Reproduction in moose at their southern range limit

Joel S. Ruprecht,* Kent R. Hersey, Konrad Hafen, Kevin L. Monteith, Nicholas J. DeCesare,
Matthew J. Kauffman, and Daniel R. MacNulty

Department of Wildland Resources and the Ecology Center, Utah State University, 5230 Old Main Hill, Logan, UT 84322, USA (JSR, DRM)
Utah Division of Wildlife Resources, Box 146301, Salt Lake City, UT 84114, USA (KRH)
Department of Watershed Sciences, Utah State University, 5210 Old Main Hill, Logan, UT 84322, USA (KH)
Haub School of Environment and Natural Resources, Wyoming Cooperative Fish and Wildlife Research Unit, Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82072, USA (KLM)
Montana Fish, Wildlife and Parks, 3201 Spurgin Road, Missoula, MT 59804, USA (NJD)
United States Geological Survey, Wyoming Cooperative Fish and Wildlife Research Unit, Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071, USA (MJK)

* Correspondent: ruprechtjoel@gmail.com

Reproduction is a critical fitness component in large herbivores. Biogeographic models predict that populations occurring at the edges of the range may have compromised reproductive rates because of inferior habitat at range peripheries. When reproductive rates are chronically low, ungulate populations may lack the resiliency to rebound quickly after periods of environmental stress, and this effect may be greatest for heat-sensitive organisms at their southern range limit. To assess the demographic vulnerability of moose (*Alces alces*), we studied relationships between reproductive rates, maternal age, and rump fat in the southernmost naturally occurring moose population in North America. For prime-aged moose in our study, pregnancy rates were high (92%), but moose aged < 3 or > 9 years had low pregnancy rates (32% and 38%, respectively). The relationship between rump fat and pregnancy was nonlinear such that a threshold of at least 2 mm of rump fat yielded a high probability of being pregnant midwinter. In contrast, among pregnant moose, the probability of both producing a calf and recruiting it until spring increased linearly with rump fat. We also conducted a meta-analysis of pregnancy and twinning rates for adult (≥ 2 years) moose across a latitudinal gradient to compare reproductive rates from our study to other populations in North America. Moose living at southern latitudes tended to have lower reproductive rates than those living in the core of moose range, implying that southern moose populations may be demographically more vulnerable than northern moose populations.

Key words: *Alces*, environmental gradient, latitude, range edge, rump fat, Shiras, Utah

Understanding vulnerability of wildlife populations to environmental change is an urgent and worldwide conservation concern (Dawson et al. 2011). Biogeographic models predict that populations inhabiting the edge of a species range are demographically more vulnerable to environmental change than populations at the range core because of inferior habitat conditions at the edge (Caughley et al. 1988; Lawton 1993; Channell and Lomolino 2000; Sagarin and Gaines 2002; Vucetich and Waite 2003). Reports of depressed reproduction in edge populations of some plants (García et al. 2000; Jump and Woodward 2003; Angert 2006) and animals (Caughley et al. 1988; Sanz 1997) support this prediction. Little is known, however, about whether this biogeographic pattern applies to cold-adapted ungulate species, especially those with populations inhabiting low-latitude edges of the geographic range of the species. Low reproduction in these edge populations may limit the extent to which they can adapt to persistent climate warming and may presage a poleward range contraction (Hampe and Petit 2005).

Moose are a cold-adapted ungulate (Renecker and Hudson 1986) with a circumpolar distribution that reaches its lowest latitude in the southern Rocky Mountains of the United States (Telfer 1984). Range loss linked to low reproduction has been reported in moose inhabiting other portions of their southern range limit in North America, which includes southern Canada

and the northcentral and northeastern contiguous United States (Murray et al. 2006; Lenarz et al. 2010). Conversely, some southern moose populations in western Canada and the northeastern United States have expanded their ranges (Foster et al. 2002; Darimont et al. 2005; Musante et al. 2010), which suggests that reproductive success is independent of latitude and that the vulnerability of a population to environmental change is not easily generalized as a function of proximity to the range edge. Notably, we have little information about the reproduction of Shiras moose (*Alces alces shirasi*), which is the Rocky Mountain subspecies that inhabits the southernmost reaches of the circumpolar distribution of the species (Bubenik 2007).

Early studies of Shiras moose presented anecdotal evidence that reproductive rates were lower in southern-edge moose populations than those in the core of moose range (Peek 1962; Houston 1968; Peek 1974). Researchers speculated that comparatively low reproductive output was either controlled by a genetic influence (Houston 1968) or arose from marginal habitat quality (Peek 1974). Despite the suggestion that moose reproductive rates vary along a north–south gradient throughout North America, the hypothesis has never been tested. An important consequence of this knowledge gap is that when low reproductive rates are documented in southern moose populations, it is unclear whether the occurrence is an anomaly or instead part of a broader pattern.

Shiras moose have experienced declines in recruitment of young in many herds in Utah, Wyoming, and Colorado in recent decades (Monteith et al. 2015). Monteith et al. (2015) observed lower recruitment after years that were warm, dry, or exhibited rapid rates of spring greenup. Such climatic conditions likely reduced forage quantity and quality, which acted to suppress maternal nutritional condition, ultimately at the expense of recruiting young (Monteith et al. 2015). Future climatic conditions in this region are expected to become warmer (Gutzler and Robbins 2011) and drier (Cook et al. 2015), which could continue to exacerbate nutritional intake for moose. Therefore, understanding the extent to which various reproductive rates are influenced by maternal body condition will help to elucidate how productivity of moose populations may change in response to a declining nutritional plane.

We had 2 objectives in the study. The 1st objective was to clarify the extent to which pregnancy, parturition, and recruitment rates are influenced by nutritional condition in Shiras moose. Rump fat is a strong predictor of nutritional condition (Stephenson et al. 1998) and subsequent reproductive success in Alaskan moose (*Alces alces gigas*—Testa and Adams 1998; Keech et al. 2000), but this pattern has not been described in Shiras moose, or more generally, moose at their southern range limit. The 2nd objective was to test the hypothesis that reproductive rates are lower for moose populations near the southern range limit by using data obtained from a meta-analysis to assess whether fecundity rates show latitudinal trends. Results from this study will contribute to a better understanding of the resiliency of this cold-adapted species to future environmental stress at its southern range limit.

MATERIALS AND METHODS

Study area.—We studied moose in 2 mountain ranges in northern Utah: the Wasatch Mountains (40.4°N, −111.3°W) and the North Slope of the Uinta Mountains (40.9°N, −110.5°W). Study areas were bounded by the North Slope and Wasatch Mountains management units and together comprised > 5,000 km^2. Moose in our study represented the southernmost naturally occurring moose populations in North America. Although moose currently occupy more southern latitudes in Colorado, those herds were introduced into the state by means of transplants from Utah (Olterman et al. 1994).

