



EVIDENCE OF SUMMER NUTRITIONAL LIMITATIONS IN A NORTHEASTERN WASHINGTON MOOSE POPULATION

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ABSTRACT: Understanding the role of summer-autumn nutrition is critically important as moose (*Alces alces*) populations decline along their southern range in North America because it influences dynamics through performance and susceptibility to predation, disease, and parasitism. To assess nutritional limitations during summer-autumn, we estimated body fat and protein reserves ($n = 61$), pregnancy rate ($n = 71$), and lactation status ($n = 59$) of adult female moose in northeastern Washington State in December 2013, 2014, and 2016. Adult pregnancy rate was depressed (79%) and correlated with loin muscle thickness, and 14% of adult moose had evidence of delayed conception. Adult moose, particularly those that had successfully raised a calf, entered winter with low energy stores. Lactating moose were thinner than non-lactating moose and overall, 79% of moose sampled had $< 9\%$ body fat, indicating at least moderate nutritional limitations linked to performance and survival. Body fat was positively related to subsequent survival, and marrow fat levels indicative of starvation or severe nutritional stress were found in 56% of femurs (10 of 18) collected. Combined, these data highlight the importance of accounting for reproductive history when interpreting nutritional condition data and the importance of sampling moose populations in autumn when interpreting the influence of seasonal habitats on subsequent productivity and mortality.

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Key Words: *Alces alces*; body condition; body fat; moose; nutrition; pregnancy; ultrasonography; Washington State.

Although huntable populations remain in most jurisdictions, moose (*Alces alces*) are currently declining across much of their range within the United States south of the 49th parallel (Timmerman and Rodgers 2017, Jensen et al. 2018), including most populations in Rocky Mountain states (Nadeau et al. 2017). Many factors are hypothesized to influence southern populations, including parasites and disease (Lankester and Samuel 2007), predation (Ross and Jalkotzy 1997, Patterson et al. 2013, Mech and Fieberg 2014), plant phenology, composition, and nutrition (Monteith et al. 2015, Ruprecht et al. 2016), and

climate change directly through heat stress (McCann et al. 2013, Lenarz et al. 2019), or more likely, indirectly through changes in host-parasite relationships (Rempel 2011, Jones et al. 2017, 2019, Pekins 2020).

Nutrition rarely impacts populations in a catastrophic, obvious manner but rather through subtle, cumulative effects across many metrics of performance (Cook et al. 2004, Hurley et al. 2014) complicating explicit identification of its effects. Inadequate nutrition impacts reproduction, sub-adult growth, and survival and also interacts with other limiting factors making animals more susceptible to predation,

disease, parasites, or heat stress and winter weather (Huggard 1993, Bender et al. 2008, Metz et al. 2012, Mattisson et al. 2014, Johnson et al. 2019), with these interactions challenging to quantify in wild populations. In addition, researchers commonly measure pregnancy rates or survival of adults; however, these performance metrics in adults are the least sensitive to nutritional limitations (Gaillard et al. 2000, Bonenfant et al. 2002, Cook et al. 2004, 2018). Adding to the complexity, measuring nutritional resources is difficult for ruminants that make decisions at a variety of scales to maximize energy or protein intake while minimizing ingestion of secondary metabolites (Hobbs and Swift 1985, Hobbs and Hanley 1990, Cook et al. 2016, Forbey et al. 2018, Shipley et al. 2020). Intake and diet quality are reflective not only of the abundance of high-quality foods (Renecker and Schwartz 1998), but also of variation in bite mass among plant species (Shipley 2007, Cook et al. 2016, Denryter 2017, Hull et al. 2020), distribution of patches, and forage density (Wickstrom et al. 1984, Spalinger and Hobbs 1992), attributes difficult to measure with standard vegetation sampling methods (Cook et al. 2016).

Alternatively, nutritional condition – formally defined as the state of body components (i.e., fat and protein) that influence an animal’s future fitness (Harder and Kirkpatrick 1994) – reflects the cumulative balance of nutritional resources, energetic expenditures, and requirements. Strategic, temporal measurements of nutritional condition of moose can provide insight into the occurrence and severity of resource limitations across seasons. Critical to field measurements of nutritional condition has been the development of techniques to estimate the ingesta-free body fat percentage (hereafter referred to as “body fat”) of live ungulates. In particular, rump fat thickness measured via ultrasonography is

consistently one of the most accurate predictors of body fat in moose (Stephenson et al. 1998), mule deer (*Odocoileus hemionus*; Stephenson et al. 2002, Cook et al. 2007), elk (*Cervus canadensis*; Cook et al. 2001a), bighorn sheep (*Ovis canadensis*; Stephenson et al. 2020), and caribou (*Rangifer tarandus*; Cook et al. *in press*). Unfortunately, measurements of body fat in moose near their southern distribution has been limited and restricted to mid-winter captures (DelGiudice et al. 2011, Oates 2016, Ruprecht et al. 2016, Newby and DeCesare 2020) constraining evaluations of summer-autumn nutritional resources shown to influence performance in moose (Hjeljord and Histol 1999, Ericsson et al. 2002, Herfindal et al. 2006a, 2006b, McArt et al. 2009, Rolandsen et al. 2017).

By the 1970s, moose numbers were sufficient to support a recreational hunt in northeastern Washington (Base et al. 2006, Harris et al. 2015) that continued as wolves repopulated parts of the region in the last decade (Harris et al. 2021). In 2016, this moose population was estimated at 5169 animals (3510–7034 [95% CI]; Oyster et al. 2018) but was declining annually in 2014–2018 based on dynamics of radio-collared adult females (Harris et al. 2021). Declines in other western states including Wyoming, Montana, and Idaho, mid-western states (Minnesota and North Dakota), and northeastern states (New Hampshire and Vermont) have been associated with multiple, often interrelated factors including disease, predation, parasitism, habitat composition, and climate change (Timmerman and Rodgers 2017). Understanding the relative influence of these factors on performance and survival of adult females and calves is a management challenge and a priority across the southern range of moose where habitat quality is of paramount importance.

Our objective was to use body condition metrics to assess evidence of summer-autumn

nutritional limitations of adult moose in north-eastern Washington and to interpret whether limitations were severe enough to influence reproduction and survival. We considered a moose population to be nutritionally limited, defined herein as nutritional inadequacies sufficient to reduce reproduction, sub-adult growth and development, or survival regardless if these inadequacies directly influence population growth trends, if 1) lactating moose had less than 12% body fat in autumn, 2) pregnancy rate of females \geq 2-years old was less than 95%, or 3) in addition to other indicators of nutritional limitations, starvation was evident in adult female moose that died over winter. These criteria were based on studies of captive and wild elk and mule deer (Cook et al. 2004, Tollefson et al. 2010, Cook et al. 2013) and of Alaskan moose linking nutritional condition to performance (Testa and Adams 1998).

