



REPRODUCTIVE PARAMETERS OF MOOSE DURING POPULATION EXPANSION IN NORTH DAKOTA

William F. Jensen¹, James J. Maskey, Jr.², Jason R. Smith³, and Eric S. Michel⁴

¹Present address: North Dakota Game and Fish Department, 100 North Bismarck Expressway, Bismarck, North Dakota 58501 USA; ²University of Mary, 7500 University Drive, Bismarck, North Dakota 58504 USA; ³North Dakota Game and Fish Department, 3320 East Lakeside Road, Jamestown, North Dakota 58401 USA; ⁴Department of Natural Resource Management, South Dakota State University, South Dakota 57007 USA.

ABSTRACT: Understanding reproductive parameters of a population is vital to management, especially during periods of population fluctuation. Therefore, our objective was to provide the first estimates of reproductive parameters such as pregnancy rates, litter size, fecundity rates, conception dates, and fetal sex ratios for a moose (*Alces alces*) population in North Dakota, USA. Between 1978 and 1986, the North Dakota Game and Fish Department necropsied 54 hunter-killed cow moose which were all harvested after the rut (10 November to 12 December). Pregnancy rates for calves (n = 7), yearlings (1.5 years, n = 6), and adults (≥ 2.5 years, n = 41) were 0%, 100% and 95%, respectively. Mean conception date was 2 October. Overall, mean litter size was 1.76 fetuses, twinning rate was 73.3%, and mean fecundity was 1.66 fetuses and 0.85 female fetuses/cow. Fetal sex ratio did not differ from the expected 50:50 ratio, but the odds of producing at least one male calf increased with dam age, but not dam weight or litter size. This population displayed reproductive parameters consistent with an irruptive and expanding moose population.

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Several parameters influence population growth rates including offspring and adult survival rates (Coulson et al. 2001, Delgiudice et al. 2006), fecundity rates (Raithel et al. 2007, Chitwood et al. 2015), offspring sex ratio (Reuterwall 1981), and adult sex ratio (Olsson and van der Jeugd 2002). Although these parameters all affect population dynamics, their relative importance varies among species and populations (Johnson et al. 2010). For moose (*Alces alces*), all have proved important when assessing population dynamics of certain populations.

Although survival and reproductive parameters greatly influence population

dynamics, biologists managing game species such as moose frequently make management decisions based upon incomplete data sets (Johnson 1996). Collecting baseline reproductive data from free-ranging moose populations is difficult for a number of reasons: 1) they can occur at low density, 2) they often occupy dense and remote habitats that complicate survey or capture efforts, and 3) their large size makes inspection of live-captured or hunter-harvested individuals logistically difficult. Lacking requisite information to guide local management, biologists often use baseline data collected elsewhere including pregnancy rate, twinning rate, and sex ratio of calves. These data

provide helpful metrics and sideboards to consider a range of reproduction, productivity, and population dynamics.

Moose began recolonizing the Pembina Hills area of northeastern North Dakota, USA in the late 1950s. By the early 1960s, a small resident population was established and the first modern hunting season occurred in 1977 (Knue 1991). This pattern of pioneering new areas of North Dakota continued, and by 1984, a hunting season extended to western North Dakota. The population further expanded during the study period, establishing into drift prairie, non-traditional moose habitat (Jensen 2001). In contrast, moose have declined substantially in recent years within our study area in northeastern North Dakota. This decline appears related to adult mortality resulting from parasitic diseases and localized overharvest (Maskey 2008). Despite recent closures in hunting seasons, the population remains low and continues to decline in this region.

Here we summarize reproductive parameters of the expanding moose population in northeastern North Dakota during 1978–1986. We provide pregnancy rates, litter size, fecundity rates, and fetal sex ratios of this irruptive population. Our objective was to summarize and interpret the basic reproductive parameters of harvested female moose to establish baseline data useful to interpret expanding, declining, and stable moose populations in North Dakota.