The North Slope Unit was characterized by high-elevation (2,500–3,500 m) montane forest with much of the suitable habitat contained within the High Uintas Wilderness. The forested areas were dominated by lodgepole pine (*Pinus contorta*) interspersed with quaking aspen (*Populus tremuloides*), and subalpine fir (*Abies lasiocarpa*) occurred at higher elevations. Forested areas were punctuated by several wide drainages that created expansive riparian willow (*Salix* spp.) communities. Lakes and marshes were common in the high-elevation areas. In contrast, the Wasatch Unit was composed of a more heterogeneous landscape and included mid- to high-elevation (2,000–3,000 m) zones, much of which was atypical moose habitat. Lower elevation areas were characterized by sagebrush steppe (*Artemisia* spp.) communities with Gambel oak (*Quercus gambelii*) and mountain mahogany (*Cercocarpus* spp.) occurring in high abundance. At higher elevations, Douglas fir (*Pseudotsuga menziesii*), lodgepole pine, and aspen became dominant. Willow communities were present but occurred in low densities throughout the Wasatch Mountains. In the eastern portion of the unit, juniper (*Juniperus* spp.) and pinyon pines (*Pinus edulis*) were common. Although habitat differed between the 2 study management units, sample size limitations required us to pool data between units.

Data obtained from the National Oceanic and Atmospheric Administration/National Climatic Data Center (NOAA/NCDC) nClimDiv dataset (Vose et al. 2014) indicated historic seasonal temperatures for the study area (Utah Northern Mountains climate division) averaged 8.1°C, 15.1°C, −0.4°C, and −5.2°C for spring, summer, fall, and winter, respectively. Historic total seasonal precipitation averaged 15.1, 10.8, 16.7, and 11.3 cm during the same seasons. Climatic conditions in the year before our study were generally warmer and drier than the historic means: temperatures averaged 9.9°C, 16.5°C, 0.8°C, and −6.8°C for spring, summer, fall 2012, and winter 2013, respectively, whereas total seasonal precipitation was 6.4, 9.3, 16.9, and 6.0 cm during the same seasons.

The North Slope was the 1st area in Utah to be colonized by moose, which occurred through natural dispersal from the Greater Yellowstone Ecosystem in the early 1900s (Wolfe et al. 2010). Moose later dispersed to other areas of the state including the Wasatch Mountains, and some herds were augmented by management translocations conducted by the Utah Division of Wildlife Resources. Although moose were introduced to parts of the state farther south than our study area, none of those herds have established viable populations; thus, the likely range limit

for moose in Utah occurs at about 40°N (Wolfe et al. 2010). Moose numbers in northern Utah increased steadily throughout the latter one-half of the 20th century until reaching an apparent ceiling in the early 1990s (Ruprecht 2016). Consistent with an irruptive paradigm of population growth, population declines occurred during the next 2 decades, thought to be the result of density dependent resource limitation (Ruprecht 2016). The statewide population is currently believed to be stable, although population density is substantially lower than it was during peak abundance in the 1990s (Ruprecht 2016).

Moose in the study area occurred sympatrically with elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), and low numbers of white tailed deer (*Odocoileus virginianus*). The decline in moose generally coincided with an increase in elk numbers (M. L. Wolfe, Utah State University, pers. comm.). Domestic sheep (*Ovis aries*) and cattle (*Bos taurus*) were present in much of the occupied moose habitat during summer. Predation is not suspected to be a limiting factor for moose in this area, although cougars (*Puma concolor*) occasionally kill adult moose in the state (Wolfe et al. 2010). Black bears (*Ursus americanus*) occur at low to moderate densities within occupied moose range within the state, and presumably some juvenile moose are lost to bears. Gray wolves (*Canis lupus*) are occasionally documented within Utah, although at present no established packs have been confirmed within the state.

Capture and handling.—We captured 120 female moose in January and February 2013 as part of a multiyear study of moose demography in Utah. Each moose was fitted with a very-high-frequency radiocollar with mortality-motion sensors (Sirtrack Ltd., Havelock North, New Zealand). We determined the pregnancy status of all captured moose using the pregnancy-specific protein B (PSPB) assay of serum obtained from blood samples collected from venipuncture (BioTracking, Moscow, Idaho—Sasser et al. 1986; Haigh et al. 1993). Of these 120 moose, we extracted the incisiform canine of 50 individuals for determination of age via cementum annuli (Matson's Laboratory, Milltown, Montana—Boertje et al. 2015). In addition, we measured maximum rump fat depth to the nearest millimeter for these 50 moose using a portable ultrasound device (Stephenson et al. 1998) and measured chest girth and body length to the nearest centimeter. Body length was measured from the planum nasale to the tip of the tail following the dorsal crest, and chest girth was measured as the circumference of the animal located immediately behind the foreleg (Hundertmark and Schwartz 1998). Ages of 13 additional moose were obtained from collared moose that died between the time of capture and data analysis, which increased the sample of known-aged moose to 63. Moose were captured and handled following protocols in accordance with applicable guidelines from the American Society of Mammalogists (Sikes et al. 2011) and approved by the Utah State University Institutional Animal Care and Use Committee (Protocol # IACUC-2365).

To determine whether each moose subsequently produced 1 or more calves, we conducted calf searches from the ground by locating each moose with telemetry during May and June. We classified a moose as nonparturient if it was not observed with a calf on multiple occasions in which observers had unobstructed views of the moose. Although we attempted to survey each moose during the peak calving period, because of logistical constraints, some moose may have produced a calf that died before being surveyed. Therefore, calving rates should be considered minimum estimates. We surveyed again the following March to estimate recruitment status for each animal known to have produced a calf. We conducted March recruitment surveys by locating radiocollared adult female moose from a helicopter and observing if calves were still present. Sample sizes differed among analyses based on available data.

Statistical analyses.—To determine whether mean maximum rump fat depths differed between moose with and without a calf at the time of capture, we used a nonparametric Wilcoxon rank sum test (Wilcoxon 1945) because rump fat data did not follow a normal distribution. We used generalized linear models (GLMs) to assess the relationship between rump fat depth (mm) in winter and pregnancy status at the time of capture, as well as subsequent parturition and calf recruitment. For the latter 2 analyses, we considered only moose that tested positive for pregnancy at the time of capture. Because maternal age can influence reproduction in moose (Ericsson et al. 2001), we evaluated whether adult female age explained variation in reproductive rates. Finally, because size of the animal can confound interpretation of rump fat, we converted the raw rump fat measurements to a scaled rump fat index using the equation developed by Cook et al. (2010). The scaled rump fat index accounts for differences in body size by using an allometric scaling equation where scaled rump fat = rump fat/0.15 × body mass$^{0.56}$ (Cook et al. 2010). We estimated the body mass of each moose using the predictive equation developed by Hundertmark and Schwartz (1998) which predicts body mass from total body length. The scaled rump fat index not only accounts for differences in body sizes among individuals within our sample but also presents our data in a format that should allow valid comparisons to larger subspecies of moose. We used the scaled rump fat conversions for all models relating body fat to reproductive rates.

We used piecewise linear splines to test for nonlinear effects of rump fat on the probabilities of each metric of reproduction. Specifically, we tested for a threshold level of rump fat beyond which the probability of reproduction abruptly changed. To determine the presence and position of fat-specific thresholds, we evaluated a set of competing GLMs. The set included models with a single knot placed at each integer from 1 to 8 mm, a model with no knot representing the hypothesis of no thresholds in reproductive rates, and an intercept-only model representing the null hypothesis that rump fat had no effect on reproduction. A knot was the join point between 2 linear splines. We selected knots a priori based on the prediction that reproductive rates should asymptote at high fat levels. Our placement of knots was consistent with guidelines for the efficient use of knots (Wold 1974; Eubanks 1984; Seber and Wild 2003). By definition, knots selected a priori are fixed (i.e., not random) variables and are therefore not estimated as parameters in models. We created variables containing a linear spline for rump fat depth

with the MKSPLINE command in STATA 13.1 (StataCorp LP 2013). Variables were constructed so that estimated coefficients measure slopes of the segments before and after a given knot. We compared GLMs using Akaike's Information Criterion adjusted for small sample size (AIC$_c$—Burnham and Anderson 2002). In addition, we assessed whether including a variable for the presence of a calf at heel at the time of capture improved model fit by using likelihood ratio tests and associated χ^2 values among nested models.

