# Alaska Department of Fish and Game Wildlife Restoration Grant

**GRANT NUMBER:** AKW-23 FY18

**PROJECT NUMBER:** 1.65

**PROJECT TITLE:** Age-specific natural mortality rates of male versus female moose

PERIOD OF PERFORMANCE: July 1, 2017 –June 30, 2018

**REPORT DUE DATE:** September 1, 2018

PRINCIPAL INVESTIGATOR: Graham Frye, Wildlife Biologist III

**COOPERATORS:** Rodney Boertje (ADF&G retired), Donald Young (ADF&G retired)

I. PROGRESS ON PROJECT OBJECTIVES DURING PERIOD OF PERFORMANCE

OBJECTIVE 1: Continue literature review on 1) moose biology and ecology at high densities; 2) indices to nutritional status of ungulates; 3) models of ungulate population dynamics;4) predator-prey ratios in relation to population dynamics of moose, caribou, sheep, wolves, and grizzly bears; 5) predator-prey relationships in multi-prey, multi-predator systems; and 6) population and harvest data on moose, caribou, sheep, wolves, and bears in Unit 20A.

ACCOMPLISHMENTS: A review of recent and relevant literature was conducted during FY 18 for the writing of the manuscript entitled "Lifetime, known-age moose reproduction in a nutritionally stressed population." Initial review of relevant literature was also begun for the manuscript entitled "Male and female moose mortality in a nutritionally stressed population."

OBJECTIVE 2: Estimate causes and age-specific rates of mortality among radiocollared male and female moose in Unit 20A. These data are expected to be useful in determining whether male moose have high survival rates in the 2- through 6-year age-classes as documented among females. These data will also be useful in evaluating when and why changes occur in population density.

ACCOMPLISHMENTS: The remaining moose alive in this study were checked during 9 months in FY 18 via fixed wing. Two of the four remaining moose died during late April and May 2018 and their collars were retrieved via helicopter in May 2018. Preliminary analyses of all mortality data collected for this project were analyzed during FY18 by Frye and Boertje.

OBJECTIVE 3: Continue to estimate and evaluate the usefulness of several reproductive and condition indices for moose in Unit 20A. In particular we need to complete age-specific reproductive rates for moose older than 9 years old. These data will also be useful in determining when and why changes occur in population density.

ACCOMPLISHMENTS: Age-specific reproductive rates were analyzed and presented in a paper submitted for publication in a scientific journal during the report period (see Objective 4 accomplishments below). Data collection on reproductive rates was completed for Project 1.65 during spring 2018.

OBJECTIVE 4: Review literature, fly aerial surveys, write annual progress reports, write final project report, and publish results in peer-reviewed journals.

ACCOMPLISHMENTS: A paper entitled "Lifetime moose reproduction in a nutritionally stressed population" was submitted to the Journal of Wildlife Management and Wildlife Monographs editors during the report period. It was subsequently sent back to the authors on 2 occasions for revision and is currently in final review prior to acceptance and publication. Aerial surveys are continuing with the objective of regularly monitoring survival of 2 remaining female moose. Meanwhile, preliminary work on the final manuscript on mortality rates is progressing and submission to a peer-reviewed journal is anticipated in FY 19.

# II. SUMMARY OF WORK COMPLETED ON PROJECT TO DATE.

This long-term project began in FY 06. See federal aid annual reports for FY 06 thru FY 17. The following papers were produced during FY 06 thru FY 18:

- 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.
- \_\_\_\_\_, G. G. FRYE, and D. D. YOUNG. (in prep). Lifetime known-age moose reproduction in a nutritionally stressed population. Journal of Wildlife Management.
- \_\_\_\_\_, M. A. KEECH, D. D. YOUNG, K. A. KELLIE, and C. T. SEATON. 2009. Managing for elevated yield of moose in Interior Alaska. Journal of Wildlife Management 73: 314–327.
- \_\_\_\_\_, K. A. KELLIE, C. T. SEATON, M. A. KEECH, D. D. YOUNG, B. W. DALE, L. G. ADAMS, and A. R. ADERMAN. 2007. Ranking Alaska moose nutrition: signals to begin liberal antlerless harvests. Journal of Wildlife Management 71: 1494–1506.

# **III. SIGNIFICANT DEVELOPMENT REPORTS AND/OR AMENDMENTS.** N/A.

# IV. PUBLICATIONS

See Appendix A for draft revised manuscript (Lifetime known-age moose reproduction in a nutritionally stressed population) submitted to the Journal of Wildlife Management on 13 August 2018.

# V. RECOMMENDATIONS FOR THIS PROJECT

Publish the attached paper on lifetime moose reproduction in the Journal of Wildlife Management during FY19. Continue to monitor survival and reproduction in the small sample of remaining elderly moose during FY19. Prepare and submit for scientific publication an article detailing long-term age-specific male vs. female moose mortality rates in central Game Management Unit 20A.

Prepared by: Scott Brainerd, Graham Frye, and Rodney Boertje

Date: 8/21/2018

# Appendix A.

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RH: Boertje et al. • Lifetime Moose Reproduction

Lifetime, Known-age Moose Reproduction in a Nutritionally Stressed Population

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**ABSTRACT** Quantifying long-term, low reproductive metrics indicative of an ungulate population's low nutritional status can help spur action to manage for moderate densities in contrast to unsustainable, high densities. We previously ranked this moose (*Alces alces gigas*) population as having the lowest nutritional status among 14 moose populations in Alaska, USA, primarily using reproductive indices (1996–2005) from moose with ages estimated by counting cementum annuli. Here, we detailed lifetime reproductive metrics from a subset of known-age female moose initially radio-collared at 9–10 months of age (7 cohorts; 1996–2002); we renewed radio-collars as necessary. We radio-tracked and observed these moose at 24- or 48-hour

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intervals for the presence of newborns during the 1998–2018 calving seasons, with meaningful annual sample sizes during 2000–2014. The number of snow-free days in the year preceding parturition had a subtle positive effect on parturition probability, but we found no evidence for effects of the preceding February and March immobilization, cohort affiliation, or the preceding winter's snow cover on the probability of a female being parturient. The probability of twinning clearly declined as the calving season progressed. Compared with moose production in populations with improved nutrition, our study population experienced low production primarily as a result of delayed maturation, occasional pauses in reproduction, and low twinning rates, not early reproductive senescence. We recorded a 28% parturition rate among 144 females 3 years of age (min. age of reproduction). Parturition rates were stable from 4 to 13 years of age ( $\bar{x} = 77\%$ ), declined at 14 years of age, and peaked at 15 years of age. Females first twinned at 5 years of age (5%), and the twinning rate increased with age, peaking at 13 years of age (25%). Overall, 136 radio-collared females with complete reproductive histories produced a mean of 5.3 calves/lifetime while being monitored a mean of 7.1 years at ages  $\geq 3$  years, although variability in individual production was high. Delaying or pausing reproduction clearly increased the parturition rate at 4 and 5 years of age. However, females that delayed first reproduction produced fewer calves/lifetime on average compared with moose that first produced at 3 years of age. Virtually all moose regularly gave birth with occasional 1-year pauses that acted to enhance production the subsequent year; the incidence of 2 consecutive nonparturient years was 24/844 =2.8%. We classified the years 2000–2014 as a period of stable, low moose nutritional status based upon low population-wide twinning rates from annual aerial transect surveys (no telemetry) flown a few days after the median annual calving dates. Detailed understanding of low reproductive metrics encouraged empowered stakeholders to allow liberal harvests of female

moose (2.0–4.4% of prehunt moose population numbers) and encouraged land managers to allow wildfires to burn 25% of the study area to improve moose carrying capacity. We helped manage a 31% decline in moose numbers during 2004–2012 by implementing liberal harvests of female moose. Elevated population-wide twinning rates in 2012, 2015, 2017, and 2018, similar to elevated levels prior to 1997, were likely a positive response to lower moose densities and improved browse after wildfires.