STUDY AREA

Our 1262 km² study area was in northeastern Washington, USA within the North-Central Rocky Mountain Forest terrestrial ecoregion on the eastern side and the Okanagan Dry Forest ecoregion on the western side (Olson et al. 2001) (Fig. 1); elevations ranged from 500 to 2200 m. Climate was characteristic of both the continental and marine types with low relative humidity and moderate temperatures during summer (mean = 16.6 °C in June – August) and cool, foggy weather during winter (mean = -2.7 °C in November – February) (USGS North America Climate; www.sciencebase.gov). Most precipitation occurred in winter and spring as measured in Colville, Washington: mean precipitation = 210 mm in November–February, 135 mm in March–May, 102 mm in June–August, and 57 mm in September–October (<https://www.usclimatedata.com/climate/colville/washington/united-states/uswa0606>). See Harris et al. (2021) for weather information during

the study period and an assessment relative to conditions Monteith et al. (2015) found were correlated with recruitment in a multi-population study.

Land ownership was a matrix of private timber inholdings (21%), private landowners (45%), and public (34% federal and state). The study area was dominated by forests (86%) in subalpine parkland, subalpine fir (*Abies lasiocarpa*), grand fir (*Abies grandis*), western red cedar/western hemlock (*Thuja plicata*/ *Tsuga heterophylla*), Douglas fir (*Pseudotsuga menziesii*), and ponderosa pine (*Pinus ponderosa*) potential vegetation zones (Appendix A; Franklin and Dyrness 1988, Cooper et al. 1991). Other communities included grasslands (subalpine meadows, Idaho fescue [*Festuca idahoensis*] and bluebunch wheatgrass [*Pseudoroegneria spicata*]) and sagebrush (*Artemisia* spp.) and bitterbrush (*Purshia tridentata*) shrublands (Integrated Landscape Assessment Project; <https://inr.oregonstate.edu/ilap>). The most common deciduous shrubs included Rocky Mountain maple (*Acer glabrum*), serviceberry (*Amelanchier alnifolia*), oceanspray (*Holodiscus discolor*), ninebark (*Physocarpus malvaceus*), Scouler’s willow (*Salix scouleriana*), fool’s huckleberry (*Menziesia ferruginea*), huckleberry (*Vaccinium* spp.), and snowberry (*Symphoricarpos* spp.), and the most common evergreen shrub was snowbrush ceanothus (*Ceanothus velutinus*) (Johnson and O’Neil 2001).

Potential moose predators included mountain lions (*Puma concolor*), black bears (*Ursus americanus*), and wolves (*Canis lupus*) that arrived in northeastern Washington by 2008 with 10 packs documented in 2013 (WDFW et al. 2019, Harris et al. 2021). White-tailed deer (*Odocoileus virginianus*) and a few elk (*Cervus canadensis*) and mule deer (*O. hemionus*) also occupied the study area. Moose hunting was permitted in the study area during all years of the study;

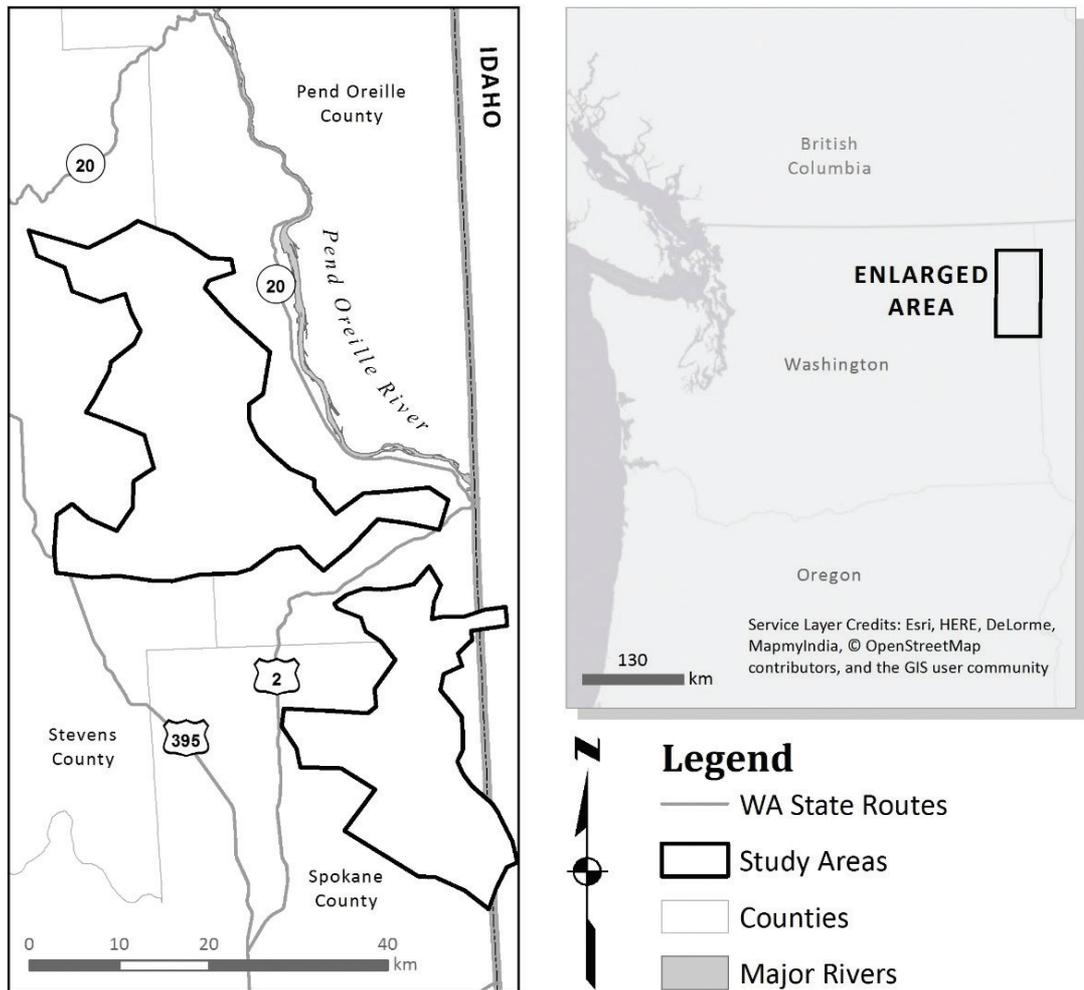


Fig. 1. Study area, defined by 95% kernel density estimates of locations of captured moose (left panel) and in context of their location in northeastern Washington (right panel). Major U.S. highways 2 and 395 are illustrated along with the Pend Oreille River. Adult female moose were captured during early December 2013, 2014, and 2016 in northeastern Washington, USA.

hunter pressure and success varied by Game Management Unit (Harris et al. 2021).

