ASSESSING AGE OF HARVESTED MOOSE PRIOR TO POPULATION DECLINES IN BRITISH COLUMBIA

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ABSTRACT: Moose populations in parts of British Columbia, Canada have been declining since about the mid-2000s with the licensed harvest dropping by more than half from 1987 to 2014. A tooth reporting program for harvested moose from 1982 to 2003 enabled us to assess the relationship between age of harvested moose and 1) time (1982–2003), 2) level of licensed harvest of bulls and cows, and 3) estimated populations prior to declines with age data collected after decline in the province. We used age data determined from cementum annuli of teeth collected from hunter returns from 72,888 moose (n = 57,376 bulls and n = 15,512 cows). We found average age of harvested bulls and cows to be 3.32 ± 0.02 and 4.99 ± 0.06 years, respectively, similar to ranges reported elsewhere in western North America. Age of bulls declined linearly by year, whereas age of cows declined in the latter half of the study period. The average age of cows harvested from 1983 to 2003 prior to the population decline (n = 2,016; mean = 3.84 years, SD = 3.03) was 7 years younger than that of a small sample of cows dying of multiple causes (harvest and natural) during the decline (n = 47; mean = 10.93 years, SD = 3.72). We acknowledge the logistical and financial constraints required to gather a representative sample of teeth from harvested moose, but recommend reimplementation of a tooth collection program to provide continuous information on the age structure of moose populations to help guide management decisions.

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Determining age from teeth of harvested ungulates provides important demographic information about populations to help guide management strategies. Understanding age and sex of ungulate populations assists with determining productivity, age-specific survival, and reproduction (Gove et al. 2002), evaluating expected population dynamics (Loison et al. 1999), and estimating maximum yield in harvested systems (Sæther et al. 2001, Clutton-Brock et al. 2002, Nilsen et al. 2005). Survivorship may also be inferred from age distribution of ungulates, though it may be biased if age structure changes during the period of survival estimation (Eberhardt 2002).

Using the age of harvested moose is common and useful in developing effective management strategies and understanding moose population dynamics (Timmerman and Buss 2007). It is used to develop standing age distributions or estimate age structure of moose populations, recognizing there is no standard population age structure because of fluctuations in survival and reproduction (Van Ballenberghe and Ballard 2007). The population age structure of moose and how it varies over time (Peterson 1977) is useful to interpret population trends because variation in survival and reproduction may be related to age structure (Solberg et al. 2000, Ericsson et al. 2001, Sæther et al. 2001). Harvest age data can also serve as an index of harvest rate and provide for assessment of its effects on sex structure and the mean age of females and males in the population (Langvatn and Loison 1999, Milner et al. 2007). Generally, the mean age of moose populations declines as harvest rate increases and relationships between mean age and population density indicate that mean ages are lower in low density populations with few older individuals (Bowyer et al. 1999).

Recent declines in moose populations in parts of North America (Timmermann and Rodgers 2017, Jensen et al. 2018) have created challenges for maintaining sustainable hunting opportunities. Populations in British Columbia have declined in ~70% of moose range in the last decade (Kuzyk et al. 2018) and licensed harvest has declined by approximately half since 1987 (Kuzyk 2016). Declines within central British Columbia coincided with a mountain pine beetle (*Dendroctonus ponderosae*) outbreak where habitat changes and increased salvage logging and road building were hypothesised to increase vulnerability to harvest and predation (Kuzyk and Heard 2014). Although British Columbia had a voluntary tooth return program for licenced resident and non-resident hunters from 1982 to 2003 to provide harvest age information, it was discontinued due to financial constraints prior to the onset of population declines in the mid 2000s.

The purpose of this study was to determine and assess change in the age of harvested moose populations in British Columbia long-term, both prior to (1982–2003) and post-population decline in the mid-2000s. This assessment used two regions in British Columbia with sufficient samples of harvested cows. Specific objectives were to: 1) estimate the mean age of moose populations and how it changed over a 21-year period, 2) assess relationships between harvest age of bulls and cows over time and levels of harvest, and 3) compare the mean age of moose populations prior to, during, and after population decline.

