Wildlife Society Bulletin 39(2):383–389; 2015 DOI: 10.1002/wsb.537

Tools and Technology

Accuracy of Moose Age Determinations from Canine and Incisor Cementum Annuli

RODNEY D. BOERTJE,[1,2] *Alaska Department of Fish and Game, 1300 College Road, Fairbanks, AK 99701-1551, USA*
MARTHA M. ELLIS,[3] *Alaska Department of Fish and Game, 1300 College Road, Fairbanks, AK 99701-1551, USA*
KALIN A. KELLIE, *Alaska Department of Fish and Game, 1300 College Road, Fairbanks, AK 99701-1551, USA*

ABSTRACT We sent 76 canines and 77 incisors (I1) from 84 known-age moose (*Alces alces*) ≥2 years old sampled from near Fairbanks, Alaska, USA (2003–2011) to Matson's Laboratory (Milltown, MT) to test G. Matson's accuracy rate in estimating moose ages. To estimate ages, G. Matson counted annuli in the cementum of root tips using a Giemsa-staining technique and assumed a birth date of 1 June. We originally radiocollared moose at 9 months of age, and we extracted teeth upon death. Estimated moose ages averaged 7.0 years using canines and 6.9 using I1 teeth (range = 2–16 year), and known ages of each sample averaged 7.1 years. The accuracy rate among 76 canines was 74% and improved to 95% when ignoring errors within 1 year of the known age; comparative results among 77 I1 teeth were 66% and 94%. By far the most frequent error was a 1-year underestimate in age, particularly for moose that died in July and August, which included the seasonal transition period associated with completing peripheral annuli formation. After controlling for −1-year errors associated with the seasonal transition period, we found evidence for errors accumulating with age. We found no significant difference in accuracy based on which tooth was sectioned. However, G. Matson observed more individually distinct annuli and regular deposition patterns in canines, compared with incisors. Thus, we recommend the more easily extracted canine for estimating moose age.

KEY WORDS age estimation, Alaska, *Alces alces*, annuli, cementum, known-age moose, moose, tooth sections.

Optimal management of moose (*Alces alces*) is dependent in part on age-specific data on body condition, parturition, and mortality (e.g., Solberg et al. 2004, Mysterud et al. 2005, Boertje et al. 2009). Thus, the need exists to acquire as accurate and precise ages from moose as possible and to document error rates (Gasaway et al. 1978). Counting the number of growth layers (annuli) in teeth to estimate animal age was first developed for marine mammals (Scheffer 1950) and then moose (Sergeant and Pimlott 1959) and other cervids (Low and Cowan 1963).

The basic premise, using the Giemsa-staining technique described here, is that a dark-stained ring, or annulus, is formed in the cementum during winter and a wider, relatively light-stained layer is formed during the growing seasons of spring and summer. However, counting the annuli and interpreting counts can be problematic and subjective, in part because the light-stained layer is complex in moose (i.e., the light-stained layer often contains small, dark-stained annuli not to be confused with the winter annuli). Also, the rate of formation of the light-stained layer varies among moose, so misinterpreting the light-stained layer on the perimeter of the tooth can result in subjective estimates of ages, particularly within 1 year of the known age. Also, the dark-stained annuli can split into multiple lines, resulting in overestimates of moose ages (Gasaway et al. 1978). Annuli also become thinner as moose age. The underlying physiological mechanisms for annual cementum growth are unknown (Grue and Jensen 1979).

Gasaway et al. (1978) tested 68 known-age moose teeth for accuracy and concluded the primary source of error resulted from difficulties in distinguishing discrete cementum annuli. More recently, Rolandsen et al. (2008) reported results from 51 known-age moose teeth and concluded that technicians should be well-trained and have access to a sample of known-age moose teeth. Fancy (1980) and Hamlin et al. (2000) reported evidence of regional bias in intraspecific clarity of cementum annuli. Dalton and Francis (1988) discussed the status and limitations of using cementum annuli counts in 16 North American jurisdictions that managed moose; they found 21 different laboratory techniques being used to prepare moose teeth, and each laboratory used a different level of effort and quality control to assign moose ages. Conclusions were that results suffered from subjective counting criteria, inadequate verification, and poor repeatability (Cumming and Evans 1978). Dalton and Francis (1988) recommended the maximum technology available to assign moose ages (i.e., histological sectioning and staining).

To contribute to the science of cementum counts, we sent known-age moose teeth to Matson's Laboratory, Milltown, Montana, USA, for histological sectioning and staining.