METHODS

Animal capture and handling

We captured adult female moose via aerial darting (Pneudart Inc., Williamsport, Pennsylvania, USA) from a Bell Jet-Ranger helicopter (Northwest Helicopters, Olympia, Washington, USA) on 16–20 December 2013 (n = 28), 2–6 December 2014 (n = 25),

and 1–6 December 2016 (n = 28); capture crews documented accompanying calves when possible. We immobilized animals with Carfentanil (3–4.5 mg) and xylazine (50 mg) in 2013 and 2014, and etorphine (7.5–15 mg) and xylazine (50 mg) in 2016. After sedation, we blindfolded moose and injected 100 mg xylazine IV to deepen anesthesia and improve muscle relaxation, administered long-acting penicillin, flunixin meglumine, and a clostridium vaccine, and

collected a blood sample. After injecting 10 mg of bupivacaine hydrochloride into the mental foramen for pain relief (Mansfield et al. 2006), we extracted an incisiform lower canine to determine age by examination of annuli (Matson's Laboratory, Milltown, Montana, USA). We fitted moose with GPS (Geographic Positioning Systems) collars transmitting a location every 23 h (Vectronic/Globalstar Survey; Vectronic Aerospace GmbH, Berlin, Germany), and subsequently reversed the immobilizing agents with 450 mg naltrexone and 700 mg tolazoline. All captures were under supervision of the Washington Department of Fish and Wildlife (WDFW) veterinarian.

On each animal, one trained observer (R. Cook) measured maximum subcutaneous rump fat thickness (MAXFAT) and longissimus dorsi (hereafter "loin") muscle thickness (to the nearest mm between the 12th and 13th ribs adjacent to the backbone) using an Ibex® Pro ultrasound with a 5.0 MHz, 7.0 cm linear probe (E. I. Medical Imaging, Loveland, Colorado, USA) (Stephenson et al. 1998, Cook et al. 2001a, 2010), and collected a rump body condition score (rumpBCS) using the elk score developed by Cook et al. (2001). We measured chest-girth circumference to the nearest cm when positioning allowed (Cook et al. 2003); otherwise, we measured from the mid-line of the sternum to the backbone and multiplied by 2.

We classified pregnancy status for most moose using a combination of serology, palpation, and ultrasonography. We collected serum samples and quantified pregnancy status using enzyme-linked immunosorbent assay for pregnancy-specific protein B (PSPB), with an optical density reading > 0.21 considered positive for pregnancy (BioTracking LLC, Moscow, Idaho, USA; Haigh et al. 1993, Noyes et al. 1997, Huang et al. 2000). Because PSPB is considered

96% accurate 40 d post-conception in elk (Noyes et al. 1997), an experienced observer also used transrectal ultrasound to visually examine the uterine contents (i.e., fluid and placentomes), a method that detects pregnancy in ruminants at ~15 d post-conception and can detect the fetal heartbeat at 21 d (Pohler et al. 2016). Therefore, we considered moose with non-pregnant PSPB levels but classified as pregnant by ultrasound, and subsequently seen with a calf the following spring, to have conceived in early to mid-November. In addition, we considered moose with no evidence of pregnancy (either method), but observed with calf the following spring, to have conceived not earlier than mid-November (i.e., a few weeks prior to capture). Because peak rut for moose occurs in late September-early October, we classified these moose as having delayed conception.

We documented whether a calf was observed at heel immediately prior to capture, and categorized lactation status by visually examining udder size and any extractable fluid. We grouped females into 3 categories: 1) currently lactating had a swollen udder and either thick milk (signifying a calf had nursed within the past 11 days; Flook 1970, Fleet and Peaker 1978, Noble and Hurley 1999) or dilute, milk-like fluid (suggesting that weaning occurred within days or weeks; unpublished data, R. Cook) was extracted from the udder; 2) non-lactating were without calf and had no evidence of a swollen udder with a small amount or no extractable clear fluid; 3) calf-at-heel females had an accompanying calf at capture with udder characteristics of a non-lactating female.

We relied on mortality signals from collars (9 h without movement) to assess the proximate cause of mortality, typically within 24 h, but up to 3 d later; if a legal harvest, we communicated with the hunter.

We surveyed mortality sites for signs of a struggle and evidence of predators (scat or tracks), performed necropsies, noted tick loads and hair loss, collected tissue samples for histopathological analysis, and collected a femur when possible; see Harris et al. (2021) for additional details on assigning proximate cause of death. We disarticulated whole femur bones from the carcass, removed most of the flesh, wrapped them twice in heavy plastic and stored them frozen for up to 8 months before extracting marrow for analysis. We split the femur on the longitudinal axis, extracted 5.6 to 50.1 g of marrow fat from the entirety of the cavity, and oven-dried samples at 75 °C to constant weight (3–5 d; Neiland 1970). We note that desiccation of marrow soon after death in warmer climates can result in overestimates of fat content; however, Kie (1978) recommended corrections only if collection was >10 d post-death, a period beyond our recovery window. See Harris et al. (2021) for a comprehensive survival analysis.

Statistical Analysis

We used the global equation in Cook et al. (*in press*) to estimate body mass from the chest-girth circumference measurement. When we could not measure circumference due to positioning, we used the average estimated body mass (350 kg) from all other adult moose. To account for the smaller body size of moose in the Northern Rockies, we allometrically scaled MAXFAT estimates to surface area with a large-animal scaling unit [$\text{MAXFAT}/(0.15 \times \text{body mass}^{0.56})$]; the scaled MAXFAT values were used to predict body fat (Cook et al. 2010). For any animal without measurable rump fat, we estimated body fat using the rumpBCS equation from Cook et al. (2001). Although not validated with moose, we believe that using rumpBCS and associated equations validated on North American elk provided biologically relevant

and useful estimates of body fat. For animals with measurable rump fat, we used a 2-sample *t*-test (PROC TTEST; SAS Institute 1988) to compare the estimates of body fat from the scaled MAXFAT equations with those derived from the equations of Stephenson et al. (1998) which integrated body size within the predictive equation for body fat.

We evaluated the effects of age at capture and of lactation status (i.e., lactating, non-lactating, and calf-at-heel) on our 3 metrics of nutritional condition (body fat, body mass, loin muscle thickness) with an analysis of covariance (SAS Institute 1988). If age was insignificant, we removed it from the model and conducted a one-way fixed effects analysis of variance (ANOVA; SAS Institute 1988) with Duncan's multiple range test. We assembled frequency histograms to illustrate differences in distribution of body fat among moose for each lactation status.

We compared means of body fat and loin muscle thickness using one-way, fixed effects ANOVA for moose classified as non-pregnant, pregnant, or pregnant but with delayed conception, and separately for moose classified simply as non-pregnant and pregnant. We used logistic regression to evaluate probability of pregnancy as a function of autumn body fat and loin muscle thickness and age. We did not evaluate body mass for these analyses because of insufficient sample size. We estimated femur marrow fat (%) of collared moose that died, graphed results over time, and interpreted these results relative to reported values for other ungulate species.

Finally, we used Cox proportional hazards models to evaluate adult survival as a function of both autumn fat and loin muscle thickness. For these analyses, we omitted 2 records in which sample animals died within 1 week after handling (no other moose died within 3 weeks of capture). We quantified

exposure as the number of days between capture and the terminal event (death or censored). Because we were interested in assessing potential effects of body condition on non-hunting mortalities, we censored hunter-harvested moose on the date of harvest. Age-at-death was not included in the survival analyses. We used the R package *coxph*, with ties among sampled animals handled using the Efron method. For all analyses of statistical hypotheses, we used a significance level of $\alpha = 0.10$ because sample sizes were small (reporting *P* values for results we consider significant), although we acknowledge this increased the probability of a Type I error.