**KEY WORDS** Alaska, *Alces*, delayed maturation, known-age, moose, parturition rates, reproduction, twinning.

Evaluating reproductive parameters of an ungulate population is important when opting to manage below ecological carrying capacity to achieve sustainable harvests and population levels (e.g., Caughley 1976; McCullough 1979, 1999). Several previous studies used moose (*Alces alces*) reproductive metrics, particularly parturition rates in the young age classes and twinning rates (number of twin births/number of parturient F), to rank nutritional status of the respective populations and proximity to carrying capacity (Blood 1974, Franzmann and Schwartz 1985, Boer 1992, Gasaway et al. 1992, Ferguson et al. 2000, Boertje et al. 2007, Gingras et al. 2014, Jensen et al. 2018). Reproductive metrics varied substantially among populations, e.g., first age of twinning ranged from 2 to 5 years of age (24–60 months) in differing populations and twinning rates varied from <10% to >65%. Several moose populations with the lowest reproductive metrics were successfully managed through implementation of temporary liberal harvests of female moose to curtail growth of the populations to prevent long-term overstocking and associated shifts in forest composition to browse-resistant species (Boertje et al. 2010, Gingras et al. 2014, Charron and Hermanutz 2017). The importance of linking increasing

herbivore numbers with declining reproductive metrics should not be underestimated, particularly when faced with the task of convincing stakeholders to allow liberal harvests of female ungulates (Boertje et al. 2009, 2017).

We previously identified several indices in our study area suggesting moose were reaching unsustainable, high densities. Boertje et al. (2007) ranked the nutritional status of our 2 subpopulations (Tanana Flats and adjacent foothills) during 1997–2005 as the lowest among 14 moose populations in Alaska, USA. Boertje et al. (2007) based this low ranking on the low twinning rate from transect surveys (7%), delayed age to first twinning (5 yr), delayed age of first reproduction (3 yr), lowest parturition rate among 3 year olds ( $\bar{x} = 29\%$ ), lowest parturition rate among mature females ( $\bar{x} = 75\%$ ), low average mass at 9–10 months of age, and high browse removal rates (Paragi et al. 2015). Also, our study population exhibited the lowest average twinning rate reported among wild, noninsular moose in North America, with the exception of certain Shiras moose (*A. a. shirasi*) populations (Schwartz 2007, Ruprecht et al. 2016).

Age-specific reproductive rates of moose are best measured by radio-collaring young, known-age cohorts. In previous studies, age-specific reproductive rates were based mostly or entirely on approximate ages based largely on counts of cementum annuli in teeth (Pimlott 1959, Markgren 1969, Sæther and Haagenrud 1983, Boer 1992, Gasaway et al. 1992, Heard et al. 1997, Ericsson et al. 2001, Ruprecht et al. 2016). Despite relatively large teeth in moose, counting cementum annuli can be problematic and subjective because of difficulties in distinguishing distinct annuli (Cumming and Evans 1978, Rolandsen et al. 2008, Boertje et al. 2015). Cementum annuli counts in moose studies have both overestimated and underestimated actual ages (Gasaway et al. 1978, Rolandsen et al. 2008, Boertje et al. 2015). Counting errors

accumulated with age and a small percentage of counts produced errors of several years, even when using the best staining techniques available and the most experienced laboratory personnel (Boertje et al. 2015).

Our objectives included examining the potential effects of immobilization, cohort affiliation, snow cover, snow-free days (SFD), and parturition date on reproduction in these nutritionally stressed moose. We also documented and discussed age-specific summaries of parturition rates, twinning rates, and production rates, and annual and lifetime summaries when appropriate to better describe a low level of moose production. We tested whether female moose in the earliest primiparous age class produced the most calves over lifetimes of  $\geq 12$  years (Schwartz et al. 1992) and  $\geq 3$  years, compared with females that delayed maturity for a year or 2. We investigated the occurrence and role of age-specific reproductive pauses because parturition rates often fluctuated annually, e.g., from 98% in 1996 to 77% in 1997 (Keech et al. 2000), and we discussed these results in relation to several published hypotheses related to reproductive pauses in ungulates. To help define whether nutritional status changed during this long-term study of aging moose, we documented annual twinning rates from population-wide aerial transect surveys (no telemetry) flown a few days after the median annual calving dates. We tested for differences in twinning rates from the population-wide versus radio-collared samples. We discussed the timing and ramifications of elevated population-wide twinning rates, because stakeholders targeted an improvement in moose reproductive metrics during this study.

#### **STUDY AREA**

The roadless study area (4,680 km<sup>2</sup> of moose habitat) was an area of concentrated moose calving, which encompassed the central Tanana Flats between the Little Delta and Wood Rivers immediately south of Fairbanks, Alaska, USA. Gasaway et al. (1983), Boertje et al. (1996, 2007,

2009), and Keech et al. (2000) previously described the study area and adjacent flats and Alaska Range foothills (Game Management Unit 20A, 13,044 km<sup>2</sup> of moose habitat) and factors limiting moose numbers during 1960–2006. Moose numbers in Game Management Unit 20A declined from 23,000 to 3,000 during 1965–1975 and subsequently increased, peaking at almost 18,000 in 2003, partly from wolf (*Canis lupus*) reductions during 1976–1982 and 1993–1994, and low grizzly bear (*Ursus arctos*) and black bear (*U. americanus*) predation relative to other moose mortality studies in Alaska (Boertje et al. 1996, 2009).

This study (1997–2018) began several years before the 2003 peak in moose density and we managed a reduction in the moose population during 2004–2012, largely through implementation of liberal harvests of female moose (2.0–4.4% of prehunt moose population numbers; Boertje et al. 2009, Young 2014). The population appeared to stabilize after early winter 2012 when harvests of female moose were largely discontinued (Young 2014, 2017).

To initiate this study, we sampled moose 9–10 months of age (1997–2003) equally from 2 subpopulations in Game Management Unit 20A. One subpopulation resided year-round in the central Tanana Flats while the other largely calved in the central Tanana Flats but resided at least during capture in late winter in the adjacent central Alaska Range foothills and mountains (2,050 km<sup>2</sup>; Boertje et al. 2007, 2009). These subpopulations had similar reproductive metrics, body weights at 9-10 months of age, and winter browse rates (Boertje et al. 2007), as well as similar maternal condition (rump-fat depths and age) and rates of calf mortality (Keech et al. 2000). Paragi et al. (2015) documented a decline in browse utilization in portions of the Tanana Flats and adjacent central foothills coincident with recent declines in moose density.

Young (2014) described the relative lack of wildfires in Game Management Unit 20A in the decades preceding this study, as well as recent influential wildfires in our study area,

particularly during 2001 (461 km<sup>2</sup>), 2009 (506 km<sup>2</sup>), and 2012 (190 km<sup>2</sup>). In total, about 25% of the study area burned during 2001–2012. Radio-collared moose with low prefire contact with a 1980 burn in the study area increased use of the burn area  $\geq$ 1–4 years following the fire; these moose shifted home ranges to include more of the burn and increased time spent in the burn (Gasaway et al. 1989).

Early winter male:100 female ratios among moose  $\geq 1$  year old averaged 31.9 during 2000–2015 (SE = 1.13, range = 23–38; Young 2014, 2017) in Game Management Unit 20A, and were sufficient to ensure synchronous breeding of females during the first estrous (Schwartz 2007). A selective male harvest strategy was implemented beginning in 2002 to protect the age structure of the male population and ensure continued breeding by mature male moose, although limited any-male harvests were occasionally allowed (Young and Boertje 2008, Young 2014). The selective harvest strategy largely protected males 2–4 years of age by restricting harvest to male moose with: 1) spike-fork antlers, 2) antlers  $\geq 127$  cm wide, or 3)  $\geq 3$  brow tines on  $\geq 1$  antler (Schwartz et al. 1992, Young and Boertje 2018).

