amount of information each individual possessed about local patterns of plant phenology, I calculated an index of surfing knowledge as follows:

Eq. 1. $$1 \quad \frac{abs(omniscient - empirical)}{abs(omniscient - naive)}$$

By comparing the surfing ability of collared individuals with those of the simulated omniscient and naïve individuals, the index of surfing knowledge not only accounts for different patterns of phenology in each landscape, but also provides a measure of how proficient individuals are at surfing relative to the surfing opportunity provided by the local environment (Fig. S1).

Species-Specific Habitat Delineation— To ensure that the simulated movements of omniscient and naïve foragers were realistic (in the sense that a simulated forager did not use locations on the landscape that a real moose or sheep would not), I delineated species-specific habitat across the study region by using resource selection functions (Manley et al. 2010). GPS collar locations from historical populations more accurately reflect migratory behavior and optimal habitat selection than the locations of recently translocated individuals who had less time to acquire information about their environment. Therefore, I parameterized resource selection functions using only the GPS locations of individuals from historical populations along with a suite of habitat and topographic variables known to be important to bighorn sheep and moose in the region (Baigas 2008, Becker 2008, Courtemanch et al. 2017; Table S2).

To delineate species-specific habitat across the study region I quantified 2nd order resource selection (Johnson 1980) using a classic use vs. availability design (Manley et al. 2010). In contrast to the more common analyses of 3rd order habitat selection, where used (observed) locations are compared to available (random) locations within a home range to infer fine-scale habitat selection, a 2nd order analysis of habitat selection compares used locations to available location across a much larger (landscape) scale to infer more broad scale selection of habitats associated with placement of the home range (Johnson 1980). Therefore, I sampled a random location across the entire study area for every observed GPS location because my goal was to identify species-specific habitat use rather than individual selection for specific habitat characteristics. After extracting covariate values to both used and available locations, I centered and scaled covariates prior to fitting generalized mixed-effect models (GLMM; Schielzeth 2010). I used forward step-wise model selection and Akaike's Information Criterion (AIC) to identify the most parsimonious resource selection function (Burnham and Anderson 2002). I further

evaluated model fit for each species by performing a K-folds cross validation (k=10, repeated 100 times; Boyce et al. 2002). K-folds cross validation indicated that the models performed well (bighorn sheep r_s=0.87±0.03, moose r_s=0.88±0.02). I considered species-specific habitat to be any raster cell with a probability-of-use value above the 50th quantile of the distribution of selection probabilities (i.e., high probability of use areas; Sawyer et al. 2009a).

Statistical Assessment of Social Learning and Culture– I used GLMs and GLMMs to quantify the effect of opportunity for cultural transmission (time in years) had on surfing knowledge (Fig. 3A), the influence of surfing knowledge on migratory propensity (Fig. 3B), and the influence of time on migratory propensity (Fig. 3C). I fit models with and without random intercepts, random slopes, and random intercepts and slopes with species (moose and bighorn sheep) as the random effect. I estimated model parameters using maximum likelihood and compared models using likelihood ratio tests (Zuur et al. 2009). Mixed effect models indicated that sheep and moose had similar intercepts and slopes in all models (P>0.5 for all log likelihood ratios). All models were statistically significant (all P<0.01). All analyses and simulations were performed in Program R (R Core Team 2014).

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Fig. S1. Illustration of how landscape suitability for migration was measured. Simulated (A) perfect green wave (i.e., phenological gradient), (B) heterogeneous landscape with no green wave, and (C) landscape intermediate to A and B, as well as observed green waves in (D) Devils Canyon, (E) Seminoe, and (F) Jackson. Brown pixels represent areas where the date of peak forage quality occurred early, whereas green pixels represent relatively late peaks in forage quality. X-axis represents the distance travelled by green waves (distance lag in km) and y-axis represents magnitude of the green wave (semivariance). Dashed lines illustrate maximum semivariance (horizontal), maximum distance lag (vertical), and the ¾ cutoff (grey) used to eliminate 'edge' effects. No relationship was found between migratory propensity and the (G) distance green waves travelled or (H) the magnitude of green waves available to all 17 populations of bighorn sheep (orange) and moose (purple), indicating that landscape characteristics alone cannot explain the presence or absence of migration.