RESULTS

We captured 69 unique female moose over 78 capture events during early December in 2013, 2014, and 2016 (Table 1). One emaciated female with severe mastitis died shortly after recapture (data from that second capture were excluded from all summaries and analyses). Mean age at first capture was

6.7 years (range = 1–14); by year, mean age at capture was 5.1 (SE = 0.8, $n = 12$), 6.0 (SE = 0.7, $n = 23$), and 8.2 years (SE = 0.7, $n = 24$) in 2013, 2014, and 2016, respectively. We estimated nutritional condition for 61 (58 unique) adult females that were ≥ 2 years old (Table 1); annual measurements were considered independent samples for the 3 animals measured 2 ($n = 1$) or 3 ($n = 2$) years apart. Only 6 moose (8%) were observed with calf and classified as currently lactating, whereas 53 (77%) were classified as non-lactating of which 16 (30%) were observed with calf.

Estimated body mass of 45 moose (29 full chest-girth, 16 half chest-girth) averaged 350 ± 49 kg and did not differ by age or by lactation status although lactating females were $\sim 10\%$ lighter than other females (Table 2). Average loin muscle thickness was 4.7 cm (range = 3.3–5.4; $n = 60$) and did not differ by lactation status or its interaction with age (Table 2), although age was related to loin muscle thickness ($F_{1,52} = 3.61$, $P = 0.063$); for each year an animal aged, loin muscle decreased 0.036 cm (Fig. 2B).

Average body fat was 7.7% (range = 0–12.2%; $n = 61$) across all animals. Lactating moose had less body fat than non-lactating moose ($F_{2,58} = 3.72$, $P = 0.030$); body fat increased from $6.5 \pm 0.5\%$ in lactating females to $8.3 \pm 0.3\%$ in non-lactating females (Table 2, Fig. 3). Eight moose (13%) had no measurable rump fat; rumpBCS was 1.25 for 2 females, 2.0 for 1 female, 2.5 for 1 female, and 2.75 for 3 females. Most moose had body fat levels indicating moderate nutritional limitations. Lactating females ($n = 6$) had a higher proportion of animals with body fat levels indicative of severe nutritional limitation than other female categories; no lactating female had body fat levels $\geq 8\%$ (Fig. 3). No significant difference was found between body fat estimates calculated with the Stephenson et al. (1998)

Table 1. Sample sizes for each measure of nutritional condition, pregnancy status, age, and lactation status for 78 moose capture events during December 2013, 2014, and 2016 in northeastern Washington, USA.

Measurement	<i>n</i> ^a
Pregnancy status	73
Age (cementum analysis)	71
Lactation status	59
Body fat (%)	61
Loin muscle thickness (cm)	60
Estimated body mass (kg)	45
Full chest-girth circumference (cm)	29
Half chest-girth circumference (cm)	16

^a, Three animals handled originally in either 2013 or 2014 were recaptured in 2016 and are included in these sample sizes. One additional recaptured female with severe mastitis was emaciated and died shortly after capture; we excluded this capture event from all analyses and summaries.

Table 2. Mean, standard error (*SE*), and sample size (*n*) of body fat, body mass, and loin muscle thickness across 3 lactation categories of moose (Lactating = had swollen udder and evidence of calf at capture; Calf-At-Heel = no evidence in udder of lactation but was seen with a calf before the capture approach; Non-Lactating = no evidence in udder of lactation and was not seen with a calf before the capture approach) captured during December 2013, 2014, 2016 in northeastern Washington, USA. Means with the same letters following them are not significantly different.

Nutritional condition	Lactating			Calf-at-heel			Non-lactating		
	Mean	<i>SE</i>	<i>n</i>	Mean	<i>SE</i>	<i>n</i>	Mean	<i>SE</i>	<i>n</i>
Body fat (%)	6.4a	0.5	6	7.1a, b	0.5	17	8.3b	0.3	38
Body mass (kg)	314.7a	23.9	3	357.4a	21.6	11	351.4a	7.5	30
Loin muscle thickness (cm)	4.5a	0.2	6	4.7a	0.1	17	4.8a	0.1	37

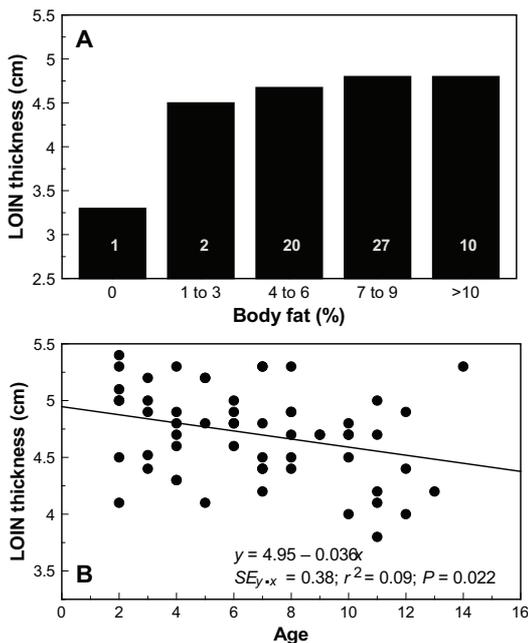


Fig. 2. Average loin muscle thickness (cm) across 5 body fat categories (Graph A) and the relationship between loin muscle thickness (cm) and moose age (years; Graph B). Female moose were captured during early December 2013, 2014, and 2016 in northeastern Washington, USA.

equation and scaled MAXFAT (Cook et al. 2010). Two trends were that estimates diverged as fat increased and body fat calculated with scaled MAXFAT was always higher (Appendix B), but this divergence was minimal at moderate to severe nutritional restriction ($\leq 9\%$ body fat).