To compare reproductive rates of moose in Utah with those of moose at higher latitudes in North America and to search for evidence of a possible range-limit effect in moose fecundity, we conducted a meta-analysis on pregnancy and twinning rates in moose. We constrained our literature review to studies that: 1) only considered animals ≥ 2 years old (Boer 1992), 2) were conducted on free-ranging moose in North America, and 3) had a specific geographic location in which a latitude could be derived (i.e., not region-wide). Once we found moose reproductive rates that met these criteria, we obtained the latitude of the study area from the text or derived it using the closest geographic feature to the center of the study area. Because moose have a circumpolar distribution, we considered high latitudes to be the range core and southern latitudes to represent the periphery or range limit. We included the method used for pregnancy or twinning determination as a categorical variable to account for potential variation arising due to the diagnostic method used. Following Schwartz (2007), methods of pregnancy determination included fetal counts that most often were conducted by examining reproductive tracts of dead moose, PSPB from serum assays, progesterone from serum assays, fecal progesterone, or rectal palpation. Methods of twinning determination were either fetal counts or direct observations of numbers of juveniles per adult female conducted during the calving period. Twinning rates were defined as the percentage of parturient females that had 2 calves. For studies that presented both pregnancy and twinning rates over the same time period, we calculated a measure of fecundity by multiplying pregnancy rate by litter size to estimate the expected number of young produced per adult female in each population. Because fecundity rates were composed of both pregnancy and twinning data, methods of fecundity determination were constructed as categorical variables with different combinations of twinning and pregnancy diagnostics, respectively. We tested the hypothesis that moose reproductive rates declined with decreasing latitude (i.e., as the population approached the southern range limit) using generalized linear mixed models with a binomial distribution for pregnancy and twinning rate and a normal distribution for fecundity. Additionally, we included a random intercept identifying the population. For studies that presented annual data on reproductive rates for more than 1 year, we retained each annual estimate in the analysis; the population-specific random intercept controlled for lack of independence between reproductive rates within the same population across multiple years. All analyses were performed in STATA 13.1 (StataCorp LP 2013).

RESULTS

Rump fat.—Rump fat depth of female moose (> 1 year old) in our study ranged from 0 to 21 mm (Fig. 1) with a mean ± *SE* of 4.5 ± 0.7 mm (*n* = 50). When converted to scaled rump fat to control for body size, scaled rump fat measurements averaged 5.0 ± 0.7 mm. Sixteen of 50 moose (32%) had a rump fat depth of 0 mm (Fig. 1). The presence of a calf at heel at the time of capture did not influence rump fat (*z* = −0.19, *P* = 0.85, *n* = 50); moose with calves at heel had a mean rump fat depth of 4.2 ± 0.8 mm (*n* = 18), and rump fat for those without calves measured 4.8 ± 0.9 mm (*n* = 32). When restricting this analysis to only prime-aged individuals (3.5–8.5 years old), moose with calves (3.7 ± 0.8 mm, *n* = 14) had less rump fat than those without calves (7.4 ± 1.2 mm, *n* = 18; *z* = 2.12, *P* = 0.033).

Pregnancy.—We acquired age-specific pregnancy rates for 63 moose > 1 year old (Fig. 2). Following the age classes defined by Boer (1992), yearling pregnancy rate was 0% (*n* = 5), and adult pregnancy rate was 74.1% ± 5.8% (*n* = 58). Nevertheless, classifying pregnancy rates into 3 age groups better highlighted the effects of age on pregnancy: moose 1.5–2.5 years old had low pregnancy rates (31.6% ± 10.9%, *n* = 18), those between
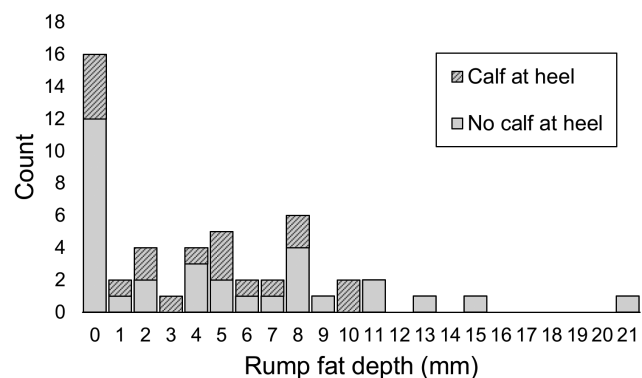

Fig. 1.—Frequencies of rump fat depths (unscaled) for 50 adult female moose (*Alces alces*) measured in northern Utah, January–February 2013. Shading indicates whether each moose had a calf at heel at the time of capture.
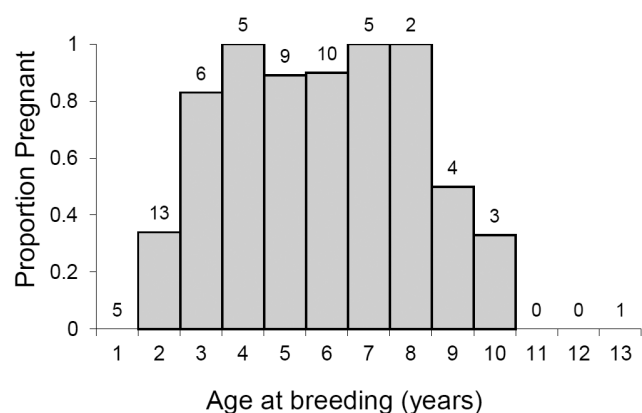

Fig. 2.—The proportion of adult female moose (*Alces alces*) pregnant by age (*n* = 63) as determined by the pregnancy-specific protein B (PSPB) in January and February 2013. Sample sizes for each age are given above each column.

3.5 and 8.5 years had high rates of pregnancy (91.9% ± 4.5%, $n = 37$), and individuals greater than 8.5 years old exhibited low pregnancy rates (37.5% ± 18.3%, $n = 8$). Hereafter, we used these breakpoints to classify each animal into 1 of 3 age classes: young (1.5–2.5 years old), prime (3.5–8.5 years old), and senescent (> 8.5 years old).

Calf production.—Of the females determined to be pregnant in winter 2013, 37% (25 of 67) were not seen with young at heel the subsequent spring. Although some calves likely died shortly after birth and before they could be surveyed, the large discrepancy between pregnancy rate and calving rate suggests at least some fetal losses occurred in utero. Anecdotal evidence further supports the notion that in utero losses occurred: in 2 instances, moose that earlier had tested positive for pregnancy status died before the parturition period, but fetuses were not present upon dissection of the reproductive tract. However, the possibility of an earlier false-positive pregnancy diagnosis cannot be ruled out. Parturition rates among all moose (i.e., regardless of pregnancy status) varied from 44% (43 of 98) in 2013, to 42% (28 of 67) in 2014, and 60% (29 of 47) in 2015. Twinning rates varied from 5% (2 sets of twins of 43 parturient females) in 2013, to 4% (1 of 28) in 2014, and 0% (0 of 28) in 2015. Over the 3 years of the study, parturition rates averaged 47% ± 3.4% ($n = 212$), and twinning rates averaged 3% ± 1.7% ($n = 100$).