Received: 26 June 2014; Accepted: 9 December 2014
Published: 20 April 2015

[1]*E-mail: rod.boertje@gmail.com*
[2]*Present address: 220 Blue Bird Circle, Kerrville, TX 78028, USA.*
[3]*Present address: United States Department of Agriculture Forest Service, Rocky Mountain Research Station, Montana State University Campus, Bozeman, MT 59717, USA.*

Known-age moose teeth had not previously been received by Matson's Laboratory. However, during 1978–2014, lab staff assigned ages to >129,500 moose teeth; and, in recent years, staff annually counted cementum annuli of >90,000 teeth of all species (Matson's Laboratory website, http://www.matsonslab.com/index.htm). Clearly, the level of experience at Matson's Laboratory is far beyond that of researchers reporting initial evaluations (Hamlin et al. 2000). In 1981, G. Matson established standardized models or interpretation procedures for tooth section analysis in most North American game and furbearer species, and he regularly added to the models in the form of criteria for recognizing sources of error and interpreting specific histological details in cementum (Matson et al. 1993). G. Matson considered the standardized analysis models as essential elements for maintaining the long-term stability of accurate and precise cementum age analyses.

Our objectives were to evaluate G. Matson's annuli counts in respect to known ages of moose and to examine accuracy rates by season and by moose age and gender. We also tested whether canines or I1 teeth provided the best estimates of moose ages. We found no previous studies that tested accuracy of ungulate ages using canines, or previous studies of moose teeth using the same techniques described here.

MATERIALS AND METHODS

During 2003–2011, we extracted paired canine and I1 teeth from 69 moose ≥2 years old, and 1 of either tooth from an additional 15 moose, for 76 total canine and 77 total I1 teeth. We extracted teeth with the aid of a dental elevator and extractor and assigned each tooth a number unique to each moose. We initially radiocollared all moose in March as 9-month-old short-yearlings (Boertje et al. 2007). We determined calves to be 9 months old by the absence of adult incisors. We knew the date of death to the nearest day or week or estimated the date as the median date between monthly winter radiotracking flights. Cause of death was evaluated for each moose (Boertje et al. 2009) and jaws were frozen until we could extract teeth. The sample consisted primarily of female moose (67%). All sampled moose lived immediately south of Fairbanks, Alaska, USA, in central Game Management Unit 20A. We previously described this moose population as having the lowest nutritional ranking among 15 moose populations in Alaska, and having the lowest reproductive rates among wild, noninsular moose populations in North America (Boertje et al. 2007). We conducted all aspects of research in accordance with acceptable methods for field studies adopted by the American Society of Mammalogists (Animal Care and Use Committee 1998, Alaska Department of Fish and Game Protocol no. 04-003).

We assigned unique random numbers to each tooth and sent each dried tooth in a separate small, paper envelope to Matson's Laboratory per the lab's instructions. We sent teeth in 6 batches from January 2004 through April 2011 with 6–63 teeth/batch. We supplied the month or season (Sep–Mar) of death as instructed by Matson's Laboratory. The sole examiner was G. Matson, who examined each tooth without prior knowledge of ages of teeth or which teeth were from the same individual.

Matson used 13 steps in processing teeth, as generally described on the Matson's Laboratory website. Specifically, Matson's Laboratory processed the teeth by cleaning in a hot water bath, wiping with a nylon mesh, decalcifying in a weak acid solution, rinsing in water, dehydrating in isopropyl alcohol, clearing in toluene, and embedding in melted paraffin (Paraplast®; Oxford Division of Sherwood Medical, Saint Louis, MO). Lab staff sectioned the embedded teeth at a 14-micron thickness using a Leica Model SP9000 rotary microtome (Leica, Buffalo Grove, IL). They mounted these sections on microscope slides, stained them with Giemsa blood stain (Ricca Chemical Company, Arlington, TX), and applied a cover glass using Hypermount resin (Shandon, Inc., Pittsburgh, PA). G. Matson counted annuli in the stained sections using a Leitz compound brightfield microscope at 40× to 160× magnifications (Figs. 1 and 2). In addition to age, G. Matson reported a letter certainty level for each specimen: A = result likely correct and B = evidence less strong and error possible.