Pregnancy rate of moose > 1 year of age ($n = 71$) was 79%; 8 of 56 pregnant moose (14%; 2–11 years old) were classified as delayed conception (Fig. 4A). For 2-year-olds specifically ($n = 8$), 87% were pregnant with 2 classified as delayed conception (Fig. 4A) and 1 of 2 yearlings was pregnant. We found no difference in body fat among animals classified as non-pregnant, pregnant, or pregnant with delayed conception. When combined, pregnant moose were fatter than non-pregnant moose (7.9% versus 6.8% body fat; $F_{1,57} = 4.98, P = 0.090$; Fig. 4A). Loin muscle thickness was smaller in non-pregnant than in all pregnant moose (4.5 cm versus 4.8 cm; $F_{1,57} = 4.98, P = 0.030$) and in pregnant moose with delayed conception (4.5 cm versus 4.9 cm; $F_{2,56} = 3.03, P = 0.056$). We found no effect of age on probability of pregnancy (Fig. 4C, 5A), although sample size was limited. Because age was not significant as an interactive covariate in models predicting pregnancy with either body fat or loin muscle thickness, we dropped age from those models. We found no effect of body fat on probability of pregnancy although the associated coefficient suggested increased probability of pregnancy as fat increased ($\beta = 0.2654$, Fig. 5B). Loin muscle thickness predicted pregnancy both in a stand-alone model

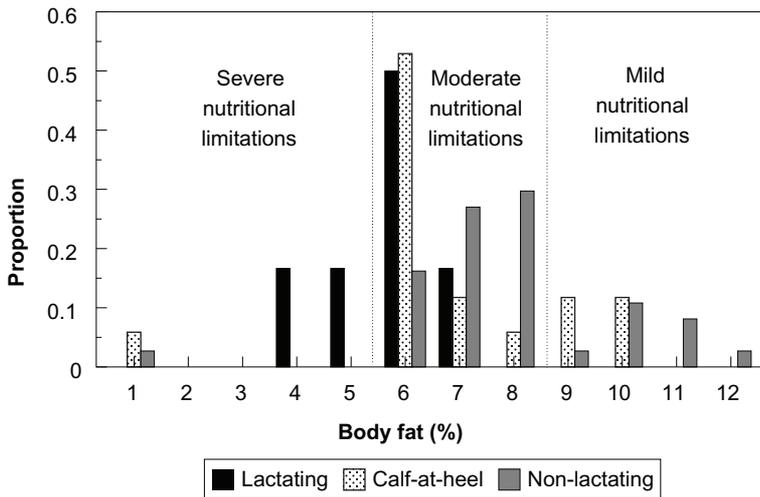


Fig. 3. Distribution of body fat (%) of adult female moose by lactation status: 1) lactating females with milk in udder, 2) non-lactating females lacking any udder characteristics of lactation and no evidence of calf at capture, and 3) calf-at-heel females with udder characteristics of non-lactating females, but were seen with a calf at the time of capture. Vertical dotted lines indicate thresholds of nutritional limitations based on elk (Cook et al. 2004). Adult female moose were captured during early December 2013, 2014, and 2016 in northeastern Washington, USA.

($\beta = 1.9229$, $P = 0.038$; Fig. 5C) and when included as a covariate with body fat (body fat: $\beta = 0.2300$, $P = 0.023$; loin muscle: $\beta = 1.8038$, $P = 0.056$).

Among the 18 moose for which we measured femur marrow fat, the proximate cause of death was predation (39%), harvest (22%), winter ticks (17%), unknown health-related (11%), and accidental (11%). Three moose (16.7%) had marrow fat levels indicative of starvation (< 12% marrow fat); these moose died in April or May (Fig. 6) and death was proximately associated with tick infestation (high tick loads, substantial hair loss, and evidence of emaciation). An additional 7 moose (38.9%) had femur fat between 12 and 80%, levels indicative of nutritional limitations that could predispose animals to predation, disease, or parasites; 4 were predated, 2 died from an accident, and 1 death was unspecified health-related. Six of these 7 moose died between February and

June (the 7th died in November). The remaining 8 (44%) moose had femur marrow fat > 80% and died primarily between July and November (Fig. 6); 3 were predated, 4 were harvested, and 1 was killed by vehicle. Of 10 moose with marrow fat < 80%, 4 successfully raised a calf the previous growing season (i.e., observed calf or lactation status); no evidence was found for the other 6 animals. The average age and range of moose with < 80% (9.4 years, range = 4–14 years) and > 80% marrow fat (8.1 years, range = 5–12 years) were generally similar.

Increased body fat reduced mortality hazard regardless of lactation or calf status at time of capture ($\beta = -0.2799$, SE = 0.1273, $Z = -2.1990$, $P = 0.028$); neither calving status nor its interaction with body fat significantly predicted mortality hazard. Neither loin thickness nor body mass were significant predictors of mortality hazard.

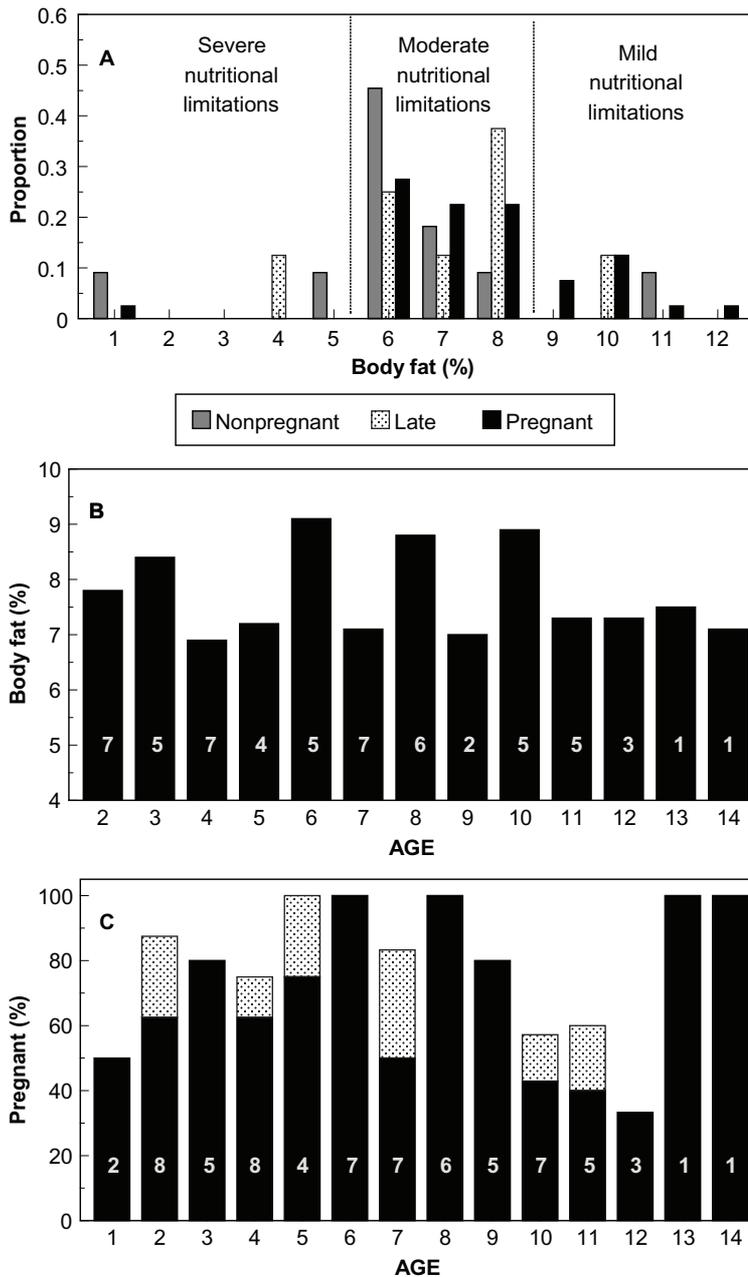


Fig. 4. Distribution of body fat (%) by pregnancy status (non-pregnant, late = pregnant but evidence suggests delayed conception, pregnant) (Graph A) where vertical dotted lines categorize expected severity of nutritional limitations associated with body fat levels based on captive elk trials (Cook et al. 2004); average body fat (%) for each age with sample sizes imbedded in each bar (Graph B); percent pregnant by age with sample sizes imbedded in each bar and moose with delayed conception distinguished by the checkered portion of each bar (Graph C). Female moose were captured during early December 2013, 2014, and 2016 in northeastern Washington, USA.