STUDY AREA

We assessed age of bulls and licenced harvest levels of moose at a provincial scale in 186 Wildlife Management Units (WMU) where hunting was authorized from 1982 to 2003. We also examined cow age and harvest, but this was limited to only two regions of the province, Region 7A and Region 3 (Fig. 1) where sufficient samples of harvested cow moose were available. In these areas moose occupy habitats in northern boreal forests, dry interior forests, and mountainous habitats (Eastman and Ritcey 1987, Meidinger and Pojar 1991) and are sympatric with mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), elk (*Cervus elaphus*), bison (*Bison bison*), and caribou (*Rangifer tarandus*) (Shackleton 1999). Moose co-exist with 4 main predators: wolves (*Canis lupus*) and black bears (*U. americanus*) throughout moose range, grizzly bears (*Ursus arctos*) in all areas except parts of the south-central interior, and cougars (*Felis concolor*) primarily in the central and southern areas (Spalding and Lesowski 1971).

METHODS

Licenced hunters voluntarily submitted a front incisor from moose harvested between 1982 and 2003, except in 1999 when the collection program was suspended temporarily. From 1982 to 1988, teeth were

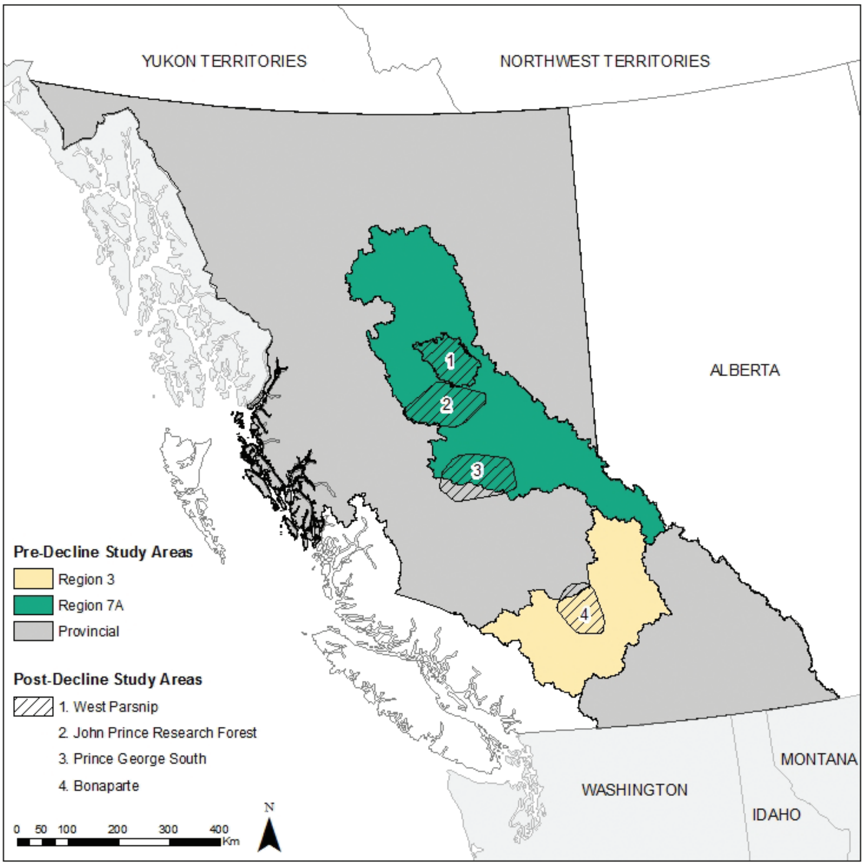

Fig. 1. Distribution of moose with licensed hunting seasons in British Columbia at the provincial scale (grey, includes Regions 7A and 3), Region 7A (green), and Region 3 (yellow). Regions 7A and 3 had licensed cow hunting seasons and included the research sites where mortality of radio-collared cow moose was monitored.