STUDY AREA

The distribution of harvested animals was between 47.10 and 48.99 °N, and 97.14 and 100.41 °W (Fig. 1). Common vegetation included prairie junegrass (*Koeleria macrantha*), indiagrass (*Sorghastrum nutans*), needle and thread grass (*Hesperostipa comata*), brome (*Bromus* spp.), wheat grass (*Agropyron* spp.), and alfalfa (*Medicago*

sativa). Common herbaceous species included sarsaparilla (*Aralia nudicaulis*), baneberry (*Actea* spp.), false lily-of-the-valley (*Maianthemum canadensis*), wild vetch (*Vicia americana*), and Virginia anemone (*Anemone virginiana*). Common woody species included green ash (*Fraxinus pennsylvanica*), box elder (*Acer negundo*), American elm (*Ulnus americana*), Russian olive (*Elaeagnus angustifolia*), plum (*Prunus* spp.), apple (*Malus* spp.), chokecherry (*Prunus virginiana*), willow (*Salix* spp.), paper birch (*Betula papyrifera*), and balsam poplar (*Populus balsamea*) (Bakke 1980, North Dakota Forest Service 2003). Mean annual temperature in northeastern North Dakota was 3 °C and annual precipitation was 51 cm (Seal bloom et al. 2011). Cervids in the area included white-tailed deer (*Odocoileus virginianus*), moose, and occasionally elk (*Cervus elaphus*). The predator base for cervids was limited to coyotes (*Canis latrans*) (Seal bloom et al. 2011). However, on rare occasions during this study (1978 to 1986), gray wolf (*Canis lupus*), Canada lynx (*Lynx canadensis*), bobcat (*Lynx rufus*), and black bear (*Ursus americanus*) were observed in northeastern North Dakota (Seal bloom et al. 2011).

METHODS

We examined 54 cow moose harvested post-rut from 10 November to 12 December in 1978 - 1986. Hunters voluntarily brought their moose in whole to a check station (i.e., prior to removal of viscera, hide, head, or legs). Whole carcass and dressed weight were measured (Jensen et al. 2013), and when possible, uteri were examined to determine reproductive status.

We used incisor eruption (Peterson 1955) to identify calves (≤ 6 months), and estimated age of older moose via cementum annuli analysis of a front incisor (Matson's Laboratory, Milltown, Montana, USA).

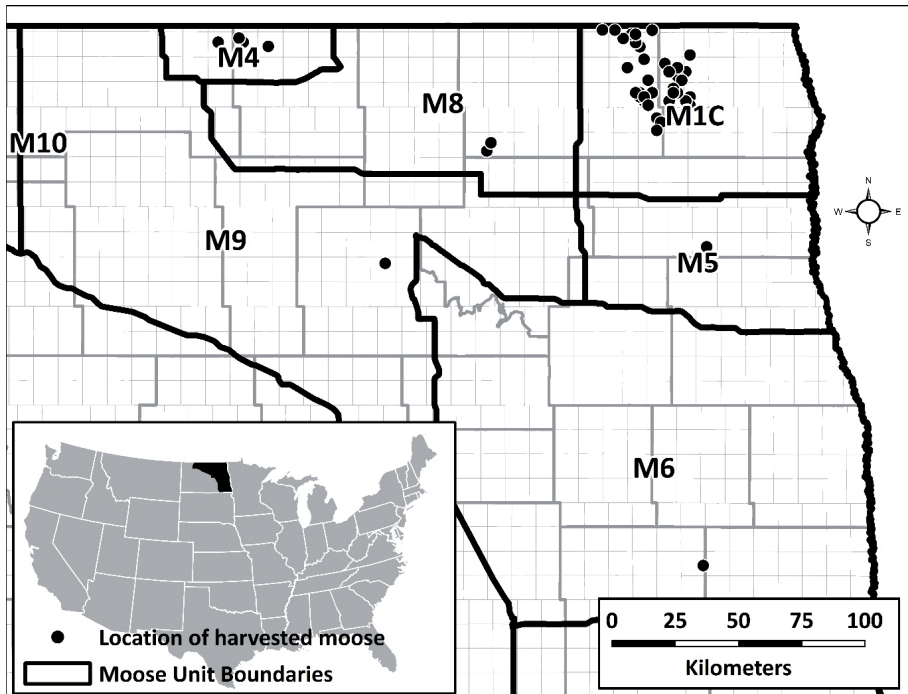


Fig. 1. Study area and locations where female moose were harvested in northeastern North Dakota, USA from 1978 to 1986.

After 1980, North Dakota Game and Fish Department (NDGFD) personnel performed these measurements (Gasaway et al. 1978, Haagenrud 1978). We also classified 5 adult cows based on their field dressed weight (≥ 290 kg; Jensen et al. 2013). To examine reproductive parameters, we separated cows into 3 age classes (calves, 1.5 years, ≥ 2.5 years; Boer 1992).