We took 2 approaches to analyzing accuracy parameters. First, we were interested in the distribution of 1-year underestimates in age related to deaths during the April–August period. This period is a seasonal transition period relevant to assigning ages (i.e., the peripheral cementum layer can be misinterpreted). Another complicating factor during the seasonal transition period was the 1 June cutoff date, or assumed birth date, used as the basis for truncating ages to whole years (Figs. 1 and 2). Thus, given a tooth with a mortality date in May, the tooth would be assigned an age from the previous year, whereas a tooth with a mortality date in June would be assigned the next year's age.

We analyzed for the midway date and associated variability of this seasonal age transition based on known ages using a generalized linear mixed model with binomial error structure

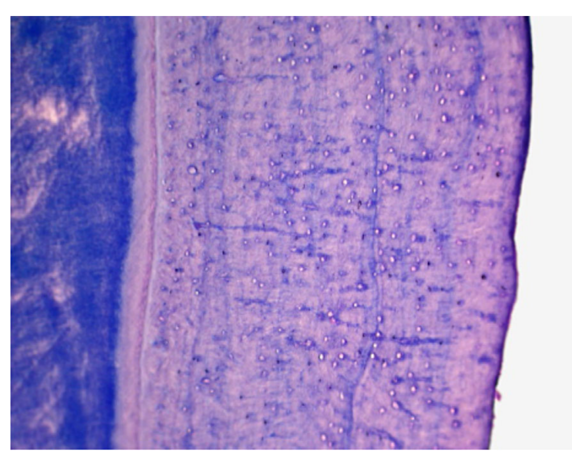

Figure 1. Photograph of sectioned canine above root tip, 100× magnification, date of death 12 January 2004, known age 5 years, moose 156 from Interior Alaska, USA. Photograph taken at Matson's Laboratory, Milltown, Montana, USA. G. Matson assigned the correct age based on counting 4 annuli—the first was formed during the second winter of life—and assuming a birth date of 1 June. We assumed canine tooth eruption occurred at the age of 1 year.

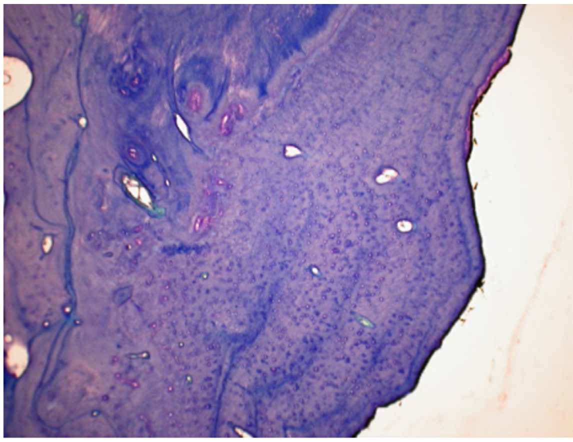

Figure 2. Photograph of sectioned incisor (I1) above root tip, 40× magnification, date of death 12 January 2004, known age 5 years, moose 156 from Interior Alaska, USA. Photograph taken at Matson's Laboratory, Milltown, Montana, USA. G. Matson assigned the correct age based on counting 5 annuli—the first was close to the core dentine and less distinct than those of subsequent winters. We assumed I1 tooth eruption occurred during the moose's first winter.

and a probit link function (Campana et al. 1995, Campana 2001). The response variable was an indicator of whether the sample was aged with the May age (previous year) or June age (next year). We included mortality date as a fixed covariate. We included individual as a random effect to account for correlation among multiple teeth sampled per moose. We did not include batch number as a covariate, based on preliminary modeling. We included teeth collected 1 April–30 October in this analysis to span the range of the seasonal transition period, and excluded any errors other than 1-year underestimates. Errors other than the most common 1-year underestimates likely originated from sources other than the seasonal age transition. For example, Rolandsen et al. (2008) reported sources of error unrelated to season because all teeth were collected during the early winter hunting season. We estimated 95% confidence intervals for derived parameters via model-based parametric bootstrap with 10,000 replicates (Bates et al. 2014).