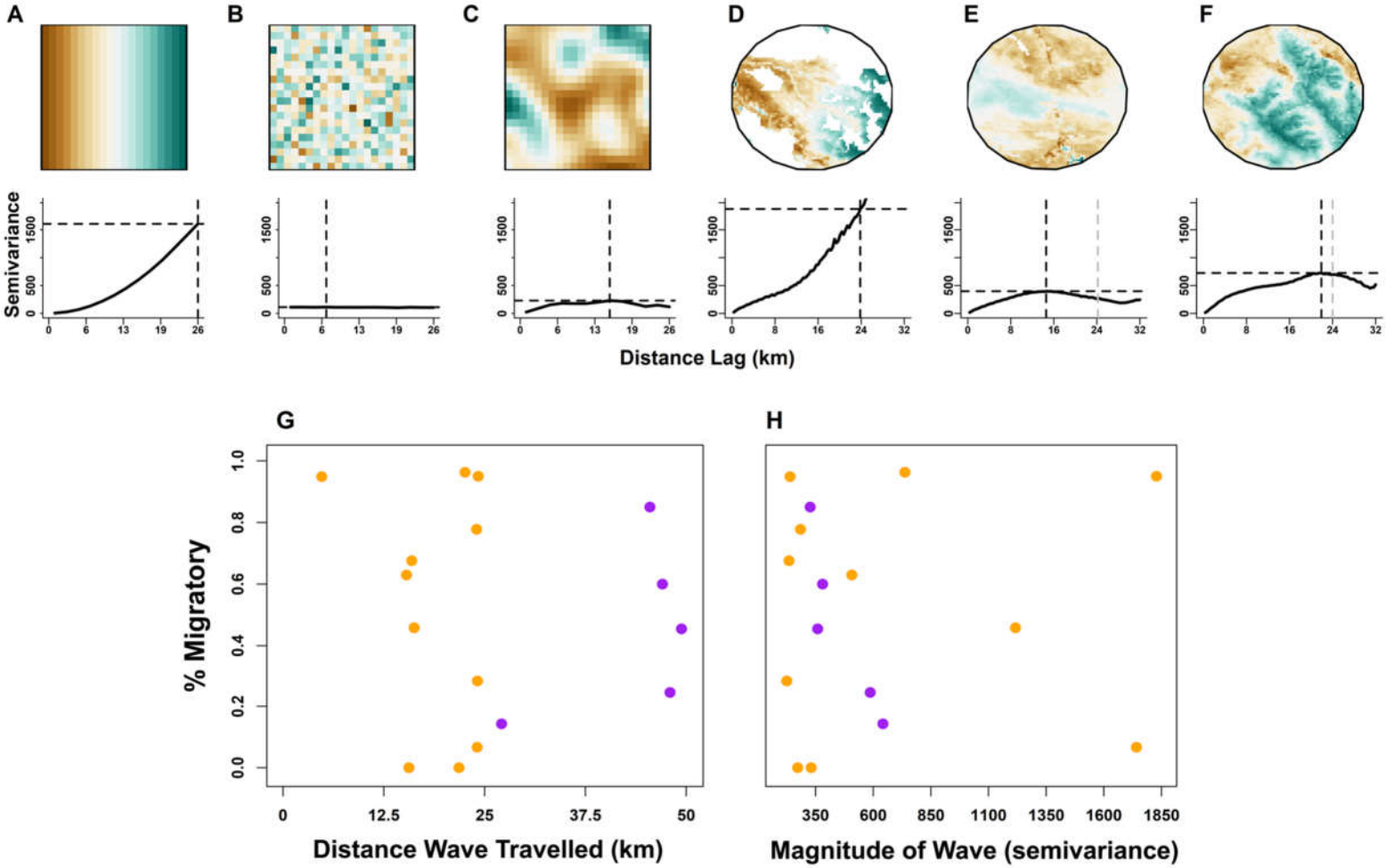

Fig. S2. Heuristic demonstration of how surfing knowledge was calculated. The phenology tracking (surfing) abilities of simulated omniscient (black circles), simulated naïve (red circles), and empirical (open circles) bighorn sheep and moose were used to calculate an index of mean surfing knowledge (green triangles). Population-level (n=17) means are plotted to illustrate the appropriateness of the surfing knowledge index for quantifying how well observed populations were able to track high-quality forage relative to simulated individuals in real landscapes. Graphically, equation 1 and the surfing knowledge index represents how close to omniscience (complete knowledge of forage quality distribution on their landscape) or naïveté (no knowledge of forage quality distribution on their landscape) empirical individuals, and hence populations, surfed green waves. Therefore, the surfing knowledge index simultaneously controls for local variation in the distribution of high-quality forage and represents how much information individuals and populations have about distribution of high-quality forage on their landscapes.