We classified moose as pregnant if we observed ≥ 1 fetus upon uteral examination. McKenzie (1989) measured body mass (0.1 g) and crown-rump length (CR: point of intersection of the coronal and sagittal sutures of the skull to the tuberosity of the ischium to the nearest mm; Armstrong 1950, Morrison et al. 1959) of 52 fetuses from 30 dams. We recorded fetal sex when genitalia were sufficiently developed, which usually occurred by 6 to 8 weeks of age ($n = 41$ fetuses from 24 dams).

We determined fetal age using the linear equations of Markgren (1969) and Crichton (1992), and then estimated conception date by backdating fetal age from the harvest date.

We calculated twinning rate, fetal sex ratios, and fecundity rates (calculated as total fetuses/dam and female fetuses/dam; Caughley 1977, Johnson 1996). We used a chi-square goodness of fit test to examine whether the observed fetal sex ratio differed from 50:50. Additionally, Jensen et al. (2013) reported that moose in North Dakota do not reach peak body mass until 5.5 years old. Thus, moose ≤ 4.5 years may have less energy to allocate towards reproduction because they are still investing resources towards somatic growth. To examine whether this occurred, we separated known-age cows into 2 age classes (1.5–4.5 years, and ≥ 5.5 years) and compared twinning

Table 1. Reproductive parameters for 54 harvested cow moose in North Dakota, USA from 1978–1986.

Age (yr)	n	% Pregnant	% Twinning	Mean Litter Size (SE)
0.5	7	0	0	0
1.5	6	100.0	0	1.00 (0.00)
≥2.5	41	95.1	85.0	1.87 (0.07)
all (≥ 1.5)	47	95.7	73.3	1.76 (0.07)

rates between classes with a χ^2 test for independence.

Finally, we constructed a multiple logistic regression model using the glm function in Program R (R Core Team 2014; version 3.1) to examine if the odds of producing at least one male calf increased with dam age or total body mass. The model also contained a covariate for litter size to control for its effect on the response variable, and evaluated with the age, total weight, and sex of fetus data from 21 known dams. We calculated the area under the receiver operating characteristic curve (AUC) for the model and evaluated its significance by comparing it to an intercept-only model with a likelihood ratio test. We considered results significant at $\alpha = 0.05$.

RESULTS

We collected data from 54 females ranging in age from ≤ 6 months to 10.5 years. Pregnancy rates were 0%, 100%, and 95.1% for calves ($n = 7$), yearlings (1.5 years, $n = 6$), and adults (≥ 2.5 year, $n = 41$), respectively. One of 2 non-pregnant cows was severely emaciated with a large beaver trap on its front leg; it was clear that the trap had impacted estrus and/or conception. The mean conception date of 45 cows was 2 October ± 8.0 d (SD; range = 3 September to 21 October).

Mean litter size of 45 cows was 1.76 ± 0.07 (SE). Mean litter size was 1.0 ± 0.0 for yearlings ($n = 6$) and 1.85 ± 0.07 for adults ($n = 39$); one adult (4.5 years) had triplets (2

female, 1 male). The combined twinning rate was 73.3% (0% of yearlings, 82% of adults; Table 1, Fig. 2). Twinning rates of 1.5 – 4.5 year-olds (0.68, $n = 28$) and ≥ 5.5 year-olds (0.85, $n = 13$) were not different ($\chi^2_1 = 1.27$, $P = 0.26$).

We determined sex of 43 (21 male and 22 female) fetuses collected from 24 adults. Fetal sex ratio did not differ from a 50:50 ratio ($\chi^2_1 = 0.5$, $P = 0.88$; Table 2, Fig. 2). Mean fecundity (# fetuses per cow) was 1.0 ± 0.0 for yearlings ($n = 6$), 1.76 ± 0.31 for adults ($n = 41$), and 1.66 ± 0.07 for all cows combined ($n = 47$). Mean fecundity of female fetuses was 0.67 ± 0.33 for yearlings ($n = 3$), 0.87 ± 0.17 for adults ($n = 23$), and 0.85 ± 0.15 for all cows combined ($n = 26$) (Fig. 2). The probability of producing at least one male calf increased with age ($\beta = 1.8$, Odds Ratio = 6.0, AUC = 0.89, $P = 0.03$, $n = 21$ dams), but not weight ($\beta = -0.02$, $P = 0.35$) or litter size ($\beta = -0.49$, $P = 0.68$; Table 3).