Second, we analyzed accuracy parameters to assess the distribution of errors unrelated to 1-year underestimates in age that originated from the seasonal transition period. We were interested in whether remaining errors depended on known age of the moose, moose gender, or tooth type (canine or I1) used for aging. The response variable was the number of years of error between the estimated age and the true age. To account for errors resulting from the seasonal transition period, we used the results of our seasonal analysis to predict the probability of being assigned the previous May age based on the mortality date for each tooth. For example, if a tooth had a predicted 50% chance of being assigned with the previous May age based on a mortality date in August, we selected a uniform random number between 0 and 1. If this random number was <0.50, we corrected the estimated age by +1 year. We then treated the entire sample of observed and corrected errors as observations from a Pascal random variable, and regressed the errors against the explanatory variables (age, gender, and tooth type) using a generalized linear mixed model with negative binomial error structure, a log link function, and an overdispersion parameter of 1 (Zeileis et al. 2008, Bates et al. 2014). Individual was included as a random effect to account for multiple teeth sampled per moose. We included direction of error as a fixed covariate to test the assumption that errors were symmetric, because the modeling approach assumed that underestimates and overestimates were equally likely. We assessed the significance of each fixed covariate using likelihood ratio tests (Bolker et al. 2009).

RESULTS

The most common age of sampled moose ≥2 years of age was 8 years (Fig. 3) with an average of 7.1 years (SE = 0.367) in each known-age sample of canine or I1 teeth (Table 1). The average estimated age was 7.0 years (SE = 0.368) for the canine sample and 6.9 years (SE = 0.367) for the I1 sample. The distribution of errors was asymmetrical (Table 1).

Among moose ≥2 years of age, G. Matson correctly assigned ages in 74% of 76 canines and 66% of 77 I1 teeth. Ignoring errors of ±1 year, G. Matson correctly assigned ages in 95% of 76 canines and 94% of 77 I1 teeth (Table 1). G. Matson provided consistent ages in paired canine and I1 teeth from 75% of 69 moose, and both ages were accurate in 58% of the 69 moose (Table 2). In addition, G. Matson assigned accurate ages to 2 calf moose (11 months of age) and 4 yearlings (14–15 months of age) by tooth inspection

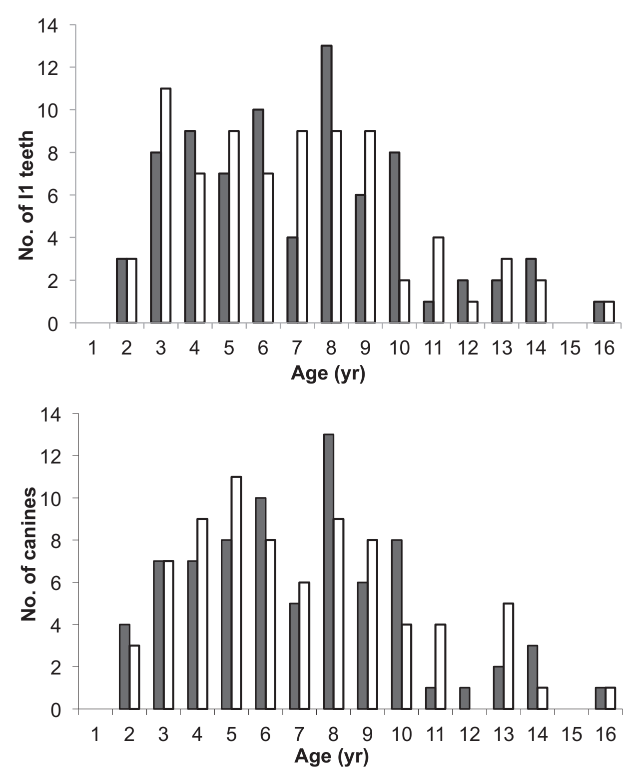

Figure 3. Distributions of known ages (shaded bars) and estimated ages (open bars) of 76 canines (bottom chart) and 77 I1 teeth (top chart). Ages were estimated by counting cementum annuli, as determined at Matson's Laboratory, Milltown, Montana, USA, 2004–2011. Moose teeth originated in Interior Alaska, USA, 2003–2011. We assumed a birth date of 1 June.

Table 1. Numbers (and percent) of moose with deviations in estimated ages from known ages using 76 canines and 77 incisors. Ages were estimated by counting cementum annuli, as determined at Matson's Laboratory, Milltown, Montana, USA, 2004–2011. Moose teeth originated in Interior Alaska, USA, 2003–2011. A birth date of 1 June was assumed, and we included only data from moose ≥2 years of age.