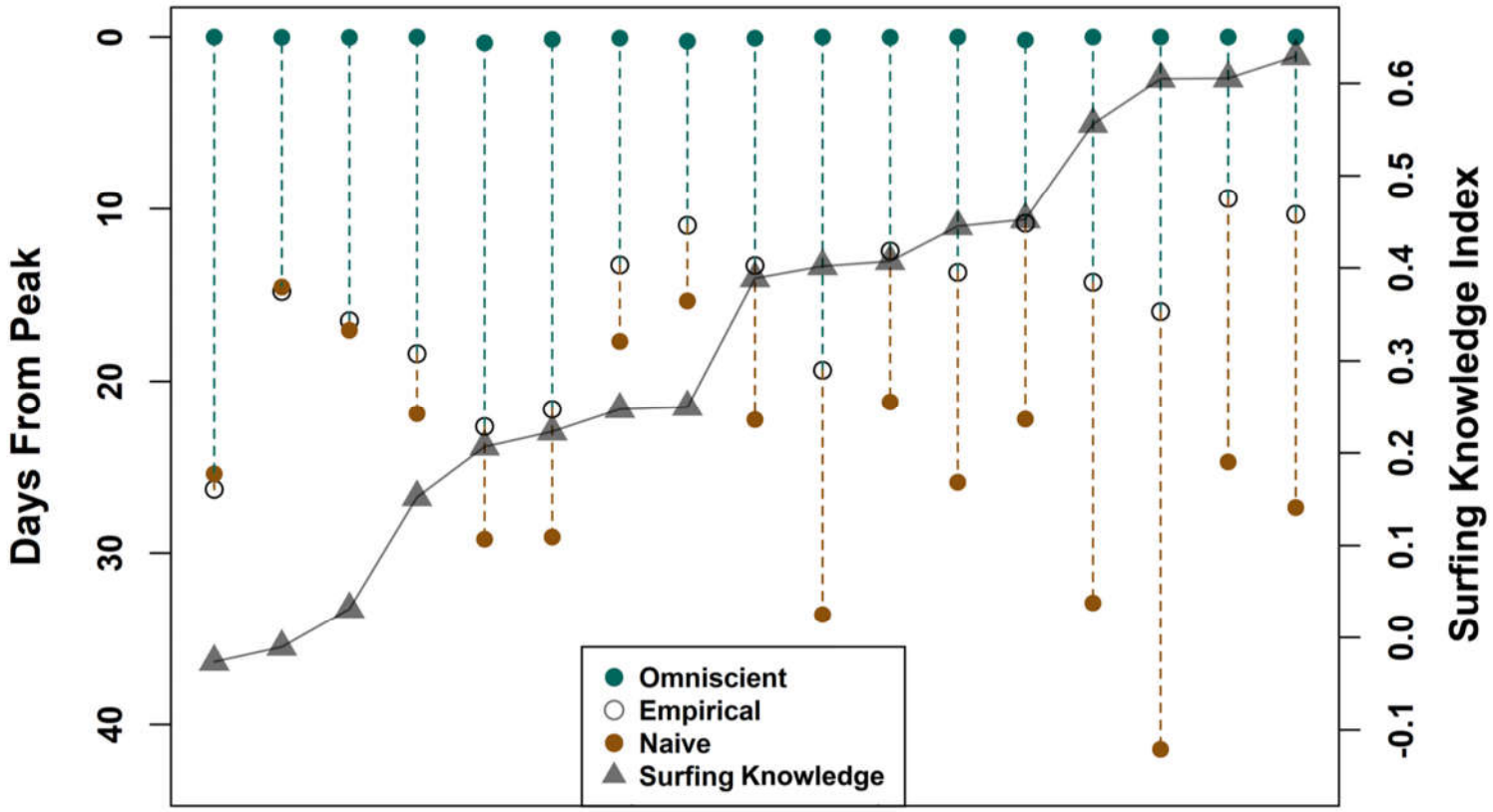

Table S1. **Data illustrating study design of translocation experiment.** For convenience in plotting and analyzing the effect of time on the migratory propensity of bighorn sheep, I use ca 1800 as year of establishment because these populations have persisted since the time European Americans settled western North America (*1*). Moose were not present in WY and ID when European-American settlers first arrived, but were rather first observed around the turn of the twentieth century (*14*). Population age is either (i) the difference between the year a population was established and the year in which GPS collars were deployed on individuals or (ii) zero if collars were deployed at the time of translocation. Double crosses (‡) reflect populations where GPS-collared bighorn sheep were translocated into previously extirpated landscapes where small populations of bighorn sheep (<200 individuals) had been established approximately three decades prior. Sample size (n) refers to the number of animal years observed (i.e., number of years individuals were monitored). Source populations of each translocation and bibliographical references describing the migratory behavior of each source population are provided.

Species	Population	Pop. Type	Pop. Age	(n)	Source Population(s)	References
Ovis canadensis	East Fork Salmon R.	historical	216	51	–	–
Ovis canadensis	Whiskey Basin	historical	212	44	–	–
Ovis canadensis	Jackson	historical	211	43	–	–
Ovis canadensis	Grand Teton	historical	209	43	–	–
Alces alces	Clearwater	historical	111	29	–	–
Alces alces	Jackson	historical	108	67	–	–
Alces alces	Sublette	historical	82	119	–	–
Alces alces	Sand Creek	historical	82	14	–	–
Ovis canadensis	N. Beaverhead Range	translocated	35	18	Salmon River, ID; Jasper National Park, AB	Idaho Fish and Game Department (*37*)