#### METHODS

#### **Moose Capture**

We captured and radio-collared female moose 9-10 months of age from 7 cohorts (1996–2002) during a 3- to 6-day period each March (range = 3-20 Mar) using procedures detailed by Boertje et al. (2007). In brief, we flew in a helicopter to dart and immobilize moose with carfentanil citrate and xylazine hydrochloride. We identified moose 9-10 months of age prior to capture based on body size, behavior, pelage, and face length; we verified age by assessing tooth eruption (Peterson et al. 1983). We recaptured radio-collared moose at 4-6 and 9-11 years of age in late February or March to renew radio-collars using immobilization procedures described by

Keech et al. (2000). Our final deployed radio-collars transmitted for 10 years (Model 605-NH transmitters on CB-8 collars, Telonics, Mesa, AZ, USA), so we did not immobilize moose >11.8 years of age. We did not administer systemic antibiotics. All aspects of this research were in accordance with acceptable methods for field studies adopted by the American Society of Mammalogists (Institutional Animal Care and Use Committee 1998, Alaska Department of Fish and Game Protocol #04-003).

### **Data Collection**

To monitor individual reproduction, we radio-tracked female moose 2–18 years of age via Piper PA-18 aircraft to detect newborns every 24 (1998) or 48 hours (1999–2018) from 11 May through mid-June (Boertje et al. 2007). We could discern most birth sites from the matting and scraping of vegetation that occurred during parturition. We excluded stillborn or nonviable calves (n = 8) from our analyses and treated the associated adult females as neither parturient nor barren.

To evaluate trend in population-wide twinning rates, we flew 1- or 2-day aerial transect surveys in Piper PA-18 or Bellanca Scout aircraft throughout the study area during 20–29 May, 2000–2018. We used no radio-telemetry. Both an observer and pilot searched for newborns; the pilot circled the plane over each litter to determine number of newborns. We flew each survey a few days after the median calving date for the respective year (Boertje et al. 2007). The median calving date was the date when 50% of the radio-collared females had given birth. During test flights on or before the median calving date, we often observed insufficient numbers of parturient females. Our objective was to observe  $\geq$ 50 parturient females. To help determine median calving dates during the early and late years of the study when our sample size of known-age radio-collared females was low, we monitored calving dates from 30–50 adult radio-

collared females from companion studies in the central and western Tanana Flats (Keech et al. 2000, Boertje et al. 2007, Frye 2017).

We estimated moose population numbers in Game Management Unit 20A using early winter aerial surveys with sightability correction factors. Boertje et al. (2009) and Young (2014, 2017) described the methods.

### **Data Analysis**

To examine the trend in parturition rates as a function of age (2–17 yr), we fit mixed-effects binary logistic regression models with age as a continuous covariate. Our response was a Bernoulli random variable indicating that parturition had occurred (1) or not occurred (0) for each radio-collared female during each year of the study. We included a quadratic term to allow flexibility in the relationship between age and parturition and to accommodate the functional form of age-specific reproduction anticipated from theory (i.e., reproductive output increasing early in life and decreasing late in life; Emlen 1970, Gaillard et al. 2017). We included a random intercept for individual in each model to account for repeat observations of the same individuals among years.

In the above modeling and in 5 similar modeling exercises below, we fit the mixedeffects binary logistic regression models in the R software environment (R Core Team 2017) with the package lme4 (Bates et al. 2015), and we generated associated plots with the R package ggplot2 (Wickham 2009). We obtained maximum likelihood estimates for parameters in generalized linear mixed models using adaptive Gauss-Hermite quadrature with 20 integration nodes, and we treated the random intercepts as a single estimable parameter in AIC calculations. We interpreted parameter estimates from logistic regression models as odds ratios (Hosmer and Lemeshow 2000), and we estimated confidence intervals for predicted probabilities via parametric bootstrapping with the aid of R packages boot (Canty and Ripley 2017) and lme4 (Bates et al. 2015). We calculated Wilson score intervals (Wilson 1927) using the R package binom (Dorai-Raj 2014).

We used the above model to address hypotheses about the effect of the preceding February or March chemical immobilization, cohort affiliation, the preceding winter's snow cover, and the duration of the preceding year's SFD on the probability of a female being parturient. We included these as fixed effects along with age, and compared models using Akaike's information criterion (AIC; Akaike 1973, Burnham and Anderson 2002). We treated capture as a binary covariate, which indicated that an adult female had been immobilized (1) or had not been immobilized (0) during the February or March preceding parturition. We treated cohort affiliation as a categorical covariate with 7 levels, representing each of the 7 cohorts in the study (1996–2002).

We quantified snow cover as an index by plotting curves from snow depth measurements during the winter preceding parturition; snow depth was recorded the first and fifteenth day of each month for which a snow depth >2.54 cm was present. We calculated the area under each winter's curve as the snow cover index (Gasaway et al. 1983) using numerical integration in the R package pracma (Borchers 2017). SFD was the number of days with snow cover <2.54 cm during the year preceding parturition. The National Oceanic and Atmospheric Administration (2017) provided snow data from the Fairbanks International Airport, Alaska, USA, which was located <1 km from the northern boundary of the study area.

In addition to modeling parturition probability as a function of age, we examined the trend in parturition rates as a function of year (2000–2014). We fit a mixed-effects binary logistic regression model and again treated parturition as a Bernoulli random variable (1 = a parturient F,

0 = a nonparturient F). We treated year as a continuous covariate and included a random intercept for individual to account for repeat observations of the same individuals among years. Based on results from the age-specific parturition model, we included SFD as a covariate in this model. We estimated the autocorrelation and partial autocorrelation (Venables and Ripley 2002) over time and found no evidence for significant temporal correlation structure. We plotted predicted values along with the observed proportions of parturient females in each year of the year–trend model. We used Wilson 95% score intervals to depict binomial uncertainty in the observed annual rates. To examine the possibility that parturition date varies with age, we also fit a linear mixed model with parturition date as a function of age, number of calves, and a random intercept for individual.

To describe the trend in twinning rates with age, we fit a mixed-effects binary logistic regression model and treated twinning as a Bernoulli random variable (1 = a parturient F with twins, 0 = a parturient F with a single calf). We included only parturient females in the twinning model. We treated age as a continuous covariate with a quadratic term, and we included a random intercept for individual in the model to account for repeat observations of the same individuals among years. As with the age-specific parturition models, we used this model to address hypotheses about the effect of the preceding February or March chemical immobilization, cohort affiliation, the preceding winter's snow cover, and the duration of the preceding year's SFD on the probability of a female giving birth to twins. We also addressed the hypothesis that parturition date affected twinning probability. We included these covariates as fixed effects along with age and used AIC to compare models. We plotted predicted values from the final model along with observed proportions of parturient females with twins in each age

class. We used Wilson 95% score intervals to depict binomial uncertainty in the observed annual rates.

In addition to trends in parturition rate (p) and twinning rate (t) for radio-collared females, we examined the trend in production rate (number of calves born/F-vr =  $p \times (1+t)$ ; Boertje et al. 2009) with age. We fit a generalized linear mixed-effects model with Tweedie response distribution (Tweedie 1984) and number of offspring as the response. We estimated the exponential parameter for the Tweedie distribution with the constraint that it fell between 1 and 2 (i.e., a compound Poisson-gamma distribution). As previously, we included a random intercept for individual in the model to account for repeat observations of the same individuals among years. Because we found an effect of SFD on parturition, we included this effect as a covariate in the production model. We computed observed production rates for radio-collared females in each age class by summing the number of offspring produced by a given age class and dividing by the number of females in that age class. We plotted predicted curves along with observed production rates for each age class. We estimated confidence intervals for each observed rate via nonparametric bootstrapping. We fit the generalized linear mixed-effects model in the in the R software environment with the package cplm (Zhang 2013) and we generated associated plots with the R package ggplot2. We obtained maximum likelihood estimates for parameters in generalized linear mixed models using adaptive Gauss-Hermite quadrature with 20 integration nodes, and we treated the random intercepts as a single estimable parameter in AIC calculations. We calculated Wilson score intervals using the R package binom.