	Deviations in years from known ages and percent of total sample (%)							
Tooth	**−2 to −4**	**−1**	**0**	**+1**	**+3 to +5[a]**	**Average known age (year)**	**Average estimated age (year)**	***n***
Canine	2 (3)	13 (17)	56[b] (74)	3[b] (4)	2 (3)	7.07	6.99	76
I1	3[b] (4)	19 (25)	51 (66)	2 (3)	2 (3)	7.09	6.87	77
Both	5 (3)	32 (21)	107 (70)	5 (3)	4 (3)			153

[a] The +3 and +5 errors came from the same respective moose.
[b] G. Matson assigned a certainty level of A (result likely correct) to all teeth, except he assigned level B (evidence less strong and error possible) to 3 canines and 1 incisor. Two of the 3 B canines had accurate ages assigned and 1 had a +1 error. The B incisor had a −2 error.

without counting annuli, based in part on knowing the month the moose died.

Underestimates of 1 year from known ages were by far the most common error (Tables 1 and 2), and these errors were most common in July and August mortalities (Table 3). We had no June mortalities. Moose that died in July were consistently assigned the previous May age, leading to frequent −1-year errors, whereas August mortalities were inconsistently assigned the previous May age (Table 3; Fig. 4). Using a regression model, we identified 13 August (SE = 5 days) as the midway point of the seasonal transition period between the estimated ages; 1 June was the expected midway point given it was the assumed birth date (Fig. 4). Before 2 July (SE = 20 days) or after 28 September (SE = 20 days), the seasonal inconsistency in assigning ages would be expected to affect <1% of teeth. Moose with −1-year errors in July averaged 10.3 years of age (Table 3).

After controlling for errors due to the seasonal transition period, we found evidence for an effect of age on the error rate (βage = 0.14, SE = 0.06, $t = 2.24$, $P = 0.02$), suggesting that errors accumulated as moose age increased (Table 4). We found no significant difference in accuracy using canine versus I1 teeth (βtooth = 0.13, SE = 0.29, $t = 0.44$, $P = 0.66$) or between male and female moose (βgender = −0.25, SE = 0.47, $t = -0.54$, $P = 0.58$). Age and gender were somewhat confounded in the sampled moose, because older moose were exclusively female as a result of lower harvest rates compared with males. Overlap in ages for male and female moose occurred from ages 3–7, with 1 male moose observed at age 10. Thus, although we found no difference based on gender, this comparison is based on relatively young moose with relatively low error rates (Table 4).

Even after correcting for a seasonal tendency toward −1-year errors, we found evidence for a difference in error rates with direction (βdirection = −0.57, SE = 0.27, $t = -2.11$, $P = 0.03$), suggesting that underestimates of age were more common than overestimates. Results of our comparisons with age, gender, and tooth type were largely robust in unidirectional models. An exception was that the unidirectional model for positive errors did not include a significant effect of age (βage = 0.18, SE = 0.18, $t = 1.02$, $P = 0.31$), which suggests a lack of evidence for increasing positive error rate with age. Explicitly testing for an interaction between age and direction of error requires a larger sample size of older moose.

Although there were fewer +1-year errors in the data compared with −1-year errors, 2 moose had consistent large positive errors in respective canine and I1 teeth (+3 year and +5 year). We lacked the sample size to test whether the accumulation of positive errors was positively correlated for individual moose (e.g., whether some moose were more prone to develop positive errors); however, this could potentially lead to a higher occurrence of large positive errors than would be expected based on our approach.

Table 2. Errors in estimated ages among paired canine and I1 teeth from 69 individual moose with known ages. Ages were estimated by counting cementum annuli, as determined at Matson's Laboratory, Milltown, Montana, USA, 2004–2011. Moose teeth originated in Interior Alaska, USA, 2003–2011. A birth date of 1 June was assumed, and we included only data from moose ≥2 years of age.

Category	No. of pairs	Percentage among 69 pairs
Both correct	40	58
Both incorrect −1 year	9	13
Both incorrect −2 year	1	1
Both incorrect +3 to +5 year	2	3
Canine correct and incisor −1 year	8	12
Canine correct and incisor −2 year	1	1
Canine correct and incisor +1 year	2	3
Incisor correct and canine −1 year	4	6
Incisor correct and canine +1 year	1	1
Incisor −1 year and canine +1 year	1	1
Total	69	100

DISCUSSION

Despite relatively large teeth in moose, we reaffirmed that moose are moderately difficult to age accurately. For example, several authors previously noted that the annuli and annuli pattern are less distinct and more irregular in moose compared with certain other species, so more subjective interpretation is required to age moose teeth (Gasaway et al. 1978, Dalton and Francis 1988, Rolandsen et al. 2008). Furthermore, using the same Matson's Laboratory techniques described here, accuracy rates were 97% for 111 known-age elk (*Cervus elaphus*) ≥2 years of age and 93% for 108 known-age mule deer (*Odocoileus hemionus*) ≥1 year of age (Hamlin et al. 2000). Both species were studied through 14 years of age and investigators found no