Rump fat and reproductive rates.—We modeled the probability of pregnancy as a function of rump fat for 50 moose for which data were available. The most parsimonious model included age and a linear spline for rump fat, indicating a threshold beyond which the effect of rump fat on pregnancy changed abruptly (Supporting Information S1). Evidence for a model describing a linear relationship between rump fat and pregnancy had considerably less support ($\Delta AIC_c = 4.23$; Supporting Information S1). The best-fit model included a threshold at 2 mm of rump fat (Table 1) such that the probability of pregnancy increased from 0 to 2 mm of rump fat, but beyond this threshold the odds of pregnancy did not change (Fig. 3a). Models with breakpoints located at 1, 3, 4, or 5 mm of rump fat also had substantial support ($\Delta AIC_c \leq 1.98$; Supporting Information S1). The combined model weight for

the top models (i.e., those that included a breakpoint between 1 and 5 mm of rump fat) was 0.77. Age had a significant effect on pregnancy such that prime-aged moose were more likely to be pregnant than young ($P = 0.018$) or senescent ($P = 0.030$) moose. A variable indicating the presence of a calf at heel at the time of capture was not significant ($P = 0.187$), and including this variable failed to improve model fit ($\chi^2_1 = 2.14$, $P = 0.143$). The final model predicted a 0.95 probability of pregnancy for moose with ≥ 2 mm of rump fat.

We surveyed 29 moose during May and June that tested positive for pregnancy and for which we had age and rump fat data. In contrast to the pregnancy model, the most parsimonious model describing the probability that pregnant moose produced young included only a linear term for rump fat. The probability of producing 1 or more calves increased linearly with rump fat ($P = 0.08$) with no apparent thresholds (Fig. 3b). The top model did not include adult female age (Supporting Information S2).

Additionally, we surveyed 21 moose the following March that tested positive for pregnancy and for which we had age and rump fat data. Similar to the parturition model, the best model describing the probability that pregnant moose recruited young until the following March included only rump fat, which was positively related to recruitment ($P = 0.05$; Fig. 3c). The top model did not include age or nonlinear terms for rump fat (Supporting Information S3).

Reproductive rates and latitude.—For the meta-analysis, 39 studies reporting 76 pregnancy rates (Supporting Information S4) and 51 studies reporting 117 annual twinning rates (Supporting Information S5) satisfied the criteria for our review (Supporting Information S6). Latitude was a significant parameter in both pregnancy ($P < 0.001$) and twinning models ($P = 0.001$); as populations increased in latitude, reproductive rates also tended to increase (Figs. 4a and 4b; Table 2). The odds of pregnancy (odds ratio = 1.059) and twinning (odds ratio = 1.058) changed at nearly the same rate with changes in latitude suggesting that for every 1° increase in latitude, the odds of pregnancy or twinning increased by 5.9% and 5.8%, respectively. The analytical or field technique of determining pregnancy and twinning rates across studies was not an important predictor in either model ($P \geq 0.17$ and $P = 0.34$ for
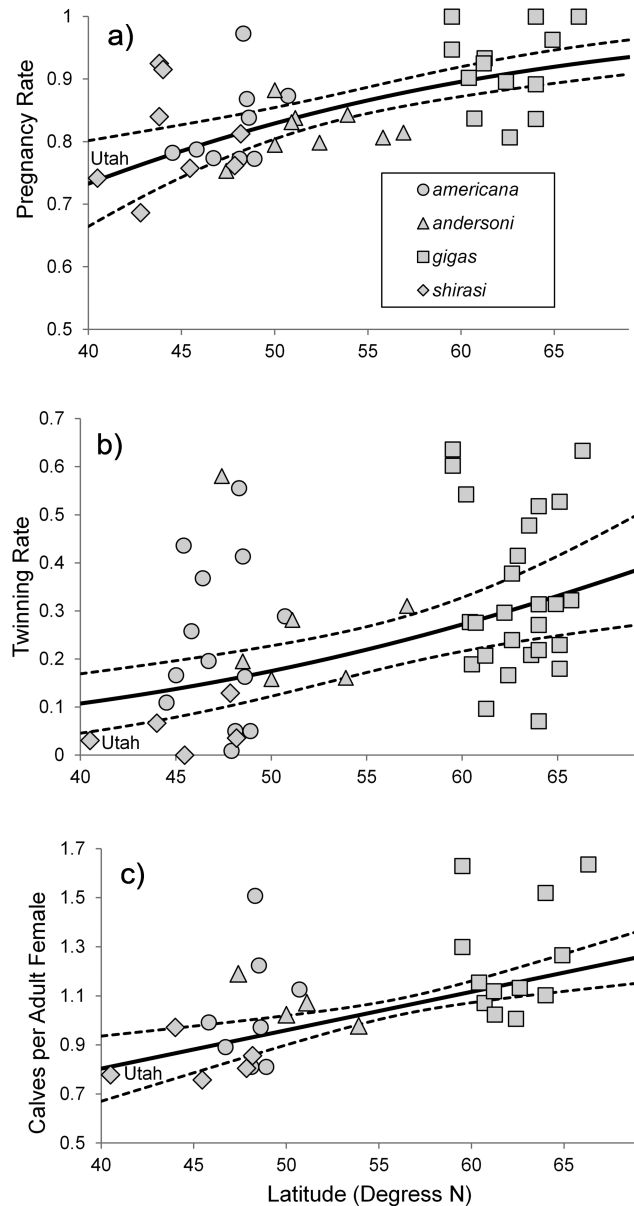
Table 1.—Parameter estimates for the best-performing generalized linear model predicting reproductive rates as a function of scaled rump fat and age for a moose (*Alces alces*) population sampled in northern Utah in 2013. Age was constructed as a categorical variable describing the age class of each moose; coefficients for this variable are given with respect to the prime age category. Sample sizes were 50, 29, and 21 for pregnancy, parturition, and recruitment, respectively. Only moose that tested positive for pregnancy in winter 2013 were included in analyses for parturition and recruitment.