To assess the effect of reproductive pauses on subsequent parturition, we fit a mixedeffects binary logistic regression model and again treated parturition as a binary response (1 = aparturient F, 0 = a nonparturient F). We treated age as a continuous covariate, which ranged from

the year following the earliest age of first parturition through the end of life (4–17 yr) and included a quadratic term for age. We treated parturition during the previous year as a binary covariate and then compared a model with an additive relationship between age and previous parturition to a model with an interaction between age and previous parturition. We included SFD as a continuous covariate because of the residual variation in parturition probability explained by SFD.

Similarly, to assess the effect of reproductive pauses on subsequent twinning, we fit a mixed-effects binary logistic regression model and treated twinning as a binary response (1 = a) parturient female with twins, 0 = a parturient female with a singleton). We treated age as a continuous covariate, which ranged from the year prior to the earliest age at first twinning through the latest age at which twinning was observed (5-15 yr) and included a quadratic term for age. We treated parturition during the previous year as a binary covariate and then compared a model with an additive relationship between age and previous parturition to a model with an interaction between age and previous parturition. We included parturition date as a continuous covariate because it was identified as important in the previous twinning model.

To examine the effect of delaying initial parturition on lifetime reproductive success, we first used the subset of our data that included females that survived  $\geq 12$  years of age, and for which we had complete reproductive histories, following Schwartz (1992). Of these females we compared lifetime reproduction of those that first gave birth at age 3 (n = 12) to those that first gave birth at age 4 or 5 (n = 29). We used a Wilcoxon rank sum test to assess the difference in central tendency between groups. Additionally, we conducted a Wilcoxon rank sum test on these groups using lifetime reproduction scaled by the number of potential reproductive years (i.e., number of newborns produced/number of yr from age 3 until death). We estimated the

differences between group location parameters (pseudo-medians) and associated 95% confidence intervals using the Hodges-Lehmann estimator ( $\Delta$ ; Hodges and Lehmann 1963, Bauer 1972). We then repeated this analysis using females that survived  $\geq$ 3 years of age for which we had complete reproductive histories, regardless of life span. For this  $\geq$ 3-year-old analysis, we censored females that died from anthropogenic causes (primarily hunting) and those with failed radios. We conducted Wilcoxon rank sum tests and calculated Hodges-Lehman estimators in the R software environment.

We examined the trend in population-wide twinning rates by fitting a binary logistic regression model to the annual results. We treated twinning as a Bernoulli random variable (1 = a parturient F with twins, 0 = a parturient F with a single calf) and year (2000–2017) as a continuous covariate. We used autocorrelation functions and partial autocorrelation functions (Venables and Ripley 2002) to check for temporal dependence between consecutive years and found no substantial autocorrelation in this time series. We plotted the fitted curve from the model along with observed proportions of parturient females with twins in each year, and we used Wilson 95% score intervals to depict binomial uncertainty in the observed annual rates.

To compare twinning rates from the population-wide versus the radio-collared samples, we fit an additional mixed-effects binary logistic regression model with 1) twinning as a binary response, 2) a binary covariate indicating whether an individual was in the population-wide or radio-collared sample, and 3) partially crossed random effects for individual and year. We used AIC to compare the fitted models and to assess whether twinning estimates were affected by the type of sample used (i.e., population-wide vs. radio-collared sample).

# RESULTS

We radio-collared 229 females 9–10 months of age in March (34–42 during 1997–2001, 22 in 2002, 11 in 2003); 144 females attained 3 years of age, the minimum age of reproduction. Capture-related mortalities totaled 5% when radio-collaring 229 females 9–10 months of age and 2% when recollaring 173 females 4–11 years of age in February or March.

We accomplished 90% of flights to detect newborns at  $\leq$ 48-hour intervals and 98% at  $\leq$ 72-hour intervals, with missed flights almost exclusively late in the calving season when new births were infrequent. It is unlikely that we missed many successful births, because we evaluated parturition status of radio-collared females on 98% of attempts. Failed attempts resulted from poor reception of a few radio signals and poor sightability, primarily after leaf emergence.

# Effects of Immobilizations, Cohort Affiliation, Snow, and Parturition Date on Moose Reproduction

We found no evidence for an effect of February or March immobilizations on subsequent May– June parturition or twinning rates (Tables 1 and 2). The parturition rate of recently immobilized females was 77.4% (n = 146 F-yr) versus 76.0% (n = 517 F-yr) among those not recently immobilized. Similarly, the twinning rate of females recently immobilized was 8.0% (n = 113 F– yr) versus 8.4% (n = 393 F–yr) among those not recently immobilized. Also, we found no evidence for effects of cohort affiliation or the preceding winter's snow cover on the probability of a female calving or twinning (Tables 1 and 2).

The number of SFD improved the parturition model, so we used the model with age and SFD as the basis for inference (Table 1). SFD had a subtle positive effect on parturition probability within the range of values observed during this study (154–204 days). An increase in

SFD of 10 days resulted in an estimated increase in the odds of giving birth by 12% (95% CI = 1-28%), while holding age constant. We found no evidence for an effect of SFD on twinning (Table 2). However, we did find evidence for an effect of parturition date on the probability of twinning (Fig. 1, Table 2). The odds of twinning decreased by 14% (95% CI: 7-20%) for every day elapsed between 11 May and 17 June, which is a cumulative decrease of 78% (95% CI = 52-89%) over a 10-day period.

### **Reproduction among Radio-collared Females**

The median calving date for all parturient females was 22 May (Fig. 2). Annual median calving dates from 2000 to 2014 (i.e., yr for which  $\geq$ 8 parturient F were sampled) ranged from 20 May to 27 May. The earliest and latest documented birth dates among radio-collared females were 11 May and 17 June, respectively. Our model of parturition date as a function of age suggested that parturition occurred 0.25 days (95% CI: 0.13–0.40) later for every year of age beyond 3 years. However, given the small magnitude of this effect relative to the observed variation in parturition dates during 2000–2014, we did not infer a biologically meaningful relationship between age and parturition date.

The mean of observed annual parturition rates was 74% (range = 53–90%) during 2000–2014 among females  $\geq$ 4 years of age; annual rates often fluctuated between consecutive years (Fig. 3). Also, young and old age moose slightly reduced the annual parturition rates in the 2 earliest years and 2 latest years of the 2000–2014 timespan (Fig. 3); the corresponding mean of observed annual parturition rates during 2002–2012 was 78% (range = 62–90%).

Age-specific parturition rates were relatively consistent from 4 to 13 years of age ( $\bar{x} =$  77%; Fig. 4). After age 13, observed age-specific rates were more variable; 56% among 14-year-olds and 92% among 15-year-olds. The 15-year-old sample (n = 13) originated from all 7

cohorts. Only 1 of 3 16-year-old moose gave birth, and the single 17-year-old moose did not give birth but did at 18 years of age in 2018. We recorded a 28% parturition rate among 144 females 3 years of age and a 69% parturition rate among all moose sampled  $\geq$ 3 years of age (n = 1,015 Fyr). We sampled 2-year-old moose only during 1998–1999 and 0 of 36 were parturient. We observed 703 birth sites where radio-collared females gave birth to apparently viable newborns; we also observed 6 newborn singletons dead at birth, 1 dwarf nonviable twin, and 1 breached birth in which the female and calf died. Given the rarity of dead newborns, including versus excluding the dead newborns in the analyses did not noticeably alter results.

The mean of annual twinning rates from parturient radio-collared females was 7% (range = 5–10%) during 2003–2010; these were the sample years when twinning rates were not biased by young and old age classes and when samples totaled 39–79 ( $\bar{x} = 58$ ) parturient radio-collared females  $\geq$ 4 years of age. Because observed twinning rates increased with age (Fig. 5) and our annual samples included aging radio-collared females, we did not depict twinning rates of radio-collared moose over time.