Table 3. Monthly distribution of 1-year underestimates of age (−1-year errors) from known ages and associated accuracy rates using 69 canines and 70 incisors. Ages were estimated by counting cementum annuli, as determined at Matson's Laboratory, Milltown, Montana, USA, 2004–2011. Moose teeth originated in Interior Alaska, USA, 2003–2011. The accuracy rate was the (no. of accurate ages)/(total no. of −1-year errors and accurate ages) expressed as a percent. Errors other than −1-year errors were not included here.

		Month												
Tooth	Parameter	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
Canine	No. −1-year errors	2		1		1		5[a]	1[b]	2			1	13
	No. accurate	7	5	6	2	4		2	1	12	2	8	7	56
	Accuracy rate (%)	78	100	86	100	80		29	50	86	100	100	88	81
I1	No. −1-year errors	3		2		1		6[a]	1[b]	4			2	19
	No. accurate	7	5	5	2	4		1	2	9	2	10	4	51
	Accuracy rate (%)	70	100	71	100	80		14	67	69	100	100	67	73
Both	No. −1-year errors	5		3		2		11	2	6			3	32
	No. accurate	14	10	11	4	8		3	3	21	4	18	11	107
	Total *n*	19	10	14	4	10		14	5	27	4	18	14	139
	Accuracy rate (%)	74	100	79	100	80		21	60	78	100	100	79	77

[a] Among the 6 moose with I1 teeth assigned −1-year errors in Jul, 4 were 10 years of age and the remaining 2 were 8 and 14 years of age. Canines from these 6 moose had identical errors, except 1 10-year-old was assigned the correct age.
[b] The single moose with a −1-year error in Aug was 6 years of age.

pattern of error relative to age or gender, and all errors were 1-year deviations from the known age. Our results differ from those of Hamlin et al. (2000) in 3 important ways; lower accuracy rates, errors accumulating with age, and a notable percentage of errors as >1-year deviations from the known age.

We share with Hamlin et al. (2000) the conclusion that there was no pattern of error relative to gender. However, G. Matson concluded that cementum annuli patterns in teeth of male elk and deer were often less complex and more distinct than those in females (Hamlin et al. 2000). We did not provide gender of moose teeth to G. Matson, and he had no experience in comparing male and female moose cementum layers.

Comparing our accuracy parameters with 2 prior studies of known-age moose is problematic, because laboratory methods differed in each study and prior investigators used mostly teeth from young moose. Acknowledging these differences, Gasaway et al. (1978) reported an accuracy rate of 56% based on 36 known-age moose ranging from 2 to 11 years of age; lab methodology included cross sectioning of I1 teeth without staining. Gasaway et al. reported 7% of errors as >1-year deviations from the known age. Also, Rolandsen et al. (2008) examined 51 known-age moose ranging from 1 to 12 years of age (mean age = 2.8 year); lab methodology included staining I1 teeth with hematoxylin. Rolandsen et al. reported accuracy rates of 49%, 71%, and 82% for 3 technicians after initial readings, without replacing poorly rated samples. After poorly rated sections were replaced and an entire second reading was conducted, accuracy rates improved to 53%, 73%, and 90%. Rolandsen et al. reported 2–6% of errors as >1-year deviations from the known age among 3 technicians after poorly rated sections were replaced, and an inverse relationship between moose age and accuracy rate when grouping moose of 1, 2, 3, and ≥4 years of age.