collected voluntarily through the Harvest Card Tooth Return Program or at hunter check stations (Hatter 1993). From 1989 to 2003 (excluding 1999), the Voluntary Tooth Return Program was made more prominent and easier to participate in as hunters received a harvest data envelope when purchasing their hunting license or by mail if they received a Limited Entry Hunting (LEH) authorization (Hatter 1993, Child et al. 2010). Hunters were requested to document date, location (Management Unit), and sex of kill on the harvest data envelope, include an incisor, and mail the pre-paid envelope to the provincial wildlife agency. Ages of bulls and cows were determined from sectioned incisor teeth (Sergeant and Pimlott 1959) by two trained wildlife staff (Child et al. 2010). There was sufficient harvest of cows in Region 7A and Region 3 to enable an assessment of cow age and harvest levels at a regional scale. We also compared ages of harvested cows (n = 2,016) in Region 3 and Region 7A from 1982 to 2003 (prior to the decline) to a small sample of cows (n = 47) dying of harvest and natural causes during the decline (2012–2018) as part of related research (Kuzyk et al. 2019, Sittler 2019). Ages were determined in a professional laboratory (Matson's Laboratory, Montana, USA) specializing in using cementum annuli to age sectioned teeth. Because teeth were aged by multiple trained individuals, we compared a sample of 35 teeth aged by a government biologist and Matson's Laboratory; 70% were aged within ±1 year of age (authors, unpublished data). The majority of difference occurred with moose ≥10 years of age because separation of annuli declines with age.

Licenced resident harvest was estimated annually in 1982 to 2003 from a provincial survey conducted with mail-out questionnaires sent to a random sample of resident moose hunters. These estimates (± 95% confidence interval) were produced from an annual average of 14,278 ± 2,732 questionnaires with an average response rate of 69.4 ± 2.7%. Non-resident licenced harvest was obtained from mandatory reports completed by guide-outfitters immediately following their hunts. Total harvest was a combination of bulls (>1 year of age), cows (>1 year of age), and calves (<1 year of age).

Trends in age of harvested moose from 1982 to 2003 were assessed by using linear, second-degree polynomial, and third-degree polynomial regression analyses. Polynomial regression analysis was used to identify possible increases and decreases in annual harvest age over time. The best regression model was selected using Akaike's Information Criteria (AIC) (Burnham and Anderson 2002).

Analysis of general harvest trends was limited by variability in annual harvest data. For simplicity, licensed harvest trends were assessed with two-sample *t*-tests to examine for difference between the estimated harvest in the first 5 years (1982–1986) and the last 5 years (1999–2003) of the study period. Pearson's correlation coefficient was used to test for relationships between bull and cow harvest age and licensed harvest levels; significance was set at $P < 0.05$.

RESULTS

The mean age of harvested bulls province-wide was 3.32 ± 0.02 years (n = 57,376) (Fig. 2), 3.17 ± 0.04 years (n = 19,610) in Region 7A (Fig. 3), and 2.96 ± 0.09 years (n = 3,226) in Region 3 (Fig. 4). Age of bulls declined linearly by year in all study areas (Table 1, Fig. 2–4). Age of bulls and harvest level were negatively correlated in Region 7A ($r = -0.69$, $P \leq 0.01$; Fig. 3), positively correlated in Region 3 ($r = 0.76$, $P \leq 0.01$; Fig. 4), but not correlated province-wide (Fig. 2).

Mean age of harvested cows (n = 15,512) was 4.99 ± 0.06 years province-wide (Fig. 2), 4.53 ± 0.07 years (n = 8,819) in Region 7A (Fig. 3), and 5.34 ± 0.19 years (n = 1,358) in Region 3 (Fig. 4). Age of harvested cows followed a second-order polynomial trend in all study areas, with age declining in the latter half of the study period (Table 2). Age and harvest level were positively correlated in Region 3 ($r = 0.44$, $P \leq 0.05$; Fig. 4), but unrelated in Region 7A (Fig. 3) and province-wide (Fig. 2). In Regions 3 and 7A, the mean age of harvested cows prior to the population decline (3.84 years, SD = 3.03; n = 2,016) was 7 years younger ($t = -12.98$, $P \leq 0.01$) than that of cows (10.93 years, SD = 3.72; n = 47) dying from a variety of causes between 2012 and 2018 during and after the decline.