Response variable	Parameter	Coefficient	SE	z	P	95% CI	
						Lower	Upper
Pregnancy	Rump fat ≤ 2 mm	2.07	0.81	2.55	0.01	0.48	3.66
	Rump fat > 2 mm	−0.11	0.16	−0.64	0.52	−0.43	0.22
	Age (young)	−2.44	1.03	−2.36	0.02	−4.74	−0.52
	Age (senescent)	−4.01	1.85	2.55	0.01	−8.20	−0.28
	Intercept	−2.02	0.87	−2.34	0.02	−3.72	−0.33
Parturition	Rump fat (mm)	0.25	0.14	1.75	0.08	−0.03	0.53
	Intercept	−0.25	0.74	−0.33	0.74	−1.70	1.21
Recruitment	Rump fat (mm)	0.33	0.17	1.98	0.05	0.04	0.66
	Intercept	−1.26	0.89	−1.42	0.15	−3.00	0.48
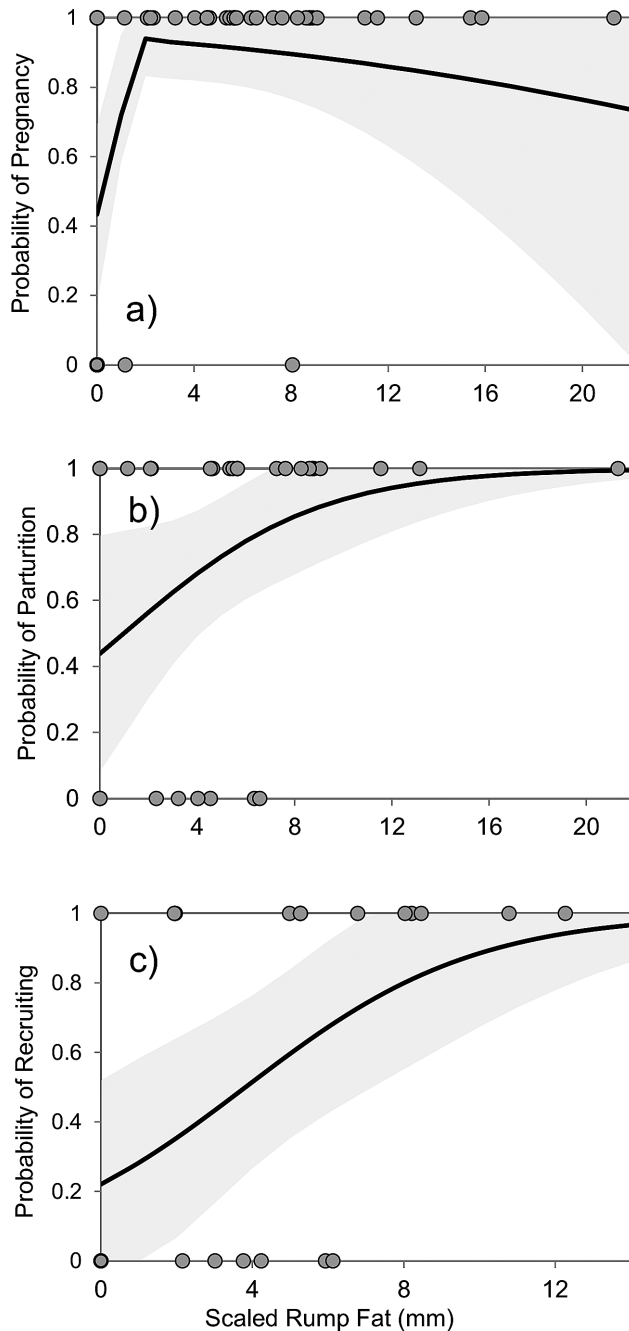
Fig. 3.—Predicted relationships between scaled winter rump fat depths and the probability of a) pregnancy ($n = 50$), b) parturition among pregnant female moose (*Alces alces*) ($n = 29$), and c) recruitment of a calf until March ($n = 21$) for moose in northern Utah in 2013. Solid lines show the model predictions of reproductive success at various levels of rump fat, and the 95% confidence interval of the prediction is given by the shaded region. Observed data points are indicated by gray circles.

Fig. 4.—Relationships between latitude and a) pregnancy rate, b) twinning rate, and c) fecundity for adult female moose (*Alces alces*) in various populations across their North American distribution. Observed proportions of reproductive rates among populations of different subspecies are represented by symbols, the prediction of reproduction rates as a function of latitude is given by the solid line, and the 95% confidence interval of the fitted line is given by dotted lines. Data points corresponding to the Utah population are labeled.

pregnancy and twinning rate determination methods, respectively; Table 2). Nevertheless, substantial, unexplained variation in both pregnancy and twining rates indicated that unmeasured factors were important (Figs. 4a and 4b). The mean pregnancy rate of all studies in our review was 85.0% ± 1.3% ($n = 39$), and the mean twinning rate was 27.4% ± 2.4% ($n = 51$).

For studies that presented data on both pregnancy and twinning rates over the same time period (29 studies reporting 48 annual estimates), we calculated fecundity, which we defined as the expected number of young produced per adult female in each population. Fecundity tended to be higher for more northern populations and exhibited a significant association with latitude ($P < 0.001$; Fig. 4c; Table 2). In this model, we found significant differences among methods used to diagnose reproductive rates (Table 2). Specifically, fecundity rates estimated from direct observation/fetal counts and direct observation/

Table 2.—Parameter estimates for generalized linear mixed models predicting reproductive rates in North American moose (*Alces alces*) populations as a function of the latitude of each population and a categorical variable indicating the method of diagnosing reproductive rates. Methods of pregnancy rate determination were: FC = fetal count; FP = fecal progesterone; PR = progesterone; RP = rectal palpation; and PSPB = pregnancy-specific protein B (reference group). Methods of twinning rate determination were: DO = direct observation and FC (reference group). Fecundity rate was calculated as the product of pregnancy rate and twinning rate; thus, methods of determination included combinations of methods used in determining both pregnancy and twinning rates; the reference group for fecundity was DO/PSPB.

Response variable	Parameter	Coefficient	SE	z	P	95% CI	
						Lower	Upper
Pregnancy	Latitude	0.057	0.013	4.45	<0.001	0.321	0.083
	FC	−0.154	0.190	−0.81	0.418	−0.527	0.219
	FP	−0.221	0.356	−0.62	0.536	−0.919	0.478
	PR	−0.416	0.359	−1.16	0.246	−1.119	0.287
	RP	−0.423	0.305	−1.38	0.167	−1.022	0.176
	Intercept	−1.134	0.649	−1.75	0.081	−2.406	0.138
Twinning	Latitude	0.057	0.017	3.26	0.001	0.023	0.091
	DO	−0.297	0.309	−0.96	0.336	−0.902	0.308
	Intercept	−4.123	0.944	−4.37	<0.001	−5.974	−2.271
Fecundity	Latitude	0.016	0.004	3.89	<0.001	0.008	0.024
	DO/FP	−0.215	0.0001	−2241.9	<0.001	−0.215	−0.215
	DO/FC	−0.268	0.081	−3.29	0.001	−0.427	−0.108
	DO/RP	−0.046	0.095	−0.48	0.63	−0.232	0.14
	FC/PSPB	−0.11	0.065	−1.66	0.096	−0.237	0.019
	Intercept	0.277	0.193	1.44	0.15	−0.100	0.655

fecal progesterone methods were significantly lower than the reference group direct observation/PSPB ($P \leq 0.001$), but other methods did not differ ($P \geq 0.09$; Table 2). After controlling for diagnostic method and including a population-specific random intercept, the model predicted that each 1° increase in latitude corresponded to 0.016 (95% $CI = 0.008$–0.024) additional young produced per adult female. Therefore, the northernmost population was expected to produce 0.48 additional young per adult female than in the southernmost population (i.e., Utah).

DISCUSSION

As with other subspecies of moose, reproductive success in Shiras moose was related to maternal fat stores (Heard et al. 1997; Testa and Adams 1998; Keech et al. 2000; White et al. 2014). Even though breeding occurred several months before we measured rump fat, rump fat and pregnancy status were clearly related. Similarly, the amount of midwinter fat stores was predictive of whether pregnant moose would eventually produce and recruit young in the following spring. Although a low threshold of rump fat during midwinter was predictive of pregnancy status, once pregnant, having more rump fat increased the probability of successfully producing and rearing viable offspring. Likewise, Testa and Adams (1998) reported an asymptote in the amount of rump fat required for pregnancy but a linear pattern between rump fat and parturition and survival of young in Alaskan moose. Milner et al. (2013) suggested that moose could conceive even in poor body condition but may later terminate pregnancies if winter conditions became limiting. Such an occurrence may partially explain the pattern we observed.