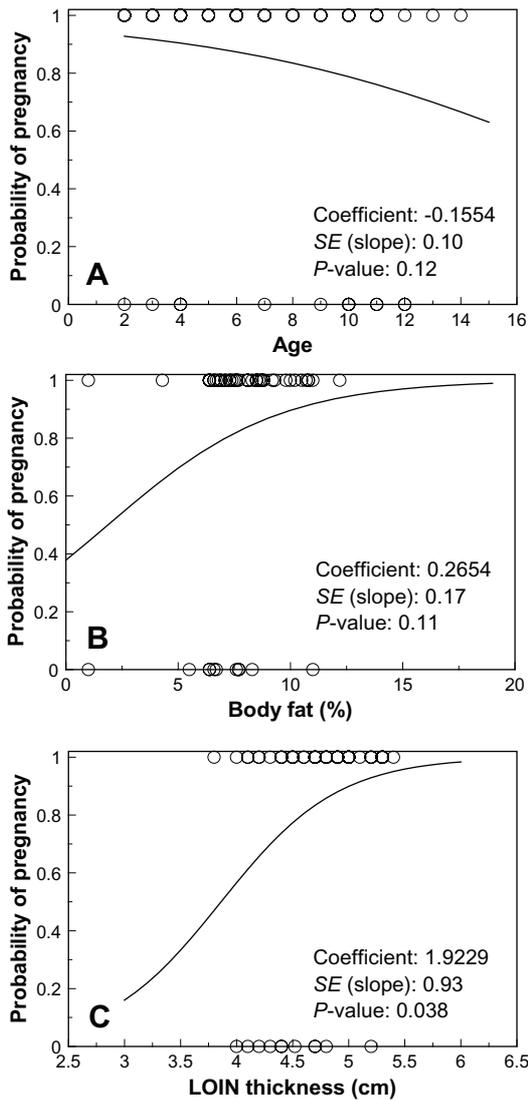


Fig. 5. Probability of pregnancy, as determined by logistic regression, based on (Graph A) age of animal (years;), (Graph B) ingesta-free body fat (%), and (Graph C) loin muscle thickness (cm). Female moose were captured during early December 2013, 2014, and 2016 in northeastern Washington, USA.

DISCUSSION

Population trends of ungulates reflect mortality and productivity, both of which are strongly influenced by habitat and summer-autumn nutrition (Cook et al. 2004, Peek 2007, Dale et al. 2008, Hurley et al.

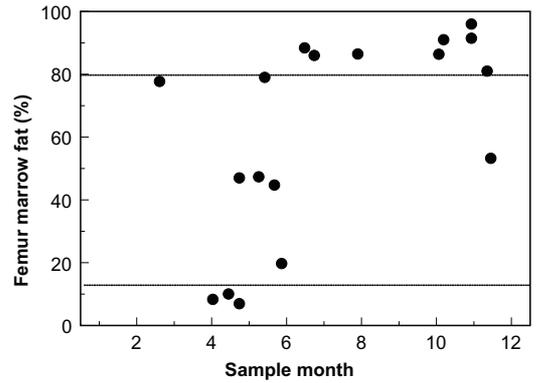


Fig. 6. Femur marrow fat (%) for collared moose that died, distributed by sample month (sample month = month + [month day/31.1]). Femur marrow fat < 12% (lower dotted horizontal line) is indicative of starvation; marrow fat between 12 and 80% is indicative of nutritional limitations that can predispose animals to predation, disease, or parasites; marrow fat > 80% (upper dotted horizontal line) indicates only that animals have > 4.6% body fat as per equations presented for elk (Cook et al. 2001a). Female moose were captured and collared during early December 2013, 2014, and 2016 in northeastern Washington, USA.

2014, Rolandsen et al. 2017). Our hypothesis that inadequate nutrition in summer and autumn limited adult moose performance in the study population was supported by several lines of evidence. In early December, 79% of moose sampled had body fat levels indicative of at least moderate nutritional limitations expected to impact performance (< 9% body fat, Cook et al. 2004; Fig. 3). Non-lactating moose were significantly fatter than lactating moose, but even non-lactating moose failed to attain body fat levels > 12%, a level indicative of little to no nutritional limitations on performance (Cook et al. 2004). Pregnancy rates were depressed (79%), correlated with protein stores, and evidence of delayed conception (i.e., breeding in early to mid- November) was found in 14% of adult moose. We documented a positive relationship between body fat and

subsequent survival, and 56% of femurs collected had marrow fat levels indicative of starvation or nutritional limitations that could predispose moose to predation, disease, or parasites (Ratcliffe 1980, Peterson et al. 1984, Mech and DelGiudice 1985, Depperschmidt et al. 1987, Sand et al. 2012). Thus, we conclude that nutritional limitations primarily operating on the summer-autumn range are of a magnitude to affect moose populations in our study area.

Our inferences depend partly on the applicability of nutritional condition indices developed in part for other ungulates, particularly elk. For example, we used a rump BCS that is unvalidated for moose. However, a version of this score showed strong relationships with body fat in 3 ungulate species (Cook et al. 2001a, 2007, *in press*) suggesting use of the elk-based BCS in combination with ultrasound measures of rump fat thickness was a biologically reasonable approach to estimate body fat in these moose. Alternatively, we could have presented rump fat data without estimating body fat (e.g., Ruprecht et al. 2016, Newby and DeCesare 2020). However, a rump fat depth of zero indicates that subcutaneous rump fat has been depleted, and thus that the animal falls outside the range of condition for which this nutritional condition index can be used (Cook et al. 2001a, 2007, 2010). Body fat can vary from 0 to 5.7% in moose with no rump fat, a range in values equivalent to rump fat measurements of 0–2.75 cm (Appendix C); hence, bias in the data would increase with an increasing proportion of “zero” animals. The proportion of moose in our data (13% of our sample) and those from other regions with no measurable rump fat demonstrate the need for additional validated indices of nutritional condition that can predict body fat in live moose with high levels of accuracy across the entire range found in wild populations.

Thresholds created from captive elk studies (Cook et al. 2004) indicate that autumn body fat levels of 6–9% in lactating adults reflect populations experiencing moderate nutritional limitations resulting in depressed pregnancy rate, delayed conception, slower juvenile growth, and increased probability of winter mortality. At body fat levels < 6%, these impacts to performance would increase in severity. Based on these criteria, our estimates of body fat indicate that most female moose in our sample were experiencing severe or moderate nutritional limitations regardless of whether they were lactating (33% severe, 67% moderate), not lactating but had a calf (6% severe, 82% moderate), or had no evidence of lactation or a calf (3% severe, 73% moderate). Only 1 moose had December body fat > 12% (a non-lactating, 6-year-old pregnant animal), a level indicative of almost no nutritional limitations if the animal had raised a calf.