Radio-collared females first produced twins at 5 years of age (5% twinning rate, n = 77). The observed twinning rate largely increased from 5 to 13 years of age and peaked at 26% (n = 28; Fig. 5). No 14-year-old females produced twins (n = 15). Twinning resumed at 15 years of age (17% twinning rate, n = 12) but was not observed in older females (Fig. 5). The mean twinning rate was 9% among parturient females 5–15 years of age (n = 561 F-yr) and 7% among those  $\geq 3$  years of age (n = 703 F-yr).

The mean annual production rate was 80% (range = 0.53-1.06 calves/number of F  $\geq$ 4 yr of age) during 2000–2014. Females  $\geq$ 3 years of age (n = 1,015 F-yr) experienced a production rate of 74% during this study, and females  $\geq$ 4 years of age (n = 871 F-yr) experienced a

production rate of 82%. Given nearly stable age-specific parturition rates and increasing agespecific twinning rates, observed production rates increased slightly from 5 to 10 years of age (Fig. 6). At ages >10 years, observed production rates were more variable, but suggested a decreasing trend (Fig. 6). A notable deviation from the pattern was the high 15-year-old production rate, because the 15-year-old age class experienced a relatively high parturition rate (92%) and twinning rate (17%).

Lifetime production for females that lived  $\geq 12$  years, scaled by number of years in the reproductive population, was greater for primiparous 3-year-olds, compared with primiparous 4- or 5-year-olds (W = 85, P = 0.01, Fig. 7). The Hodges-Lehmann estimator suggested that females primiparous at age 3 produced 0.17 (95% CI = 0.03–0.30) more calves/year than those primiparous at age 4 or 5. Using observed data over lifetimes of  $\geq 12$  years, primiparous 3-year-olds produced a mean of 0.91 calves/year (SE = 0.062, n = 12 F) versus 0.77 calves/year (SE = 0.034, n = 26 F) for primiparous 4-year-olds and 0.59 calves/year (SE = 0.580, n = 3 F) for primiparous 5-year-olds. The Hodges-Lehmann estimator suggested that primiparous 3-year-olds produced 2.0 (95% CI: 1.0–4.0) more calves than primiparous 4- or 5-year-olds.

Results were similar when comparing lifetime reproductive success without restricting the analysis to females with life spans  $\geq 12$  years. Lifetime production scaled by number of years in the reproductive population was greater for primiparous 3-year-olds compared with primiparous 4- or 5-year-olds (W = 251.5, P = 0.002, Fig. 7). The Hodges-Lehmann estimator suggested that primiparous 3-year-olds produced 0.16 (95% CI = 0.07–0.26) more calves/year than primiparous 4- or 5-year-olds. In terms of total reproductive output, primiparous 3-year-olds produced 2.0 (95% CI = 0.04–3.0) more calves over a lifetime than primiparous 4- or 5-yearolds. Average lifetime production rates were similar among the 6 cohorts with the largest sample sizes (n = 16-25 3-yr-olds, 1996–2001 cohorts). Those cohorts produced a mean of 4.6–5.9 calves/lifetime when monitored a mean of 6.1–7.9 years at ages of  $\geq$ 3 years. Overall, 136 radio-collared females with complete reproductive histories produced a mean of 5.3 calves/lifetime when monitored a mean of 7.1 years at ages of  $\geq$ 3 years.

# **Delaying or Pausing Reproduction**

Delaying or pausing reproduction was a mechanism that ensured a higher birth rate in the subsequent year (Fig. 8). Among 4- to 15-year-olds, 90% calved after a reproductive pause (n =270 F-yr) compared to a parturition rate of 70% among females that had calved the previous year (n = 576 F-yr). The model that included an interaction between age and previous reproduction (AIC = 857.1) was better supported by the data than the model treating these terms as additive (AIC = 862.0) or the model that excluded the previous reproduction term (AIC = 938.6). The interaction model indicated that the effect of previous reproduction was strongest among young females (Fig. 8). For example, 91% (95% CI: 83–95%) of primiparous 4-year-olds calved (n =89) versus only 47% (95% CI: 32–63%) of 4-year-olds that had calved the previous year (n =38). The difference in parturition probability between moose that had and had not given birth the previous year was less for moose  $\geq 6$  years of age than for those 4 and 5 years of age (Fig. 8). Despite the decreased magnitude of these differences with age, observed parturition rates were higher for previously nonparturient moose than previously parturient moose within all age classes for which comparisons were possible, with the exception of females 15 years of age (Fig. 8). However, substantial overlap of confidence intervals for moose  $\geq 10$  years of age resulted from smaller differences in point estimates and smaller sample sizes.

Females 5–15 years of age were more likely to pause the year prior to giving birth to twins versus singletons; 44% of females paused in the year prior to a twin litter (n = 50 F-yr) versus 30% prior to a singleton litter (n = 459 F-yr). In contrast, females were regularly parturient the year after producing twins (68%, n = 40 F-yr) or singletons (73%, n = 382 F-yr). Only 2 females had twins in consecutive years; the females were initially 9 years of age and from different cohorts. The model of twinning that included previous parturition as an additive term (AIC = 313.9) was better supported by the data than the model treating previous parturition as an interaction with age (AIC = 316.9) or the model without the previous parturition term (AIC = 316.0). After accounting for the effects of age and parturition date, a reproductive pause increased the odds of a parturient female giving birth to twins by 212%; however, the precision of this estimated increase was low (95% CI: 10–466%).

Virtually all sampled moose regularly gave birth at  $\geq 3$  years of age with only occasional single-year pauses. We observed only 24 cases of 2 consecutive nonparturient years (n = 21 F) among 844 cases of 2 consecutive years of potential births (n = 137 F), so the incidence of 2 consecutive nonparturient years was 2.8%. In 8 of these 24 cases, females delayed reproduction until 5 years of age, and in 7 cases females were  $\geq 10$  years of age. In addition, we observed only 2 cases of 3 consecutive nonparturient years (n = 2 F) among 708 cases of 3 consecutive years of potential births (n = 123 F), so the incidence of 3 consecutive nonparturient years was 0.3%. One of these 2 nonparturient females was recovering from a severe neck wound.

### **Population-wide Twinning Rates from Annual Aerial Transect Surveys**

We relied on twinning rates from annual population-wide aerial May transect surveys to describe twinning rates and nutritional status over time (Fig. 9), because the earliest and latest years of sampling radio-collared females for twins were biased by young and old radio-collared females

(Fig. 5). To test for potentially low twinning rates during the population-wide surveys, from possible interim increased calf mortality, we compared the population-wide and radio-collared data sets during 2003–2010, when we had adequate samples of radio-collared parturient females not biased by young and old ages. The respective mean annual population-wide twinning rate was 8%, which was similar to the 7% mean annual twinning rate from the unbiased radio-collared samples. Likewise, our comparative twinning models, which accounted for repeated measures of individuals and unmodeled annual variation, indicated no difference in twinning probability between the population-wide and radio-collared samples during 2003–2010 or 2003–2013. The model with an indicator variable, representing the respective sample, was not as well supported by the data (AIC = 340.5) as an intercept-only model (AIC = 338.5), indicating that this covariate was noninformative. Thus, population-wide twinning surveys did not appear biased by early mortality of calves.

During 2000–2014, annual population-wide, transect surveys indicated stable, low twinning rates ( $\bar{x} = 9\%$ , range = 3–11%), with the exception of an anomalously high rate (22%) during 2012 (Fig. 9). We inferred a largely stable, low nutritional status in the population during 2000–2014. Stable, low population-wide twinning rates also provided evidence for a stable age structure. In addition to 2012, we recorded elevated twinning rates from population-wide surveys in 2015 (23%), 2017 (16%), and 2018 (16%), indicating an improving nutritional status in the final years of the study, when moose numbers had declined to the lowest levels (Fig. 9) and sample sizes of radio-collared parturient moose were too small to be relevant (n = 8 in 2015 and  $n = \le 2$  in 2017 and 2018).