In accordance with other studies (Sand 1996; Heard et al. 1997; Ericsson et al. 2001), maternal age was an important determinant of pregnancy rates in moose as both young and old age classes exhibited lower pregnancy rates than prime-aged moose (Fig. 2). Although yearling moose can become pregnant (Schwartz and Hundertmark 1993), none of the 5 yearlings in our study were pregnant. Because reproduction is more costly to younger moose, which may encounter a tradeoff between reproduction and growth (Sæther and Heim 1993; Sand 1996), our results suggest that yearling moose in our study avoided reproduction in favor of growth. Moose > 9 years old in our sample had lower pregnancy rates than prime-aged individuals, although our sample contained few moose in the old age category. In contrast to the influence of age on pregnancy, age appeared to be a less important factor in determining calving or recruitment success, although our analyses were limited by sample size for moose of older ages.

Moose in our study population in Utah had scaled rump fat depths in midwinter of 5.0 mm, and roughly 1/3 had no measurable rump fat. Until more comparisons can be made with other Shiras moose populations, it is unclear to what extent this fat level suggests nutritional limitation. In ungulates, fat stored in the rump region is among the last of subcutaneous fat reserves to deplete (Cook et al. 2010); however, moose with no measurable rump fat can still possess between 0% and 5.6% ingesta-free body fat (IFBF—Stephenson et al. 1998). Therefore, data from moose that had no measurable rump fat inherently lack resolution and cannot precisely predict percent body fat. We therefore consider rump fat to be a simple but imperfect index of body condition and caution that animals with no measurable rump fat are not directly comparable to one another. Although no methods currently exist to estimate IFBF in moose without measurable rump fat (Cook et al. 2010), our analyses suggest that the threshold in rump fat for midwinter pregnancy is above the point at which subcutaneous fat reserves have been depleted.

Because we measured rump fat during January and February, these measurements represent the nutritional state of animals

near the midpoint between conception and parturition. However, the timing of measurements did not represent the peak nutritional state of an animal (i.e., autumn) and consequently, certain findings require careful interpretation. For example, we found no overall statistical difference in rump fat between adult females with and without calves at the time of handling. Adult female moose provisioning 1 or more calves during summer would logically enter winter with lower fat stores due to energetic demands of lactation. Because ungulates entering winter with more fat may ultimately metabolize more fat over winter than thinner individuals (Cook et al. 2013), by midwinter any differences in rump fat between moose with and without calves at heel may have been obscured. Additionally, the lack of an effect may have resulted from low statistical power due to small sample size. Nonetheless, our findings suggest that rump fat measured midwinter still can be valuable in terms of explaining variation in reproductive success.

Reproductive rates for adult moose tended to be lower as populations approached the southern range limit, although those trends varied widely. Latitude per se likely has no effect on reproductive rates of moose, but instead it reflects other factors that vary with latitude, e.g., climate, density dependence, primary productivity, genetics, or predation pressure. Regardless of the latitude of the population, a qualitative assessment suggests populations situated at the extreme southern range limit have below-average adult pregnancy rates: Utah (74%—this study), SW Wyoming (69%—K. L. Monteith and M. J. Kauffman, University of Wyoming, pers. comm.), NE Minnesota (75%—Severud et al. 2015), Michigan (74%—Dodge et al. 2004), New Hampshire (78%—Musante et al. 2010), and New Brunswick (79%—Boer 1987). This result is consistent with biogeographic models suggesting that edge populations may have compromised fitness.

Moose may maintain relatively high pregnancy rates despite environmental variation but instead decrease litter size in response to declining nutrition (Gasaway et al. 1992; Gingras et al. 2014). Therefore, the product of pregnancy rate and litter size may be more confirmatory in determining if southern moose indeed are less productive. Our review of moose fecundity across North America (calculated from studies presenting both pregnancy and twinning rates) also indicated a trend of fewer young per adult female in populations at lower latitudes.

Our evaluation cannot elucidate the mechanism underpinning lower reproductive rates among southern moose populations, but it suggests an overarching and relevant pattern. Fecundity in moose often has been attributed to habitat quality (Franzmann and Schwartz 1985; Gingras et al. 2014), because like other temperate ungulates, moose are capital breeders and rely partially on somatic reserves to support demands associated with reproduction. Consequently, reproductive rates should reflect habitat quality. At high latitudes, characteristics of the summer growing season allow for production of higher quality forage for moose (Sand et al. 1995; Langvatn et al. 1996; Herfindal et al. 2006); therefore, the latitudinal gradient in reproductive gradients we observed may be caused by a north–south gradient in forage quality. This hypothesis is in accordance with the environmental gradient theory, which predicts that

habitat quality becomes marginal at range edges, often leading to lower population performance (Caughley et al. 1988; Talley 2007; Sexton et al. 2009). Furthermore, cold-adapted species at their equatorial range limit may be even more susceptible to nutritional limitation when potential for thermal stress is considered (Monteith et al. 2015). Nevertheless, the large amount of variation in our data, regardless of the latitudinal position of the population, indicates that other local factors associated with environmental characteristics or other external factors also are important (Talley 2007; Sexton et al. 2009).

Alternatively, if southern moose populations occur at higher densities relative to their carrying capacity than more northern populations (Peek 1974; Post 2005), density dependence feedbacks may heighten nutritional limitation. Monteith et al. (2015) suggested that recently established moose populations in the United States Rocky Mountains have experienced irruptive population growth, and some populations could exceed carrying capacity. Furthermore, in many southern moose populations including Utah, wolves and grizzly bears (*Ursus arctos*) have been extirpated and consequently, moose are not limited by these predators. As such, lower predation on southern moose populations may allow them to reach higher densities than in northern areas with more abundant predators (Wang et al. 2009).

Reproductive rates for Shiras moose in our review were consistently low when compared to other subspecies, which accords with early researchers who postulated such an effect could be intrinsic to the subspecies (Houston 1968; Stevens 1970; Peek 1974). In particular, Shiras moose have among the lowest twinning rates in our review (Fig. 4b). Testa and Adams (1998) did not detect an effect of maternal body condition on the probability of twinning in moose, and instead they proposed that phenotypic traits such as age and body size may be related to instances of twinning. Others, however, reported that maternal body mass was associated positively with production of twins (Schwartz and Hundertmark 1993; Sand 1996). Because Shiras moose are smaller bodied than other North American subspecies (Bubenik 2007), twinning rates of Shiras moose may be limited inherently by body size, and body size itself may be driven by either environmental or genetic differences among southern and northern populations (Herfindal et al. 2014).

Finally, decreased productivity of southern moose populations may represent the evolution of a reproductive strategy that maximizes individual fitness in response to local environmental characteristics (Araújo et al. 2015). Importantly, juvenile survival may be higher in moose populations nearest the equatorial range limit (Ferguson 2002). Because winter severity increases juvenile mortality in moose (Thompson 1980; Keech et al. 2000; Sivertsen et al. 2012), as environments become less seasonal in southern latitudes, calf survival rates generally increase (Sand 1996; Ferguson 2002). Additionally, in southern regions where wolves and grizzly bears are absent, young moose may face lower predation risk than in predator abundant areas in the north. Therefore, lower productivity in southern moose may be offset by an increase in juvenile survival and consequently may not depress population growth.

If calf survival rates are indeed higher for southern moose, then female moose may not invest in larger litter sizes but instead allocate available resources into a single calf with high odds of survival. Therefore, a southern moose could optimize fitness by trading additional offspring for a higher probability of survival of a singleton, a potential form of conservative bet-hedging (Olofsson et al. 2009).