Adult moose in this population, particularly those that had successfully raised a calf, entered winter in a susceptible state (i.e., to predation, winter weather, parasites, or disease). In addition to low pregnancy rates, ungulates in poor body condition or negative energy balance may delay ovulation (Cook et al. 2001b, 2013, Johnson et al. 2019, this study) which can lead to delayed parturition dates thereby increasing the probability of neonatal mortality due to predation or other causes (Keech et al. 2000, Testa 2002, Johnson et al. 2019); Testa et al. (2000) found a 6.3% increase in neonatal mortality with each day’s delay of parturition in moose. Body fat of our moose was positively related to subsequent survival, and of 8 moose (ages 4–12 years old) with autumn condition data that died within 6 months of capture, 63% entered winter with either < 7% body fat or loin thickness \leq 4.4 cm. Marrow fat levels indicative of starvation in 3 of 18 femurs further confirm

these findings. However, despite entering winter with low fat reserves, femur marrow fat patterns across the annual cycle indicate the peak of mortality from starvation in our sample did not occur until April, suggesting moose were employing strong compensatory mechanisms to survive most of winter. For example, as plants senesce and available energy declines in autumn, northern ungulates reduce organ size as a compensatory strategy. Because organs account for 70% of resting energy use but comprise only about 10% of body mass, relatively small reductions in body mass due to reductions in organ size result in relatively large declines in metabolic energy requirements for winter maintenance (Ramsey and Hagopian 2006). May and June femur marrow fat suggested that moose were recovering at this time, but many did not exceed 5% body fat until mid-to late June.

Body fat is a critical reserve for temperate ungulates because it is a more concentrated and efficient source of energy than protein (Robbins 1993) and, unlike protein reserves, nearly all fat reserves can be utilized (Cahill 1970, Watkins et al. 1992). However, understanding how both fat and protein influence productivity and survival may be useful (Torbit et al. 1985, Hilderbrand et al. 1999, Parker et al. 2005), particularly at times of the year when body fat levels are low. Loin muscle thickness has been related non-linearly to body fat in elk (i.e., declining slowly at high levels of body fat and more rapidly at low levels of body fat; Cook 2000), leading researchers to use this measurement to identify survival thresholds (i.e., relative to probability of starvation). We found a similar relation between loin muscle thickness and body fat in sampled moose (Fig. 2A) and that loin muscle thickness was correlated to probability of pregnancy. Non-pregnant moose had smaller loin muscles (Fig. 5C) suggesting moose in our

study area were utilizing protein reserves at a level that affected performance even before winter.

Our data provide justification for additional research into the adequacy of summer ranges, but we also urge caution when interpreting nutritional condition data without concurrent information on other factors that influence energy and protein reserves in ungulates. Nutritional condition in one season may influence nutritional condition in subsequent seasons, a “carry-over” effect documented in elk (Cook et al. 2013), mule deer (Monteith et al. 2013, 2014), moose (White et al. 2014), and caribou (Dale et al. 2008). Thus, nutritional condition in late winter or spring may be more closely related to levels the previous autumn (and reproductive status) than to winter weather or nutritional resources of the winter ranges. In addition, energy costs of lactation are 2–3 × greater than for maintenance metabolism (Oftedal 1985, Robbins 1993, Cook 2002, National Research Council 2007), thus lactating ungulates are usually thinner than their non-lactating counterparts (Testa and Adams 1998, Keech et al. 2000, Crouse 2003, Cook et al. 2013, White et al. 2014) in nutritionally inadequate environments. In contrast, non-lactating females are a heterogeneous mix of individuals that are not pregnant (having the lowest requirements during summer and thus highest nutritional condition), those that lose a calf early (having the second lowest requirements during summer; often in high nutritional condition), and those that lose a calf late in the growing season (nutritional requirements and thus nutritional condition often equivalent to a lactating female). As such, inferences of the nutritional value of habitats based on nutritional condition of non-lactating females can be ambiguous and misleading (Cook et al. 2013). These patterns emerged in our sample; moose with no evidence of lactation

or a calf were not only fatter on average but had greater variation: their body fat range was 11.2 % (1.0–12.2%), whereas the range of body fat for thinner lactating females was only 3.4% (4.3–7.7%). Because moose are relatively solitary, observations of calf-pregnance are routinely used to indicate reproductive status of females although a variety of issues, including sightability bias, could influence the reliability of those observations. Although we expected a wide range of body fat in non-lactating moose, we also found high variation in animals not lactating but with a calf (1.0–10.2% body fat), suggesting certain moose may have been classified incorrectly. For example, one moose was seen with 2 juveniles and yet she had one of the highest estimates of body fat (18 mm MAXFAT = 10% body fat) suggesting the observed offspring may have been yearlings (Testa 2004). This uncertainty in determining reproductive history, even in early December, increases as winter progresses, complicating interpretation of nutritional condition data (see Bergman et al. 2020).

Measuring nutritional condition of moose can provide insights into seasonal and geographical patterns of nutritional limitations and the severity of these limitations but cannot identify the ecological states and processes that explain why populations may be nutritionally stressed (Shipley et al. 2020). Although moose did expand into our study area and ultimately occupy it at moderately high density by the early 2010s, recent studies of nutritional condition and forage resources from other ungulate species have indicated that nutritional limitations severe enough to substantially reduce performance in ungulates prevail across the northwestern United States.

In the Inland Northwest, lactating elk had low levels of autumn body fat similar to our moose (e.g., ~5–7% body fat on average),

with some populations displaying depressed pregnancy rates and delayed conception (Cook et al. 2013), and at least 2 showing evidence of adult and juvenile starvation mortality in winter (Cook et al. 2013, Johnson et al. 2019). Horne et al. (2019) reported summer nutritional influences on juvenile elk survival across much of Idaho, and Proffitt et al. (2016) reported significant influences of inadequate summer nutrition on elk populations in western Montana. Several studies that evaluated forage resources using tame ungulate foraging studies in the region found that dietary quality, particularly digestible energy content of ingested forage and their nutrient intake rates, were generally inadequate to fully support requirements of lactating females for deer and elk (Cook et al. 2014, 2016, 2018, Hull et al. 2020, Ulappa et al. 2020). Additional studies reported levels of forage quality and quantity in summer that were likely to negatively impact performance, including in western Montana (Proffitt et al. 2016), North Idaho (Monzingo 2020), and southwestern Washington (Geary et al. 2017). Inadequate nutrition during the growing season impacted population growth in mule deer (Hurley et al. 2014) and moose (Schrempp et al. 2019) in Idaho and mule deer in central Oregon (Peek et al. 2002). We found no data on body fat in moose during autumn in jurisdictions along the southern extent of their range in North America to compare with our study. But, our body fat estimates in early December (ave. = 7.7%) were lower than estimates from other regions obtained later in winter. For example, body fat averaged ~10–11% in February-March depending on winter severity in Minnesota (DelGiudice et al. 2011), ~8% in mid-February for females with calves and ~9.3% for those without in northwestern Ontario (Crouse 2003), and ranged from ~1 to 10.5% for individual moose in mid-February in Wyoming (Oates 2016).