### DISCUSSION

Our study and 2 former studies reported no effect on moose reproduction subsequent to immobilization (Feb–Apr) after darting from helicopters with carfentanil citrate and xylazine hydrochloride (Larsen and Gauthier 1989, Lowe and Aderman 2014). In both former studies, moose reproductive rates were high compared with results reported here. Similarly, Neumann et al. (2011) found no long-term impacts of chemical immobilization on moose activity patterns. We recommend continued use of these capture and collaring methods to study moose population dynamics, at least among moose 4–11 years of age (i.e., the ages at which we recaptured F). In contrast, Côté et al. (1998) found negative effects of chemical immobilization on reproduction in mountain goats (*Oreannos americanus*). These contrasting results underscore the importance of making species-specific and method-specific assessments about the impacts of chemical immobilization on study populations.

The lack of an effect of cohort affiliation on parturition probability suggests that females in the study experienced similar conditions or were able to buffer against environmental variation, regardless of when they entered the study. Extreme snow cover conditions have been found to affect spring condition of moose in our study area, particularly with snow depths >90 cm (Coady 1974, Gasaway et al. 1983, Boertje et al. 1996). Repetitive deep snow cover for several winters also adversely affected nutritional condition and reproduction of moose in Minnesota (Mech et al. 1987, McRoberts et al. 1995). The lack of effect of the preceding year's snow cover on parturition probability during our study suggested that reproduction was unaffected within the range of observed winter snow conditions. Snow depths were <90 cm during our study (1998–2017) and the range of relevant snow index values was only 1.3–2.8 versus 3.1–5.3 during previous severe winters (Gasaway et al. 1983, Boertje et al. 1996).

We tested for the effect of the snow-free period on the subsequent year's parturition probability because the duration of the snow-free period had a strong effect on caribou (*Rangifer tarandus*) parturition rate across North America after the relatively short period of SFD during 1992, caused by the eruption of Mount Pinatubo in April and May of 1991 (Bergerud et al. 2008; Boertje et al. 2012, 2017). Compared with the response in caribou, moose in the central Tanana Flats exhibited a much subtler response to the short period of SFD in 1992, e.g., a 0% 1993 twinning rate, yet normal early winter 1993 recruitment (42 calves:100 F  $\geq$ 28 months of age; Boertje et al. 1996). During 1992, SFD totaled only 126 compared to a range of 154–204 ( $\bar{x} =$ 174.9, SD = 10.54) in years relevant to this study (1997–2016).

In previous Alaska studies, mean parturition dates were found to be slightly earlier for moose giving birth to twins versus singletons (Bowyer et al. 1998, Boertje et al. 2007). However, to our knowledge, a substantial declining trend in twinning probability with parturition date has not been previously described. This pattern has implications for monitoring population-wide moose twinning rates. We recommend consistent timing of twinning surveys a few days after the respective median calving dates for accurate comparisons within or between populations over time. When the median calving date is unknown, we recommend that surveys be flown later rather than earlier because early surveys have resulted in inadequate sample sizes and because twinning rates decline after early calving. We conclude that the reliability of twinning surveys will depend on survey timing and the magnitude of early calf mortality. Sigouin et al. (1997), Bowyer et al. (1998), and Keech et al. (2011) summarized data on the timing and synchrony of moose calving from 6 other Alaska and Yukon (Canada) moose populations. Timing of calving in our study was earlier or similar to observations reported elsewhere, and synchrony of calving was similar among studies. Predation was the major cause of calf mortality in our study area.

Bears killed all 5 of the 81 radio-collared newborns that died during the first 3–9 days of life, and no calves died in the first 2 days of life (Keech et al. 2000; M. A. Keech, Alaska Department of Fish and Game, unpublished data).

Compared with moose production in populations with improved nutrition (Boertje et al. 2007, Schwartz 2007), our study population experienced low production primarily as a result of delayed maturation, occasional pauses in reproduction, and low twinning rates, rather than early reproductive senescence. For example, our finding of moose reproductive senescence at 14 years of age was similar to that reported in several studies of moose with improved nutrition. Heard et al. (1997), Ericsson et al. (2001), and Schwartz (2007) reported moose reproductive senescence beginning at 13–14 years of age. Our observed rebound in parturition and twinning rates at 15 years of age was also reported in a Southwest Alaska study, which reported the highest moose nutritional status in Alaska (Lowe and Aderman 2014); however, in that study observed parturition rates began to decline at 12 years of age and sample sizes were relatively small.

Ericsson et al. (2001) provided evidence for reproductive senescence in moose. In our study, the elevated reproductive rates for 15-year-old females (n = 13) and the small number of moose surviving beyond age 15 (n = 3) resulted in high uncertainty in observed rates for the oldest age classes (Figs. 4–6). Given the small number of females surviving to reproductively senescent ages, we conclude that reproductive senescence played a minor role in population dynamics. Liberalized harvest of female moose was an important additive factor affecting moose longevity in this study (Boertje et al. 2009, Young 2014). Although our data are from a long-term longitudinal study, we did not explicitly seek to disentangle between-individual from within-individual processes underlying senescence (Nussey et al. 2008). Our results should be interpreted as changes in population-level reproductive rates with age, which may not reflect

patterns in individual-level physiological senescence (Vaupel and Yashin 1985, Gaillard et al. 2000). Moreover, age-specific estimates are conditional on survival to each age class, and covariation between survival and reproduction at the individual level may obscure patterns of senescence within populations (Cam et al. 2002).

Potential contributing factors for the unexpected elevated 15-year-old production rate in this nutritionally stressed population included increased reproductive capability following a notable pause at 14 years of age (Figs. 4–6), delayed maturation (Boertje et al. 2007), relatively few calves produced/lifetime (Fig. 7; Schwartz 2007), terminal investment in reproduction (Gadgil and Bossert 1970, Pianka and Parker 1975, Clutton-Brock 1984), terminal allocation to reproduction (Weladji et al. 2010), and selective disappearance of low-quality individuals with age (Hamel et al. 2009). These potential mechanisms do not contradict the apparent pattern of reproductive senescence in our study, as reproductive senescence can co-occur with processes that increase reproductive output at older ages (Weladji et al. 2010, Hamel et al. 2012, Gaillard et al. 2017).

We examined several hypotheses that were tested for ungulates elsewhere. Sæther and Haagenrud (1983) rejected the hypothesis that delaying puberty for a year would benefit the subsequent year's reproductive rate in moose, e.g., they concluded that primiparous 4-year-old females would have similar reproductive rates compared with 4-year-old females that were primiparous at 3 years of age. Although ages of puberty differed among populations, Davis et al. (1991) and Boertje et al. (2017) found similar results for caribou, as did Festa-Bianchet (1989) for bighorn sheep (*Ovis canadensis*), and Richard et al. (2017) for Pyrenean chamois (*Rupicapra pyrenaica pyrenaica*). However, our data provide support for this hypothesis; primiparous 4-year-old moose (n = 89) had a parturition probability of 91% (95% CI = 83–95%) versus 47%

(95% CI = 32–63%) among 4-year-olds primiparous at 3 years of age (n = 38). We surmised that greater support for this hypothesis may occur where ungulates are relatively nutritionally stressed, as concluded by Clutton-Brock et al. (1983) for red deer (*Cervus elaphus*) and Hamel et al. (2010) for mountain goats. More generally, Stearns (1992) hypothesized that poor environmental conditions should increase the cost of reproduction in iteroparous organisms. In our study, nutritional stress was evident, e.g., age of first reproduction was delayed to 3 years of age, compared to 2 years of age in most studies of moose (Boertje et al. 2007, Schwartz 2007).