DISCUSSION

North American moose populations have varied dramatically through time (Peterson 1999, Post et al. 2002, Lenarz et al. 2010), with highest densities within a relatively narrow band of primary habitat roughly 300 to 750 km wide stretching from central Alaska across the central portion of the prairie provinces to the upper Great Lakes, to the northeastern states and Maritime provinces. Although this area composes about 30% of overall moose range

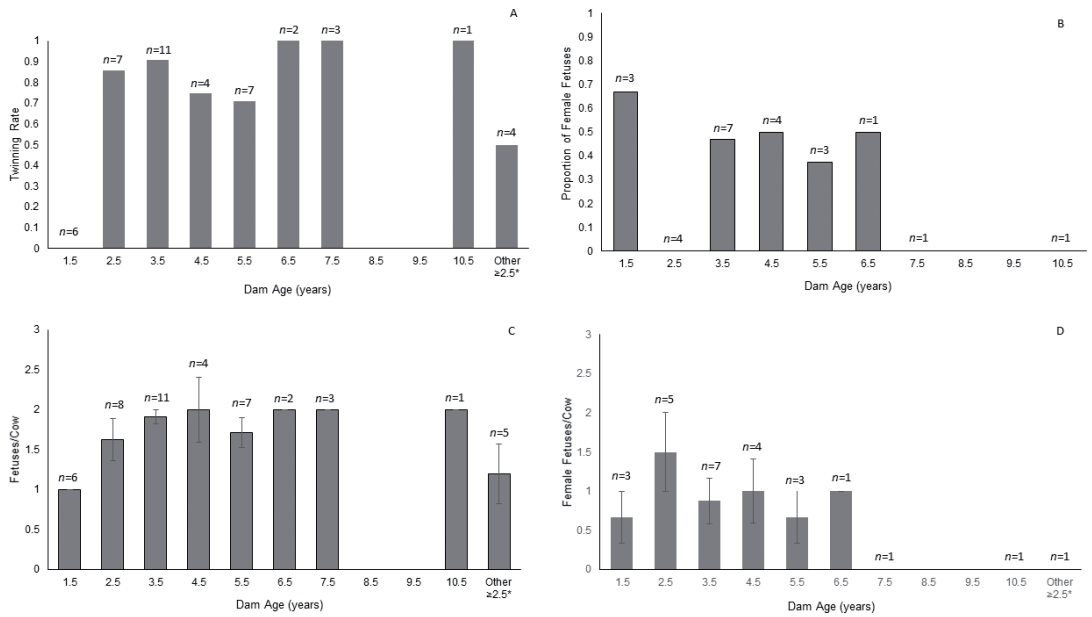


Fig. 2. Reproductive parameters for harvested cow moose in North Dakota from 1978 to 1986. A) Twinning rate of 45 cow moose; * indicates classification as adult but without exact age estimate. B) Proportion of litters comprised of female fetuses ($n = 24$ cows). C) Fecundity (total fetuses/cow) of 47 cow moose; * indicates classification as adult but without exact age estimate. D) Fecundity (female fetuses/cow) based on the examination of 26 cow moose; * indicates classification as adult but without exact age estimate.

Table 2. Sex ratios of fetuses recovered from 24 known-age moose in North Dakota, USA from 1978–1986.

Age (yr)	n	Sex of Fetus		% Female
		Male	Female	
1.5	3	1	2	66.7
≥ 2.5	21	20	20	50.0
All	24	21	22	51.2

Table 3. Statistics associated with the multiple logistic regression used to examine the relationships between male calf production and dam age, dam body weight, and litter size for 21 dams (≥ 1.5 yr) sampled from 1981–1985 in North Dakota, USA.

Variable	β	SE	Odds Ratio	P	Model Significance	AUC
age	1.8	0.84	6.0	0.03	$\chi_3^2 = 10.0, P = 0.02$	0.89
body weight	-0.02	0.02	0.98	0.35		
litter size	-0.49	1.2	0.61	0.68		

in North America, an estimated 89% of the North American population is found within this band of primary habitat (Jensen et al. 2018). Moose evolved as a pioneering species that disperses into recently created disturbed areas, such as those created by fire or timber operations (Peek 1974, 1998). Moose dispersing into new areas of North Dakota thus represent novel populations and provide a valuable opportunity to study reproductive rates of irrupting populations.