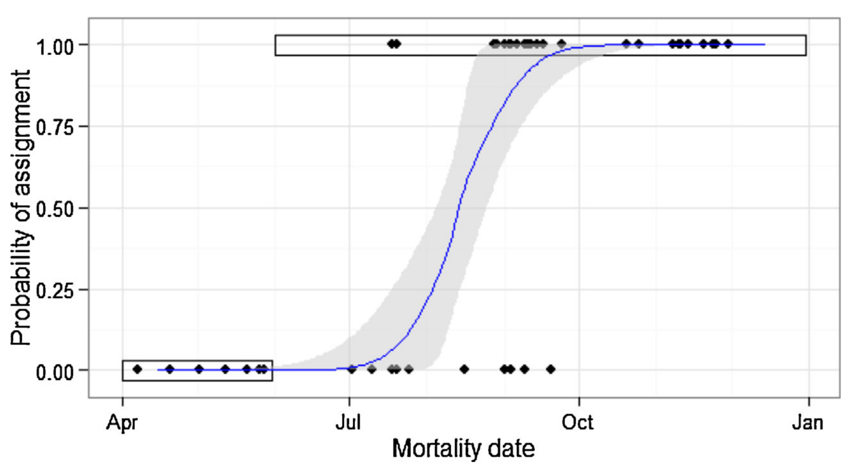

Figure 4. Probability that moose teeth (canine and I1) were assigned the June age based on mortality date. Ages were estimated by counting cementum annuli, as determined at Matson's Laboratory, Milltown, Montana, USA, 2004–2011. Moose teeth had known ages and originated in Interior Alaska, USA, 2003–2011. Line and shaded region represent predicted assignment and 95% confidence intervals based on a regression model. Points indicate observed assignments based on estimated ages. The assumed birth date, used as a cutoff mortality date for assigning age, was 1 June; thus, the correct age assignments, shown in the boxed regions, were 0 prior to 1 June and 1 after 1 June. Incorrect age assignments, shown as unboxed points, were 1-year underestimates of the known age.

Table 4. Predicted accuracy rates of age estimation and confidence intervals (CI) by age of moose (estimated using 76 canines and 77 incisors from known-age moose), based on a reduced regression model where known age was the only fixed covariate. Ages were estimated by counting cementum annuli, as determined at Matson's Laboratory, Milltown, Montana, USA, 2004–2011. Teeth were collected in Interior AK, USA, 2003–2011. We included individual as a random covariate and both positive and negative errors.

Moose known age (year)	*P* of no errors	95%CI	*P* of errors ≥1 year	95%CI	*P* of errors ≥2 year	95%CI
2	0.876	0.80–0.93	0.125	0.06–0.21	0.017	0.00–0.04
3	0.864	0.79–0.92	0.135	0.08–0.21	0.020	0.00–0.04
4	0.853	0.79–0.91	0.147	0.09–0.21	0.023	0.00–0.04
5	0.841	0.78–0.89	0.160	0.11–0.22	0.027	0.01–0.04
6	0.827	0.77–0.87	0.174	0.12–0.23	0.031	0.01–0.05
7	0.812	0.76–0.86	0.188	0.14–0.24	0.036	0.02–0.05
8	0.796	0.74–0.84	0.204	0.15–0.26	0.042	0.02–0.06
9	0.778	0.72–0.83	0.222	0.16–0.28	0.050	0.02–0.08
10	0.760	0.68–0.83	0.240	0.17–0.32	0.059	0.03–0.10
11	0.740	0.65–0.82	0.260	0.18–0.35	0.069	0.03–0.12
12	0.719	0.61–0.81	0.280	0.18–0.39	0.082	0.03–0.15
13	0.698	0.57–0.81	0.303	0.18–0.44	0.096	0.03–0.19
14	0.674	0.52–0.81	0.326	0.19–0.49	0.113	0.03–0.23
15	0.650	0.46–0.80	0.349	0.19–0.53	0.129	0.03–0.27
16	0.626	0.42–0.80	0.372	0.19–0.58	0.149	0.03–0.33

Gasaway et al. (1978) illustrated sources of error in photographs of sectioned moose teeth, and showed that in some teeth all cementum layers were difficult to identify, and multiple layers were occasionally deposited annually. Indeed, 2 moose in our sample had consistent deviations of +3 and +5 years in both the respective canines and I1 teeth. Also, 1 moose had a consistent deviation of −2 years in both the canine and I1 teeth. Rolandsen et al. (2008) reported that a 7-year-old moose was estimated to be 1, 3, and 4 years of age by 3 technicians. Then, after providing a section of a second I1, the moose was aged as 6 years of age by all 3 technicians. Before any new sections were provided the technicians, overall repeatability in 2 tests was 97% for all 3 technicians estimating ages among 51 moose teeth.

We recommend future investigators select a canine tooth, rather than an I1, to estimate age of moose. Annuli and annuli patterns in canines were more distinct and less complex than in I1 teeth, and canines were easier to extract than I1 teeth. Also, in live moose, extracting an incisor is more invasive and leaves a gap in the biting surface. However, with current sample sizes, we were unable to detect a significantly improved accuracy rate using canine versus I1 teeth. Prior to this study, the standard tooth for estimating moose age was the I1 (Dalton and Francis 1988), although molars have also been used because canines and incisors were often missing from weathered specimens collected on Isle Royale (Wolfe 1969).