Clutton-Brock et al. (1983) reported that 4- to 6-year-old and  $\geq$ 14-year-old red deer females were most likely to show reduced fecundity the year following successful reproduction, compared with 7- to 13-year-old females. Our results were similar; 4- to 5-year-old and 14-yearold moose showed reduced fecundity following successful reproduction (Fig. 8). In both studies, females that had not reproduced in the previous year produced relatively high parturition rates for all reproductive age classes through age 14 (Fig. 8). Clutton-Brock et al. (1983) argued that the costs of reproduction in ungulates should be measured in terms of effects upon subsequent reproductive success, particularly in long-term studies where changing environmental factors may contribute to better understanding. We concur. However, Hamel et al. (2012) found that reproductive costs in bison (*Bison bison*) were manifested in lower calf weights in years following reproduction, but not in lower probability of reproducing.

Sæther and Haagenrud (1983) rejected the hypothesis that the lowest moose production rate would be found the year following twinning. We concur with this rejection; instead, we found a low parturition rate of 56% the year prior to producing twins versus 74% the year following twinning. We surmised that adult females benefitted from a pause in production that favored twinning, and that low survival of either twin or both twins favored production rates the year following twinning. Keech et al. (2000) documented lower annual survival of twins versus singletons in our study area, and a 53% annual calf survival rate after radio-collaring 81 newborns during 1996–1997.

Lactation costs can reduce subsequent reproduction, particularly where nutritional status is low. For example, Testa and Adams (1998) reported lowered pregnancy rates among female moose accompanied by a calf in early winter, and moose nutritional status ranked low in their study area (Boertje et al. 2007). Also, Swenson et al. (2007) reported that female moose that lost young calves produced more calves the following year compared with moose that retained calves. In contrast, Sand (1998) found no effect of lactation to autumn on the next year's parturition rate, although the current year's twinning rate affected the next year's parturition rate. We had hoped to measure the effects of retaining calves for a year on subsequent individual production rates by noting yearling offspring associations with radio-collared females each May. However, after examining annual association data from paired radio-collared newborns of radiocollared adult females (Keech et al. 2000), we found that several surviving yearlings were no longer associated with their adult females in May. In other cases, radio-collared offspring had not survived to 11 months of age, yet their adult radio-collared females were in close, regular association with unrelated yearlings.

Thus, we had no reliable data on the survival of calves of our known-age radio-collared females to assess costs of raising a calf. However, Keech et al. (2000) and Boertje et al. (2009) detailed causes of mortality and relatively high rates of survival among radio-collared newborn calves born in our study area. Because most calf mortality occurred in spring and summer, early winter calf:older female ratios could be an index to the relative added costs of raising a calf. For example, mean early winter calf:100 older female ratios of 30.6 (SE = 0.91, range = 26-36)

during 2000–2014 indicated similar to slightly higher calf:older female ratios and therefore lactation costs in our study area compared with much of Alaska where reproductive rates were higher (Boertje et al. 2007, 2009; Harper and McCarthy 2014; Young 2014). We surmised that lactation costs were likely not substantially inhibiting reproduction in our study area but contributed to some minor degree to moose nutritional stress. Overused browse from documented high browse rates was clearly an additional and likely primary factor reducing reproductive metrics and body weights in our study area (Boertje et al. 2007, Paragi et al. 2015).

Our findings were not consistent with Schwartz's (2007) general hypothesis that delaying first reproduction for an extra year enhances lifetime birth rates. Schwartz (1992) provided the only previous data (n = 7 captive F moose with lifetimes of  $\geq 12$  yr); 4 females primiparous at 2 years of age produced 1.5 calves/year versus 1.9 calves/year for 3 females primiparous at 3 years of age. In contrast, we concluded that lifetime ( $\geq 12$  yr) reproductive performance was greater for females primiparous at 3 years of age (0.92 calves/yr) than for those primiparous at 4 or 5 years of age (0.74 calves/yr; Fig. 7). Similarly, when considering females with lifetimes of  $\geq 3$  years, those primiparous at age 3 had greater reproductive success (0.89 calves/yr) than those that delayed reproduction until ages 4 or 5 (0.72 calves/yr). These results suggest that early primiparity is a strategy that can increase lifetime reproductive success in moose, regardless of lifespan. In contrast, cumulative costs of early reproduction have been found to decrease late-life reproductive performance in some birds (Orell and Belda 2002, Aubry et al. 2009).

Total lifetime production varied substantially among individuals (range: 5–14 calves in a lifetime  $\geq$ 12 yr), indicating fundamental differences in individual reproductive potential. Although mean lifetime production was only 5.3 calves among moose  $\geq$ 3 years of age, some individuals produced 2–3 times that number of calves. Individual reproductive heterogeneity has

potential implications for the dynamics of vertebrate populations (Johnson et al. 1986, Lebreton 2005), and may play an important role in maintaining population-level production rates when reproduction is nutritionally limited.

Given a gradual 31% intentional, managed reduction in moose numbers in our study area and adjacent areas from 2003 to 2012 (Fig. 9; Young 2014), stakeholders anticipated that twinning rates would simultaneously gradually recover to elevated levels of 15–22% common during 1989–1996 (Boertje et al. 2007). Instead we saw recovered twinning rates (16–23%) in the latter part of this study during 2012, 2015, 2017, and 2018 following a 15-year period (1997– 2011) of lower rates (3–11%,  $\bar{x} = 7\%$ ; Fig. 9, Boertje et al. 2007). Apparently, stakeholders should not necessarily expect an immediate or consistent increase in moose reproductive metrics simultaneous to gradual decreases in moose density (Fig. 9; Blood 1974). Factors contributing to a lack of short-term response in moose nutrition in our study area included carry-over effects from a history of long-term, elevated moose densities (Boertje et al. 1996, 2007) with excessive browsing that favored nonbrowse species (e.g., *Alnus* spp.; Butler et al. 2007), and possibly the immediate reduction in browse for a few growing seasons after recent wildfires (Young 2014, Paragi et al. 2015).

Moose managers can now better describe and discuss with empowered stakeholders the lower age-specific, lifetime reproductive metrics associated with low moose nutrition, and managers should have a more convincing position when attempting to temporarily increase annual harvests of female moose to improve moose nutrition or maintain an improved moose nutritional status. Our managed 5,000 reduction in moose numbers with initial signs of improving nutrition (Fig. 9) was clearly more responsive and responsible management compared with enduring the consequences of a 20,000 decline in moose numbers from overabundance, as documented in the same area during 1965–1975 (Gasaway et al. 1983).

### MANAGEMENT IMPLICATIONS

When managers are faced with increasing ungulate densities or already high densities, we recommend continuous monitoring of reproductive metrics for several consecutive years, because metrics fluctuated between years at low and improving nutritional status. In our study, population-wide twinning surveys provided the most cost-effective data indicating overabundance. In lieu of twinning surveys, relatively low or declining production rates from age-specific primiparous females and the subsequent year's production rate are likely to provide the most convincing data to help spur action to manage for moderate, sustainable ungulate densities.

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Associate Editor:

### **FIGURE CAPTIONS**

Figure 1. Relationship between the probability of moose twinning and parturition date during 1999–2017, central Tanana Flats, Alaska, USA. Females were 3–17 years of age initially radiocollared at 9–10 months of age (cohorts 1996–2002, n = 51 twin births among 703 parturient Fyr). Data are from aerial radio-tracking flights at 48-hour intervals from 11 May to mid-June. Probabilities were predicted from a mixed-effects binary logistic regression model. Fitted curves are depicted for age classes that were observed producing twins. Gray bars represent the proportion of parturient moose observed producing twins during 5-day periods throughout the parturition season.

Figure 2. Frequency distribution of parturition dates (non-leap yr dates) during 1999–2017 of known-age radio-collared female moose 3–17 years of age (cohorts 1996–2002, n = 703 F-yr), central Tanana Flats, Alaska, USA. Data are from aerial radio-tracking flights at 48-hour intervals from 11 May to mid-June. The dashed line represents the overall median calving date of 22 May.