Ovis canadensis	S. Beaverhead Range	translocated	35	10	Salmon River, ID	Idaho Fish and Game Department (*37*)
Ovis canadensis	N. Lemhi Range	translocated	32	45	Salmon River, ID; Jasper National Park, AB	Idaho Fish and Game Department (*37*)
Ovis canadensis	S. Lemhi Range	translocated	30	25	Whiskey Basin, WY	Idaho Fish and Game Department (*37*)
Alces alces	Snowy Range	translocated	20	57	Jackson, WY	Brimeyer and Thomas (*43*)
Ovis canadensis	Elk Mountain	translocated	8	10	Georgetown, CO	Parr (*32*), Colorado Parks and Wildlife (*34*)
Ovis canadensis	Devils Canyon	translocated	0	44	Whiskey Basin, WY; Junction Sheep Range Provincial Park, BC; Missouri River Breaks, MT	Hickey (*35*), Sugden (*36*), Kauffman et al. (*39*)
Ovis canadensis	Laramie Range	translocated	0‡	42	Whiskey Basin, WY; Paradise-Perma, MT	Beyer (*33*)
Ovis canadensis	Seminoe Range	translocated	0‡	45	Junction Sheep Range Provincial Park, BC; Devils Canyon, WY	Clapp (*38*)

Table S2. Parameters used to build resource selection functions. Parameter names match those presented in Table S3. All parameters were derived from 30m resolution raster data. For all discrete parameters, I calculated "distance to" (in meters) and "focal" (sum of the number cells within a 1km circular moving window) parameters in ArcGIS (Environmental Systems Research Institute, Redlands, CA). Data references are both the raster data sources as well as the ArcGIS and Program R tools used to derive metrics from the data. Parameter references are literature from which the important parameters were identified. Species "BS" refers to bighorn sheep and "M" refers to moose. Asterisks indicate variables that were excluded from final RSF models through the model selection procedure.