The mean annual harvest was 11,302 ± 736 moose province-wide (Fig. 2), with 3,355 ± 202 moose in Region 7A (Fig. 3) and 550 ± 117 moose in Region 3 (Fig. 4). Harvest trends were stable province-wide ($P \geq 0.05$; Fig. 2) and in Region 7A ($P \geq 0.10$; Fig. 3), but declined in Region 3 ($P \leq 0.05$; Fig. 4). The mean annual bull harvest was 8,975 ± 568 province-wide (Fig. 2), 1,926 ± 195 in Region 7A (Fig. 3) and 429 ± 80 in Region 3 (Fig. 4).

The trend in bull harvest was considered stable province-wide ($P \geq 0.10$; Fig. 2), increased in Region 7A ($P \leq 0.01$; Fig. 3)

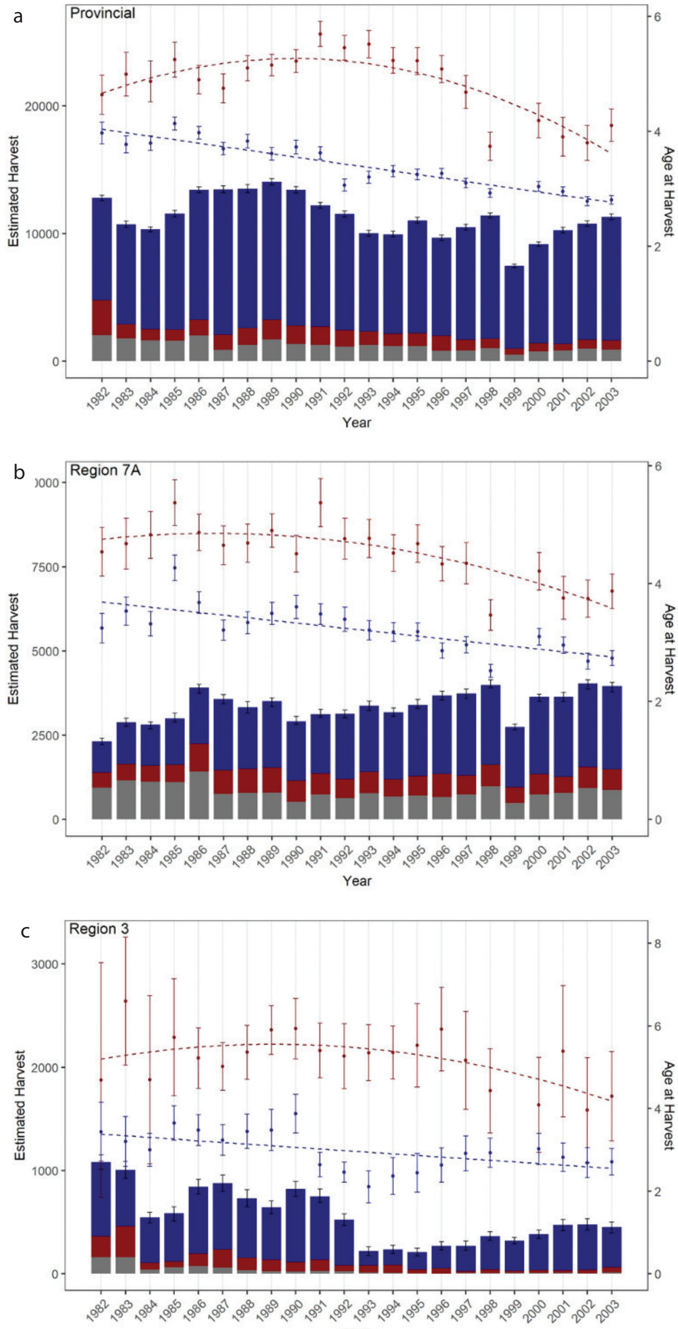

Fig. 2. Moose harvest data in 1982–2003, British Columbia, Canada. (A) Average age of bull (blue dots) and cow (red dots) moose and estimated provincial harvest (blue bar for bulls, red bar for cows, grey bar for calves) of moose Error bars are 95% confidence intervals. (B) Average age of bull (blue dots) and cow (red dots) moose and estimated harvest (blue bar for bulls, red bar for cows, grey bar for calves) of moose in Region 7A in British Columbia from 1982 to 2003. Error bars are 95% confidence intervals. (C) Average age of bull (blue dots) and cow (red dots) moose and estimated harvest (blue bar for bulls, red bar for cows, grey bar for calves) of moose in Region 3 in British Columbia from 1982 to 2003. Error bars are 95% confidence intervals.

Table 1. Comparison of AIC values associated with regression analyses used to evaluate trends in age of harvested moose age in 1982–2003, British Columbia, Canada. Grey indicates top selected model. Polynomial = degree of polynomial; df = degrees of freedom; AIC = Akaike's Information Criterion.

Study Area	Sex	Polynomial	df	AIC
Province	Bulls	1	3	−15.08
	Bulls	2	4	−13.08
	Bulls	3	5	−13.86
	Cows	1	3	33.55
	Cows	2	4	17.18
	Cows	3	5	18.71
Region 7A	Bulls	1	3	8.26
	Bulls	2	4	8.97
	Bulls	3	5	7.06
	Cows	1	3	19.07
	Cows	2	4	14.32
	Cows	3	5	13.82
Region 3	Bulls	1	3	25.46
	Bulls	2	4	25.78
	Bulls	3	5	25.43
	Cows	1	3	41.88
	Cows	2	4	38.87
	Cows	3	5	40.83