Figure 3. Annual moose parturition rates during 2000–2014 of female moose 4–17 years of age initially radio-collared at 9–10 months of age (cohorts 1996–2002, n = 854 F-yr), central Tanana Flats, Alaska, USA. Data are from aerial radio-tracking flights at 48-hour intervals from 11 May to mid-June. Points represent observed proportions of radio-collared females with newborn calves, and labels are numbers of radio-collared females observed each year. Error bars represent 95% Wilson score intervals for each year's observed proportion. The gray line is a fitted curve

from a mixed-effects binary logistic regression model and the gray shading is the associated 95% confidence band.

Figure 4. Trend in age-specific parturition rates during 1998–2017 of female moose 2–17 years of age initially radio-collared at 9–10 months of age (cohorts 1996–2002, n = 1,051 F-yr), central Tanana Flats, Alaska, USA. Data are from aerial radio-tracking flights at 24- (1998) or 48-hour (1999–2017) intervals from 11 May to mid-June. Points represent observed proportions of radio-collared females with newborn calves, and labels are numbers of radio-collared females observed in each age class. Error bars represent 95% Wilson score intervals for each year's observed proportion. The gray line is a fitted curve from a mixed-effects binary logistic regression model and the gray shading is the associated 95% confidence band.

Figure 5. Trend in age-specific twinning rates during 1999–2017 for female moose 3–16 years of age initially radio-collared at 9–10 months of age (cohorts 1996–2002, n = 703 parturient F-yr), central Tanana Flats, Alaska, USA. Data are from aerial radio-tracking flights at 48-hour intervals from 11 May to mid-June. Points represent observed proportions of parturient radio-collared females with twins, and labels are numbers of parturient radio-collared females observed in each age class. Error bars represent 95% Wilson score intervals for each year's observed proportion. The gray line is a fitted curve from a binary mixed-effects logistic regression model and the gray shading is the associated 95% confidence band.

Figure 6. Trend in age-specific production rates during 1998–2017 for female moose 2–17 years of age initially radio-collared at 9–10 months of age (cohorts 1996–2002, n = 1,051 F-yr), central

Tanana Flats, Alaska, USA. Data are from aerial radio-tracking flights at 24- (1998) or 48-hour (1999–2017) intervals from 11 May to mid-June. Points represent the observed number of newborn calves/radio-collared female, and labels are numbers of radio-collared females observed in each age class. Error bars represent bootstrapped 95% confidence intervals for each year's observed production rate. The gray line is a fitted curve from a generalized linear mixed model with a Tweedie response distribution and the gray shading is the associated 95% confidence band.

Figure 7. Lifetime reproductive success (LRS) as a function of age at first reproduction during 1999–2017 for female moose initially radio-collared at 9–10 months of age (cohorts 1996–2002), central Tanana Flats, Alaska, USA. Data are from aerial radio-tracking flights at 48-hour intervals from 11 May to mid-June. The top panels represent LRS for females that survived  $\geq 12$  years of age and for which complete reproductive histories were known (n = 41). The bottom panels represent LRS for females  $\geq 3$  years of age with complete reproductive histories and that died from natural, nonhuman causes (n = 74). Values in the left panels are numbers of total offspring produced and values in the right panels are scaled by the number of years elapsed from age 3 (the min. age of reproduction) through death. Points are estimates from the Hodges-Lehman estimator and error bars are the associated 95% confidence intervals.

Figure 8. Probability of parturition as a function of age and previous year's reproduction during 1999–2017 in female moose initially radio-collared at 9–10 months of age (cohorts 1996–2002, n = 1,015 F-yr), central Tanana Flats, Alaska, USA. Data are from aerial radio-tracking flights at

48-hour intervals from 11 May to mid-June, 1999–2017. Error bars represent 95% confidence intervals. We estimated fitted curves with a mixed-effects binary logistic regression model.

Figure 9. Early winter moose numbers and corresponding population-wide twinning rates relevant to the study area, 2000–2018. Top panel depicts changes in moose abundance in Game Management Unit 20A (13,044 km<sup>2</sup> of moose habitat), which encompasses the central Tanana Flats and adjacent foothills, Alaska, USA. The gray line is a cubic regression spline (Wood 2011) fit to the data to describe the trend in abundance. Bottom panel depicts the trend in population-wide annual moose twinning rates from aerial transect surveys (no telemetry) in the central Tanana Flats. Surveys were 1- or 2-day surveys flown 20–29 May, a few days after the respective years' median calving dates. Data labels are numbers of female moose observed with  $\geq$ 1 calf (*n* = 960 F-yr). Error bars represent 95% Wilson score intervals for each year's observed proportion. The gray line is a fitted curve from a binary logistic regression model and the gray shading represents the associated 95% confidence band.

Table 1. Comparison of models representing hypotheses about factors potentially affecting
moose parturition, 1999–2017, central Tanana Flats, Alaska, USA. We used binary mixed-effects
logistic regression to model parturition as a function of a fixed-age effect (modeled as a
quadratic effect), other fixed effects hypothesized to influence parturition, and a random
intercept representing individual identity. We present the maximized log-likelihood (LL),
number of parameters (*K*), Akaike's information criterion (AIC), and difference in AIC between
a given model and the top-ranked model (ΔAIC).

Covariates	LL	K	AIC	ΔΑΙΟ
Age + Snow-free days <sup>a</sup>	-597.4	5	1204.9	0.0
Age	-600.1	4	1208.2	3.3
Age + Immobilization <sup>b</sup>	-599.9	5	1209.8	4.9
Age + Snow cover <sup><math>c</math></sup>	-600.0	5	1209.9	5.0
$Age + Cohort^d$	-597.1	10	1216.2	11.3
NULL <sup>e</sup>	-675.3	2	1354.7	149.8

8 <sup>a</sup> The number of days during the preceding year with snow cover <2.54 cm.

9 <sup>b</sup> Indicator of whether an individual was chemically immobilized during February or March

10 preceding parturition.

<sup>c</sup> Index of snow cover during the winter preceding parturition.

- <sup>d</sup> Cohort affiliation (1996–2002).
- <sup>e</sup> Model fit as a function of a constant with a random intercept.

14

15 Table 2. Comparison of models representing hypotheses about factors potentially affecting

16 moose twinning, 1999–2017, central Tanana Flats, Alaska, USA. We used binary mixed-effects

17 logistic regression to model twinning as a function of a fixed-age effect (modeled as a quadratic

18 effect), other fixed effects hypothesized to influence twinning, and a random intercept

19 representing individual identity. We present the maximized log-likelihood (LL), number of

20 parameters (*K*), Akaike's information criterion (AIC), and difference in AIC between a given

21 model and the top-ranked model ( $\Delta AIC$ ).

Covariates	LL	K	AIC	ΔΑΙΟ
Age + Parturition date	-158.6	5	327.2	0
Age	-169.3	4	346.5	19.3
Age + Immobilization <sup>a</sup>	-169.3	5	348.6	21.4
Age + Snow-free days <sup>b</sup>	-169.6	5	349.2	22.0
Age + Snow cover <sup>c</sup>	-169.6	5	349.2	22.0
$Age + Cohort^d$	-167.0	11	355.9	28.7
NULL <sup>e</sup>	-181.5	2	367.0	39.8

<sup>a</sup> Indicator of whether an individual was chemically immobilized during February or March

23 preceding parturition.

<sup>b</sup> The number of days during the preceding year with snow cover <2.54 cm.

<sup>c</sup> Index of snow cover during the winter preceding parturition.

- <sup>d</sup> Cohort affiliation (1996–2002).
- <sup>e</sup> Model fit as a function of a constant with a random intercept.

28	Article Summary: Our moose population experienced low production primarily as a result of
29	delayed maturation, occasional pauses in reproduction, and low twinning rates, not early
30	reproductive senescence. Detailed understanding of low moose reproductive metrics encouraged
31	land managers to allow wildfires to improve moose carrying capacity and encouraged
32	stakeholders to manage for decreasing moose numbers, which eventually led to improved moose
33	twinning rates.

34 35



Figure 1.



Figure 2.



Figure 3.



Figure 4.



Figure 5.



Figure 6.



Figure 7.



Figure 8.



Figure 9.