Parameter	Data Type	Data Reference	Parameter Reference	Species
Topographic				
Escape Terrain	Discrete		Sappington et al. (2007)	BS
Topographic Roughness*	Continuous	National Elevation Dataset , Evans (2017)	Sappington et al. (2007)	BS
Elevation	Continuous	National Elevation Dataset	Baigas (2008), Becker (2008), Courtemanch et al. (2017)	BS, M
Linear Aspect	Continuous	National Elevation Dataset, Evans et al. (2014)	Baigas (2008), Becker (2008), Courtemanch et al. (2017)	BS, M
Slope	Continuous	National Elevation Dataset, ESRI	Baigas (2008), Becker (2008), Courtemanch et al. (2017)	BS, M
Slope^2	Continuous	National Elevation Dataset , ESRI	Baigas (2008)	M
Compound Topographic Index	Continuous	National Elevation Dataset, Evans et al. (2014)	*sensu* Becker (2008)	M
Topographic Position Index*	Continuous	National Elevation Dataset, Evans (2017)	*sensu* Courtemanch et al. (2017), Valdez and Krausman (1999)	BS
Heat Load Index	Continuous	National Elevation Dataset, Evans et al. (2014)	Monteith et al. (2015)	M
Habitat				
Willow	Discrete	National Land Cover Database	Baigas (2008), Becker (2008), Valdez and Krausman (1999)	BS, M
Wetland	Discrete	National Land Cover Database	Baigas (2008), Becker (2008), Valdez and Krausman (1999)	BS, M
Shrub	Discrete	National Land Cover Database	Baigas (2008), Becker (2008), Valdez and Krausman (1999)	BS, M
Grass	Discrete	National Land Cover Database	Baigas (2008), Becker (2008), Courtemanch et al. (2017)	BS, M
Conifer Forest	Discrete	National Land Cover Database	Baigas (2008), Becker (2008), Courtemanch et al. (2017)	BS, M
Deciduous Forest	Discrete	National Land Cover Database	Baigas (2008), Becker (2008), Courtemanch et al. (2017)	BS, M
Mixed Deciduous-Conifer Forest	Discrete	National Land Cover Database	Baigas (2008), Becker (2008), Courtemanch et al. (2017)	BS, M
All Forest	Discrete	National Land Cover Database	Baigas (2008), Becker (2008), Courtemanch et al. (2017)	BS, M

Table S3. **(A) Bighorn sheep and (B) moose resource selection functions.** All variables were centered and scaled prior to model fitting, meaning parameter estimates (β coefficients) reflect relative effect sizes.

A

Sheep RSF Models	Intercept	Escape Terrain Distance	Grass Distance	Wetland Distance	Forest Focal	Shrub Distance	Willow Distance	Escape Terrain Focal	Grass Focal	Shrub Focal	DF	LogLik	AICc	Delta	Weight
Model 9	-7.58	-18.72	-3.22	-2.04	0.34	-1.29	-1.24	0.74	1.50	1.14	11	-3663.32	7348.65	0.00	1.00
Model 8	-7.44	-18.62	-3.19	-1.97	-0.64	-1.81	-1.20	0.66	0.63	-	10	-3704.81	7429.64	80.99	0.00
Model 7	-7.50	-18.53	-4.16	-1.94	-0.96	-1.34	-1.09	0.73	-	-	9	-3772.59	7563.19	214.54	0.00
Model 6	-9.17	-23.82	-4.48	-1.84	-0.91	-1.10	-1.01	-	-	-	8	-3913.72	7843.45	494.80	0.00
Model 5	-8.90	-22.90	-4.50	-2.64	-0.86	-1.22	-	-	-	-	7	-4060.27	8134.55	785.90	0.00
Model 4	-8.38	-22.07	-4.31	-2.69	-0.91	-	-	-	-	-	6	-4257.70	8527.41	1178.76	0.00
Model 3	-8.44	-19.63	-6.68	-2.81	-	-	-	-	-	-	5	-4589.90	9189.81	1841.16	0.00
Model 2	-7.78	-18.98	-7.02	-	-	-	-	-	-	-	4	-5431.03	10870.07	3521.42	0.00
Model 1	-6.60	-20.61	-	-	-	-	-	-	-	-	3	-7846.09	15698.18	8349.53	0.00
Intercept	0.00	-	-	-	-	-	-	-	-	-	2	-13449.83	26903.66	19555.01	0.00