Our results suggest that demographic rates of moose can vary along geographic gradients, even for pregnancy rate that previously has been considered invariable and robust to environmental conditions (Boer 1992). We also documented the important role of maternal body fat in reproductive success in Shiras moose. These findings suggest that southern moose populations may be demographically vulnerable due to low reproduction. This vulnerability could be particularly important if environmental conditions continue to reduce forage quality for moose (Monteith et al. 2015) and result in even lower production of young.

Acknowledgments

Supporting Information

The Supporting Information documents are linked to this manuscript and are available at Journal of Mammalogy online (jmammal.oxfordjournals.org). The materials consist of data provided by the author that are published to benefit the reader. The posted materials are not copyedited. The contents of all supporting data are the sole responsibility of the authors. Questions or messages regarding errors should be addressed to the author.

Supporting Information S1.—Model selection results for candidate models predicting the probability of pregnancy in adult moose in Utah, 2013.

Supporting Information S2.—Model selection results for candidate models predicting the probability of parturition among pregnant adult moose in Utah, 2013.

Supporting Information S3.—Model selection results for candidate models predicting the probability of recruiting a calf until March for pregnant adult moose in Utah, 2013.

Supporting Information S4.—Results of a literature review on pregnancy rates of adult moose in North America.

Supporting Information S5.—Results of a literature review on twinning rates of adult moose in North America.

Supporting Information S6.—Data sources used in meta-analysis of pregnancy and twinning rates of adult moose in North America.

Literature Cited

Angert, A. L. 2006. Demography of central and marginal populations of monkeyflowers (*Mimulus cardinalis* and *M. lewisii*). Ecology 87:2014–2025.

Araújo, R., et al. 2015. Trade-offs between life-history traits at range-edge and central locations. Journal of Phycology 51:808–818.

Boer, A. H. 1987. Reproductive productivity of moose in New Brunswick. Alces 23:49–60.

Boer, A. H. 1992. Fecundity of North American moose (*Alces alces*): a review. Alces Supplement 1:1–10.

Boertje, R. D., M. M. Ellis, and K. A. Kellie. 2015. Accuracy of moose age determinations from canine and incisor cementum annuli. Wildlife Society Bulletin 39:383–389.

Bubenik, A. B. 2007. Behavior. Pp. 173–221 in Ecology and management of the North American moose (A. W. Franzmann and C. C. Schwartz, eds.). 2nd ed. University Press of Colorado, Boulder.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information theoretic approach. 2nd ed. Springer-Verlag, New York.

Caughley, G., D. Grice, R. Barker, and B. Brown. 1988. The edge of the range. Journal of Animal Ecology 57:771–785.

Channell, R., and M. V. Lomolino. 2000. Dynamic biogeography and conservation of endangered species. Nature 403:84–86.

Cook, R. C., et al. 2010. Revisions of rump fat and body scoring indices for deer, elk, and moose. Journal of Wildlife Management 74:880–896.

Cook, R. C., et al. 2013. Regional and seasonal patterns of nutritional condition and reproduction in elk. Wildlife Monographs 184:1–45.

Cook, B. I., T. R. Ault, and J. E. Smerdon. 2015. Unprecedented 21st century drought risk in the American Southwest and Central Plains. Science Advances 1:1–7.

Darimont, C. T., P. C. Paquet, T. E. Reimchen, and V. Crichton. 2005. Range expansion by moose into coastal temperate rainforests of British Columbia, Canada. Diversity and Distributions 11:235–239.

Dawson, T. P., S. T. Jackson, J. I. House, I. C. Prentice, and G. M. Mace. 2011. Beyond predictions: biodiversity conservation in a changing climate. Science 332:53–58.

Dodge, W. B., S. R. Winterstein, D. E. Beyer, and H. Campa. 2004. Survival, reproduction, and movements of moose in the western Upper Peninsula of Michigan. Alces 40:71–85.

Ericsson, G., K. Wallin, J. P. Ball, and M. Broberg. 2001. Age-related reproductive effort and senescence in free-ranging moose, *Alces alces*. Ecology 82:1613–1620.

Eubanks, R. 1984. Approximate regression models and splines. Communications in Statistics Theory and Methods 13:433–484.

Ferguson, S. H. 2002. The effects of productivity and seasonality on life history: comparing age at maturity among moose (*Alces alces*) populations. Global Ecology and Biogeography 11:303–312.

Foster, D. R., G. Motzkin, D. Bernardos, and J. Cardoza. 2002. Wildlife dynamics in the changing New England landscape. Journal of Biogeography 29:1337–1357.

Franzmann, A. W., and C. C. Schwartz. 1985. Moose twinning rates: a possible population condition assessment. The Journal of Wildlife Management 49:394–396.

GARCÍA, D., R. ZAMORA, J. M. GÓMEZ, P. JORDANO, AND J. A. HÓDAR. 2000. Geographical variation in seed production, predation and abortion in *Juniperus communis* throughout its range in Europe. Journal of Ecology 88:435–446.

GASAWAY, W. C., R. D. BOERTJE, D. GRAVGAARD, D. G. KELLYHOUSE, R. O. STEPHENSON, AND D. G. LARSEN. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. Wildlife Monographs 120:1–59.

GINGRAS, J., S. COUTURIER, S. D. CÔTÉ, AND J. P. TREMBLAY. 2014. Opposite responses of body condition and fertility in adjacent moose populations. The Journal of Wildlife Management 78:830–839.

GUTZLER, D. S., AND T. O. ROBBINS. 2011. Climate variability and projected change in the western United States: regional downscaling and drought statistics. Climate Dynamics 37:835–849.

HAIGH, J. C., W. J. DALTON, C. A. RUDER, AND R. G. SASSER. 1993. Diagnosis of pregnancy in moose using a bovine assay for pregnancy-specific protein B. Theriogenology 40:905–911.

HAMPE, A., AND R. J. PETIT. 2005. Conserving biodiversity under climate change: the rear edge matters. Ecology Letters 8:461–467.

HEARD, D., S. BARRY, G. WATTS, AND K. CHILD. 1997. Fertility of female moose (*Alces alces*) in relation to age and body composition. Alces 33:165–176.

HERFINDAL, I., H. HAANES, E. J. SOLBERG, K. H. RØED, K. A. HØGDA, AND B. E. SÆTHER. 2014. Moose body mass variation revisited: disentangling effects of environmental conditions and genetics. Oecologia 174:447–458.

HERFINDAL, I., E. J. SOLBERG, B. E. SÆTHER, K. A. HØGDA, AND R. ANDERSEN. 2006. Environmental phenology and geographical gradients in moose body mass. Oecologia 150:213–224.

HOUSTON, D. B. 1968. The Shiras moose in Jackson Hole, Wyoming. Grand Teton Natural Historical Association Technical Bulletin 1:1–110.

HUNDERTMARK, K. J., AND C. C. SCHWARTZ. 1998. Predicting body mass of Alaskan moose (*Alces alces gigas*) using body measurements and condition assessment. Alces 34:83–89.

JUMP, A. S., AND F. I. WOODWARD. 2003. Seed production and population density decline approaching the range-edge of *Cirsium* species. New Phytologist 160:349–358.

KEECH, M. A., R. T. BOWYER, J. M. VER HOEF, R. D. BOERTJE, B. W. DALE, AND T. R. STEPHENSON. 2000. Life-history consequences of maternal condition in Alaskan moose. Journal of Wildlife Management 64:450–462.