and declined in Region 3 ($P \leq 0.05$; Fig. 4). The mean annual cow harvest was 1,079 ± 210 province-wide (Fig. 2), 597 ± 44 in Region 7A (Fig. 3), and 84 ± 31 in Region 3 (Fig. 4). The cow harvest trend was stable ($P \geq 0.\ 05$) province-wide (Fig. 2) and in Regions 7A (Fig. 3) and 3 (Fig. 4) throughout the study period.

DISCUSSION

The average age of harvested moose by licensed hunters in British Columbia from 1982 to 2003 was 3.3 and 5.0 years for bulls and cows, respectively. These data were collected prior to population declines that began in the mid-2000s and later in parts of the central interior (Kuzyk et al. 2018), and similar to those reported elsewhere in western North America. For example, in Alberta the average age of harvested bulls was 2.5–2.7 years in heavily hunted areas and 3.5 years where hunting pressure was lighter (Lynch 2006). We also found that the majority (66%) of bull moose harvested in British Columbia was ≤3 years old. In Alaska, 84% of harvested bull moose on the Kenai Peninsula was ≤3 years old (Schwartz et al. 1992), and on Kalgin Island Bowyer et al. (1999) found a relationship between the mean age of moose and population density such that, at low density, the mean age of both bulls and cows was ~2 years, increasing to ~3 years at higher densities.

We found a higher average age for harvested cows than bulls in Regions 3 and 7A. The mean age of harvested cows (5 years) in British Columbia was lower than that in Alberta where the average age was 7.2 years in an area with minimal First Nations harvest (Lynch 2006). The different population age structure of cows in British Columbia and Alberta in those respective timeframes suggests that either cow mortality rates were higher in British Columbia due to natural causes and/or higher harvest pressure (licensed and/or First Nation), or that calf recruitment rates that affect age structure differed in the two areas. We found a higher average age of harvested cows than reported by Bowyer et al. (1999) in Alaska (i.e., 2–3 years) in a heavily harvested population where the objective was to reduce population density.