B.1

Moose RSF Models	Intercept	Wetland Distance	Grass Focal	Mixed Forest Distance	Decid. Forest Distance	Wetland Focal	Willow Distance	Shrub Distance	Willow Focal	Conifer Forest Focal	Heat Load Index	Conifer Forest Distance	Mixed Forest Focal	Grass Distance	Slope^2
Model 16	-3.39	-4.87	-1.84	-7.27	2.43	1.22	-1.71	-0.83	0.67	0.20	0.29	-0.66	-0.23	0.17	-0.12
Model 15	-3.36	-4.85	-1.81	-7.24	2.42	1.24	-1.71	-0.77	0.70	0.26	0.30	-0.66	-0.22	0.17	-0.12
Model 14	-3.36	-4.84	-1.80	-7.25	2.41	1.23	-1.70	-0.78	0.69	0.27	0.29	-0.68	-0.22	0.17	-0.09
Model 13	-3.38	-4.87	-1.83	-7.26	2.40	1.24	-1.71	-0.77	0.69	0.26	0.27	-0.65	-0.22	0.16	-
Model 12	-3.42	-4.80	-1.92	-7.33	2.42	1.25	-1.71	-0.75	0.69	0.25	0.27	-0.65	-0.22	-	-
Model 11	-3.38	-4.87	-1.91	-7.15	2.42	1.25	-1.68	-0.78	0.69	0.26	0.27	-0.65	-	-	-
Model 10	-3.46	-4.90	-1.85	-7.69	2.43	1.29	-1.70	-0.81	0.63	0.37	0.27	-	-	-	-
Model 9	-3.42	-4.83	-1.79	-7.74	2.41	1.29	-1.63	-0.88	0.65	0.40	-	-	-	-	-
Model 8	-3.46	-4.56	-2.04	-8.22	2.56	1.24	-1.71	-0.78	0.53	-	-	-	-	-	-
Model 7	-3.36	-4.47	-2.07	-7.85	2.63	1.43	-2.13	-0.75	-	-	-	-	-	-	-

Model 6	-3.39	-4.80	-1.98	-7.94	2.59	1.41	-1.97	-	-	-	-	-	-	-	-
Model 5	-3.17	-6.30	-1.99	-7.47	2.24	1.55	-	-	-	-	-	-	-	-	-
Model 4	-3.59	-8.17	-2.12	-5.53	1.94	-	-	-	-	-	-	-	-	-	-
Model 3	-2.50	-6.72	-2.23	-2.73	-	-	-	-	-	-	-	-	-	-	-
Model 2	-2.10	-7.18	-2.26	-	-	-	-	-	-	-	-	-	-	-	-
Model 1	-1.54	-6.71	-	-	-	-	-	-	-	-	-	-	-	-	-
Intercept	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-

B.2

Moose RSF Models	Compound Topographic Index	Shrub Focal	DF	LogLik	AICc	Delta	Weight
Model 16	-0.10	-0.09	18	-4760.10	9556.22	0.00	0.59
Model 15	-0.09	-	17	-4761.53	9557.08	0.86	0.39
Model 14	-	-	16	-4765.58	9563.19	6.97	0.02
Model 13	-	-	15	-4768.94	9567.91	11.69	0.00
Model 12	-	-	14	-4774.70	9577.42	21.20	0.00
Model 11	-	-	13	-4799.79	9625.60	69.38	0.00
Model 10	-	-	12	-4825.70	9675.41	119.19	0.00
Model 9	-	-	11	-4880.85	9783.72	227.50	0.00
Model 8	-	-	10	-4949.27	9918.56	362.34	0.00
Model 7	-	-	9	-5026.49	10070.99	514.77	0.00
Model 6	-	-	8	-5196.47	10408.95	852.73	0.00
Model 5	-	-	7	-5574.88	11163.77	1607.55	0.00
Model 4	-	-	6	-6108.91	12229.83	2673.61	0.00
Model 3	-	-	5	-6948.51	13907.03	4350.80	0.00
Model 2	-	-	4	-7740.81	15489.62	5933.40	0.00
Model 1	-	-	3	-9766.79	19539.58	9983.36	0.00
Intercept	-	-	2	-15463.42	30930.84	21374.62	0.00

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