Clarifying the pathways through which forage quality and quantity influence seasonal nutrition, nutritional condition, and productivity may be essential for developing complete and holistic landscape assessments and resource planning on behalf of moose (Rowland et al. 2018). In the northwestern United States, for example, forage quality, particularly digestible energy content, of ungulate diets and their forage intake rates are significantly higher in early seral communities (Geary et al. 2017, Barker et al. 2019) than in mid- and late seral forest communities (Cook et al. 2014, 2016, 2018, Hull et al. 2020, Ulappa et al. 2020). In addition, digestible energy content of ungulate diets tends to be too low to satisfy requirements of lactating females and their calves, with a nutritional “bottleneck” occurring in late summer, an effect that is significantly exacerbated in vegetation communities with low forage biomass levels (Cook et al. 2014, 2016, Ulappa et al. 2020) and in populations existing at high densities.

In northern Idaho and the Blue Mountains Ecoregion in northeastern Oregon, estimated levels of biomass considered acceptable for large ungulates varied widely during summer and early autumn depending on forest type and canopy cover. In most forest zones, biomass levels of perennial forbs plus deciduous shrubs in mid- and advanced seral stages were generally < 200 kg/ha (Cook et al. 2014, Monzingo 2020), a level too low to support instantaneous intake rates that can satisfy daily dry matter, digestible energy, and digestible protein requirements in elk (Wickstrom et al. 1984, Cook et al. 2014, 2016). In early seral communities with < 40% overstory canopy cover, biomass levels of perennial forbs plus deciduous shrubs in both ecoregions were 2–5 × greater than in mid- and late-seral stages, and more likely to satisfy nutritional requirements of large ungulates. In our study area, 75% of all forested stands had canopy

closure > 40% (Appendix A). Among the more productive, higher elevation, and more mesic forests, 80% had canopy closure > 40% (Appendix A).

Combined, these studies suggest that moose in our study area existed in an environment that provided marginal to inadequate forage resources during summer. We suspect that, in part, this is due to long-term fire suppression and reduced logging on federal lands that have and continue to reduce early seral communities (Hessburg and Agee 2003, Haugo and Welch 2013, Schrempp et al. 2019), and thus forage resources for moose in this region. Moose populations have increased after wildfires and other stand-replacing disturbances over vast landscapes, attributable at least in part to higher pregnancy and twinning (Spencer and Chatelain 1953, Hansen et al. 1973, Irwin 1974). Although moose in northeastern Washington appear to be in a post-irruptive state (Harris et al. 2021), broad-scale habitat manipulations that promote early seral communities, particularly in productive, moist forests, may be required to increase nutritional condition and performance of this population if that is a management goal.

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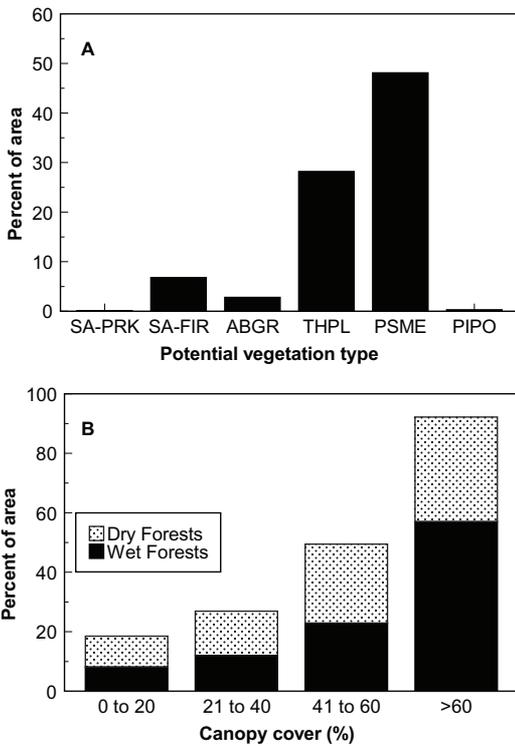
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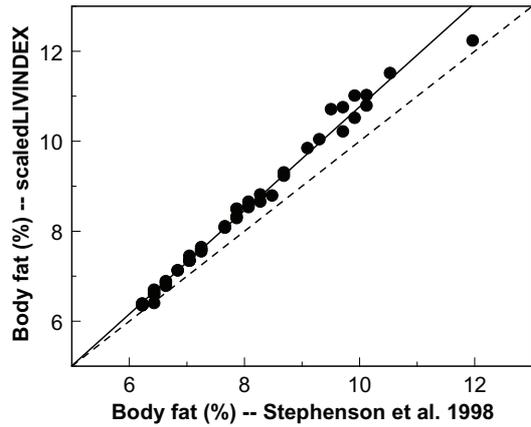
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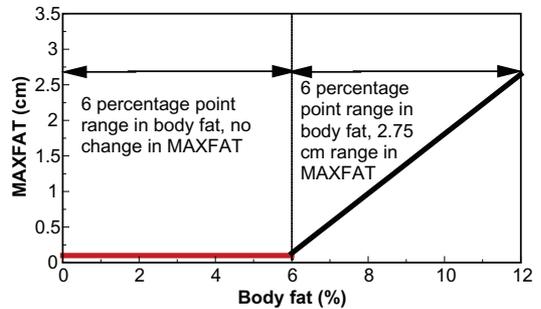
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Appendix A. Percent of study area, defined by 95% kernel density estimates of locations of captured moose, in each of 6 forested types (SA-PRK = subalpine fir-parkland, SA-FIR = subalpine fir, ABGR = Grand fir, THPL = western red cedar, PSME = Douglas fir, PIPO = Ponderosa pine; Graph A) and by canopy cover classes grouped as wet forests (SA-PRK + SA-FIR + ABGR + THPL) or dry forests (PSME + PIPO) (Graph B). Adult female moose were captured during early December 2013, 2014, and 2016 in northeastern Washington, USA.



Appendix B. Difference in predicted body fat (%) for female moose captured in northeastern WA, USA during early December (2013, 2014, and 2016) between the original Alaskan moose equation which integrated body size in the development of the prediction equation (Stephenson et al. 1998), and one where MAXFAT is scaled for surface area prior to predicting body fat (Cook et al. 2010); the dashed line is a 1:1 reference line.



Appendix C. Using data from this study, we demonstrate that moose with no measurable rump fat can range from 0 to 5.7% body fat, a range in body fat no different from rump fat measurements ranging from > 0 to 2.75cm. Representing this range with the single value of zero introduces a bias into the data set; the greater the proportion of animals with no measurable rump fat, the more biased the nutritional condition data.