The average age of harvested cows in Region 3 and Region 7A prior to the population decline was younger (3.84 years) than that of radio-collared cows (10.93 years) that died of all causes (i.e., predation, hunting, health, natural accident) in portions of both regions from 2012 to 2018 (Kuzyk et al. 2019, Sittler 2019). A more accurate comparison would use only harvested radio-collared cows, but sample size of this group was insufficient. In the latter study, most moose died at an older ager than cows harvested prior to the decline in Regions 3 and 7A, suggesting that a preponderance of older individuals were radio-collared as most mortality was unrelated to age. For these radio-collared cows, the average age of death was 11 years by predation (11 years for wolves, 10 years for bears, and 14 years for cougar), 9 years for apparent starvation, and 9 years at harvest (Kuzyk et al. 2019). These data suggest that the individuals captured and monitored for research purposes reflected the age structure of a moose population skewed to older individuals, assuming captures were random. Calf survival and recruitment may be a primary factor explaining moose population declines, which provides additional support for an age structure skewed toward older individuals, especially if lower calf recruitment occurred over a period of several years (Kuzyk et al. 2018). Aerial survey data within the research areas indicate that calf recruitment rates were lower in recent years (Kuzyk et al. 2019). An alternative explanation is that age at death is not reflective of the age structure of the standing moose population because older cows are more vulnerable to certain mortality causes, including predation as suggested elsewhere (Peterson 1977, Montgomery et al. 2014). Further, the risk of mortality from all causes other than harvest increases with age and becomes most apparent after 10 years of age (Ericsson and Wallin 2001).

Harvest trends of bull moose were stable province-wide, increased in Region 7A, and decreased in Region 3. Surveys in the southern part of 7A indicated that stable populations (Hatter 1999) and improved hunter access may have contributed to the increasing harvest trend. The primary cause of lower bull harvests in Region 3 was due to season changes that purposefully reduced the harvest level. In 1984, the 55-day General Open Season (GOS) for any bull was reduced to 24 days which reduced harvest initially, and in 1993 the any bull GOS was closed and replaced with a Limited Entry Hunt (LEH) for bulls and an antler-restricted GOS for spike/fork bulls. Ultimately, the trends in bull harvest in Region 3 were unrelated to population trends during this timeframe. Cow harvests were stable province-wide and in Regions 7A and 3.

We found a positive correlation between age and harvest level of bulls in Region 3, a negative correlation in Region 7A, and no relationship at the provincial level. The sharp decline in average age of harvested bulls in Region 3 in the early 1990s reflected unsustainable harvest as evidenced by a declining bull ratio during that timeframe, and provided the rationale for the substantial season changes in 1993. Thereafter, lower harvest age of bulls was mostly due to implementation of the GOS focused on yearling bull moose (i.e., spike/fork GOS). Increasing trends in bull harvest age through the late 1990s and early 2000s were correlated with an increasing population indicated by aerial surveys during that period. The negative relationship between age and harvest level in Region 7A is consistent with the idea that as harvest increases, population age structure declines. The average bull age in Region 7A suggests that harvest pressure was lower in this region than in Alberta (Lynch 2006) and Alaska (Schwartz et al. 1992).

No significant relationship was found between age and harvest level of cows province-wide or in Region 7A. An unexpected positive correlation was found in Region 3 that contrasted with stratified random block survey data (RISC 2002) indicating that moose populations were increasing; harvest of antlerless moose was purposely reduced for reasons other than trends in moose numbers. Although licensed harvests of antlerless moose were stable to declining, First Nation harvest levels were unknown and if increasing, would reduce the mean age of cows. Alternatively, this trend may reflect the addition of younger animals to the moose population; here, moose populations increased as mean age began to drop and concurrent survey data indicated higher calf:cow ratios in many units during mid-winter surveys (i.e., 50–71 calves/100 cows). However, this is in contrast to when mean age increases with increasing density in a harvested population (Bowyer et al. 1999) and our results with bull harvests.

We acknowledge the logistical and financial constraints required to gather a representative sample of teeth from harvested moose, but recommend reinitiating a tooth collection program in British Columbia. Harvest age provides critical information about moose populations and insight regarding population trends when combined with age data from unlicensed harvests and non-hunted animals. Population management decisions that consider harvest level, hunter effort, and hunt structure would benefit measurably from such data, especially in areas where survey data is lacking or difficult to obtain.

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