LANGVATN, R., S. D. ALBON, T. BURKEY, AND T. H. CLUTTON-BROCK. 1996. Climate, plant phenology and variation in age of first reproduction in a temperate herbivore. Journal of Animal Ecology 65:653–670.

LAWTON, J. H. 1993. Range, population abundance and conservation. Trends in Ecology and Evolution 8:409–413.

LENARZ, M. S., J. FIEBERG, M. W. SCHRAGE, AND A. J. EDWARDS. 2010. Living on the edge: viability of moose in northeastern Minnesota. Journal of Wildlife Management 74:1013–1023.

MILNER, J. M., F. M. VAN BEEST, E. J. SOLBERG, AND T. STORAAS. 2013. Reproductive success and failure: the role of winter body mass in reproductive allocation in Norwegian moose. Oecologia 172:995–1005.

MONTEITH, K. L., R. W. KLAVER, K. R. HERSEY, A. A. HOLLAND, T. P. THOMAS, AND M. J. KAUFFMAN. 2015. Effects of climate and plant phenology on recruitment of moose at the southern extent of their range. Oecologia 178:1137–1148.

MURRAY, D. L., ET AL. 2006. Pathogens, nutritional deficiency, and climate influences on a declining moose population. Wildlife Monographs 166:1–30.

MUSANTE, A. R., P. J. PEKINS, AND D. L. SCARPITTI. 2010. Characteristics and dynamics of a regional moose *Alces alces* population in the northeastern United States. Wildlife Biology 16:185–204.

OLOFSSON, H., J. RIPA, AND N. JONZÉN. 2009. Bet-hedging as an evolutionary game: the trade-off between egg size and number. Proceedings of the Royal Society of London, Series B: Biological Sciences 276:2963–2969.

OLTERMAN, J. H., D. W. KENVIN, AND R. C. KUFELD. 1994. Moose transplant to southwestern Colorado. Alces 30:1–8.

PEEK, J. M. 1962. Studies of moose in the Gravelly and Snowcrest Mountains, Montana. Journal of Wildlife Management 26:360–365.

PEEK, J. M. 1974. On the winter habitats of Shiras moose. Canadian Naturalist 101:131–141.

POST, E. 2005. Large-scale spatial gradients in herbivore population dynamics. Ecology 86:2320–2328.

RENECKER, L. A., AND R. J. HUDSON. 1986. Seasonal energy expenditures and thermoregulatory responses of moose. Canadian Journal of Zoology 64:322–327.

RUPRECHT, J. S. 2016. The demography and determinants of population growth in Utah moose. M.S. thesis, Utah State University, Logan.

SÆTHER, B. E., AND M. HEIM. 1993. Ecological correlates of individual variation in age at maturity in female moose (*Alces alces*): the effects of environmental variability. Journal of Animal Ecology 62:482–489.

SAGARIN, R. D., AND S. D. GAINES. 2002. The 'abundant center' distribution: to what extent is it a biogeographical rule? Ecology Letters 5:137–147.

SAND, H. 1996. Life history patterns in female moose (*Alces alces*): the relationship between age, body size, fecundity and environmental conditions. Oecologia 106:212–220.

SAND, H., G. CEDERLUND, AND K. DANELL. 1995. Geographical and latitudinal variation in growth patterns and adult body size of Swedish moose (*Alces alces*). Oecologia 102:433–442.

SANZ, J. J. 1997. Geographic variation in breeding parameters of the Pied Flycatcher *Ficedula hypoleuca*. Ibis 139:107–114.

SASSER, R. G., C. A. RUDER, K. A. IVANI, J. E. BUTLER, AND W. C. HAMILTON. 1986. Detection of pregnancy by radioimmunoassay of a novel pregnancy-specific protein in serum of cows and a profile of serum concentration during gestation. Biology of Reproduction 35:936–942.

SCHWARTZ, C. C. 2007. Reproduction, natality, and growth. Pp. 141–171 in Ecology and management of the North American moose (A. W. Franzmann and C. C. Schwartz, eds.). 2nd ed. University Press of Colorado, Boulder.

SCHWARTZ, C. C., AND K. J. HUNDERTMARK. 1993. Reproductive characteristics of Alaskan moose. Journal of Wildlife Management 57:454–468.

SEBER, G., AND C. WILD. 2003. Nonlinear regression. John Wiley and Sons, New York.

SEVERUD, W. J., G. D. DELGIUDICE, T. R. OBERMOLLER, T. A. ENRIGHT, R. G. WRIGHT, AND J. D. FORESTER. 2015. Using GPS collars to determine parturition and cause-specific mortality of moose calves. Wildlife Society Bulletin 39:616–625.

SEXTON, J. P., P. J. MCINTYRE, A. L. ANGERT, AND K. J. RICE. 2009. Evolution and ecology of species range limits. Annual Review of Ecology, Evolution, and Systematics 40:415–436.

Sikes, R. S., W. L. Gannon, and the Animal Care and Use Committee of the American Society of Mammalogists. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 92:235–253.

Sivertsen, T. R., A. Mysterud, and H. Gundersen. 2012. Moose (*Alces alces*) calf survival rates in the presence of wolves (*Canis lupus*) in southeast Norway. European Journal of Wildlife Research 58:863–868.

StataCorp LP. 2013. STATA: data analysis and statistical software. Version 13. StataCorp LP, College Station, Texas.

Stephenson, T. R., K. J. Hundertmark, C. C. Schwartz, and V. V. Ballenberghe. 1998. Predicting body fat and body mass in moose with ultrasonography. Canadian Journal of Zoology 76:717–722.

Stevens, D. R. 1970. Winter ecology of moose in the Gallatin Mountains, Montana. Journal of Wildlife Management 34:37–46.

Talley, T. S. 2007. Which spatial heterogeneity framework? Consequences for conclusions about patchy population distributions. Ecology 88:1476–1489.

Telfer, E. S. 1984. Circumpolar distribution and habitat requirements of moose (*Alces alces*). Pp. 145–182 in Northern ecology and resource management (R. Olson, R. Hastings, and F. Geddes, eds.). University of Alberta Press, Edmonton, Alberta, Canada.

Testa, J. W., and G. P. Adams. 1998. Body condition and adjustments to reproductive effort in female moose (*Alces alces*). Journal of Mammalogy 79:1345–1354.

Thompson, I. W. 1980. Effects of weather on productivity and survival of moose in northeastern Ontario. Alces 16:463–481.

Vose, R. S., et al. 2014. Improved historical temperature and precipitation time series for US climate divisions. Journal of Applied Meteorology and Climatology 53:1232–1251.

Vucetich, J. A., and T. A. Waite. 2003. Spatial patterns of demography and genetic processes across the species' range: null hypotheses for landscape conservation genetics. Conservation Genetics 4:639–45.

Wang, G. M., et al. 2009. Density dependence in northern ungulates: interactions with predation and resources. Population Ecology 51:123–132.

White, K. S., N. L. Barten, S. Crouse, and J. Crouse. 2014. Benefits of migration in relation to nutritional condition and predation risk in a partially migratory moose population. Ecology 95:225–237.

Wilcoxon, F. 1945. Individual comparisons by ranking methods. Biometrics Bulletin 1:80–83.

Wold, S. 1974. Spline functions in data analysis. Technometrics 16:1–11.

Wolfe, M. L., K. R. Hersey, and D. C. Stoner. 2010. A history of moose management in Utah. Alces 46:37–52.