Pregnancy and twinning rates vary amongst moose populations. For example, in his summary, Boer (1992) found that adult pregnancy rate averaged 84.2% for North American moose, whereas Ruprecht et al. (2016) reported a rate of 74.1% for moose along the southern extent of moose range. Similar pregnancy rates are reported for populations in Alaska (76–97%; Schwartz 1998), Quebec (87–90%; Ferguson et al. 2000), and Norway (60%; Solberg et al. 2002). The pregnancy rate (95.1%) of adults in our study is as high as reported elsewhere, but that of North Dakota yearlings (100%; albeit only 6 animals) is higher than reported by Ruprecht et al. (2016; 0%) and Boer (1992) (range = 17.7–64.5%). Our results are more similar to a population that expanded (irrupted) nearly simultaneously in New Hampshire where ovulation rates of yearlings ($n = 187$) and adults ($n > 500$) were 63 and >90%, respectively, during the first 10 years of harvest (Adams and Pekins 1995, Bergeron et al. 2013).

Similarly, the overall twinning rate of 82% (including one litter of triplets) for females ≥ 2.5 years old was considerably higher than reported in other North American populations in Alaska (17–65%; Schwartz 1998), Minnesota (32–58%; Severud et al. 2014, 2015), New Hampshire (6–21%; Musante et al. 2010), and various Canadian provinces (41–49%; Ferguson et al. 2000). We also found no trade-off between

reproduction and somatic growth as twinning rates were similar for 1.5–4.5 and ≥ 5.5 year-olds. Boer (1992) reported that moose populations below carrying capacity display yearling pregnancy rates of 64.5%, adult pregnancy rates of 84.2%, and adult twinning rates of 44.1%. We found up to 35% higher values in our study population that was below carrying capacity on high-quality habitat, arguably values representative of an expanding, irruptive population.

Our mean fecundity rates were also similar to those measured in other studies with a few notable exceptions. For example, mean fecundity was 0.97 female calves/adult (≥ 4.5 years) in south-central Alaska (Testa 2004), and 0.93 - 1.35 for multiparous (i.e., calved previously) adults in Norway (Saether et al. 1996). However, these populations and data were unique as the Alaskan females first reproduced at 3-years of age, and the Norwegian sample only included multiparous females; we could not control for prior reproductive status. The mean pregnancy and fecundity rates of our adults were considerably higher than reported for many populations along the southern range boundary of moose (Ruprecht et al. 2016), as well as populations found at more northern latitudes; albeit, summary data rarely account for the specific dynamics of populations. Nonetheless, our fecundity rates clearly indicate that the study population was highly productive, if not maximal, and reflective of an irruptive population.

Although older dams were more likely to produce litters that included males, multiple intrinsic and extrinsic factors influence the sex ratio of offspring in several species. Intrinsic factors such as maternal body mass and maternal body condition affect offspring sex ratio (Verme 1969, 1983, Schwartz and Hundertmark 1993, Cameron 2004, Sheldon and West 2004, Cameron and Linklater 2007, Borowik and Jędrzejewska 2016).

Extrinsic factors such as weather during gestation (Post et al. 1999) and timing of conception (Holand et al. 2006, Veeroja et al. 2010) are also influential, and may act individually or in concert making it difficult to detect general patterns in the offspring sex ratio of moose (Boer 1992). Regardless, we found a relationship between fetal sex ratio and maternal age structure (more male calves with age) which could possibly influence population dynamics, as measurable shifts in the sex ratio can alter population growth rates of moose (Reuterwall 1981). However, our analysis was of limited sample size ($n = 21$ across age classes) and we recommend further monitoring before considering any management strategy to alter the age structure of the population (Schwartz and Hundertmark 1993).

These reproductive data from the 1970s and 1980s are representative of an expanding and irruptive population that contrasts with the population currently declining in North Dakota (Timmermann and Rodgers 2017). They arguably represent maximal productivity of a moose population, and their interpretation are critical when comparing to like data from stable or fluctuating populations. Quantifying baseline reproductive parameters such as pregnancy rates, twinning rates, fecundity, and fetal sex ratios is necessary to interpret population change and whether a given harvest prescription is sustainable. Given the recent decline of North Dakota moose, continued monitoring of these reproductive parameters and female age distribution is critical to best evaluate population dynamics and guide management strategies.

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