G. Matson predicted increased aging complications for teeth collected during April–August, when the peripheral annulus can be misinterpreted. Given that we observed the lowest accuracy rates in July and August, we concur. Similarly, Sauer (1973) reported a high variation in completion dates (Feb–Jun) for formation of winter cementum layers in white-tailed deer (*O. virginianus*). We hypothesized that the low nutritional state of our moose, compared with other wild, noninsular populations in North America (Boertje et al. 2007), could have delayed winter annuli completion and complicated July annuli counts, particularly counts in older moose given their thinner annuli. Most investigators avoid April–August tooth collections, choosing instead to collect teeth from harvested moose during September or early winter, when better accuracy appears to be achieved (Table 3; Hamlin et al. 2000).

Moose in different environments may well have different eruption periods and different annuli formations, so we encourage others to publish results to broaden the scope of understanding accuracy parameters in moose. Ready access to a professional lab has many advantages for researchers, including standardized methodology and potential for testing repeatability among highly trained technicians.

ACKNOWLEDGMENTS

G. Matson deserves special acknowledgement for graciously estimating moose ages without financial compensation. We also thank C. Roberts and N. Pamperin for assisting with tooth extraction, and particularly M. Keech and C. T. Seaton for assistance with radiocollaring moose. We thank Associate Editor E. Rominger, reviewer C. Rolandsen, and an anonymous reviewer for their comments on previous drafts of this manuscript; as well as S. Brainerd, G. Matson, L. McCarthy, and B. Taras. We are indebted to L. McCarthy for formatting this manuscript for submission.

LITERATURE CITED

American Society of Mammalogists Animal Care and Use Committee. 1998. Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. Journal of Mammalogy 79:1416–1431.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2014. lme4: linear mixed-effects models using Eigen and S4. R package version 1.1-6. http://cran.r-project.org/web/packages/lme4/index.html. Accessed 4 Dec 2014.

Boertje, R. D., 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.

Boertje, R. D., 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.

Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J. S. White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology and Evolution 24:127–135.
Campana, S. E. 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. Journal of Fish Biology 59:197–242.
Campana, S. E., M. C. Annand, and J. I. McMillan. 1995. Graphical and statistical methods for determining the consistency of age determinations. Transactions of the American Fisheries Society 124:131–138.
Cumming, H. G., and R. Evans. 1978. Repeatability of incisor cementum age determinations for moose. Proceedings of the North American Moose Conference and Workshop 14:68–88.
Dalton, W. J., and G. D. Francis. 1988. The status of applied moose aging technology. Alces 24:69–77.
Fancy, S. 1980. Preparation of mammalian teeth for age determination by cementum layers: a review. Wildlife Society Bulletin 8:242–248.
Gasaway, W. C., D. B. Harkness, and R. A. Rausch. 1978. Accuracy of moose age determinations from incisor cementum layers. Journal of Wildlife Management 42:558–563.
Grue, H., and B. Jensen. 1979. Review of the formation of incremental lines in tooth cementum of terrestrial mammals. Danish Review of Game Biology 11:1–48.
Hamlin, K. L., D. F. Pac, C. A. Sime, R. M. DeSimone, and G. L. Dusek. 2000. Evaluating the accuracy of ages obtained by two methods for Montana ungulates. Journal of Wildlife Management 64:441–449.
Low, W. A., and I. McT. Cowan. 1963. Age determination of deer by annular structure of dental cementum. Journal of Wildlife Management 27:466–471.
Matson, G., L. Van Daele, E. Goodwin, L. Aumiller, H. Reynolds, and H. Hristienko. 1993. A laboratory manual for cementum age determination of Alaska brown bear premolar teeth. Matson's Laboratory, Milltown, Montana, USA, and Alaska Department of Fish and Game, Anchorage, USA. http://www.matsonslab.com/images/publications/Alaska_Brown_-Bear_First_Premolar_Teeth.pdf. Accessed 4 Dec 2014.
Mysterud, A., F. J. Solberg, and N. G. Yoccoz. 2005. Ageing and reproductive effort in male moose under variable levels of intrasexual competition. Journal of Animal Ecology 74:742–754.
Rolandsen, C. M., E. J. Solberg, M. Heim, F. Holmstrøm, M. I. Solem, and B.-E. Sæther. 2008. Accuracy and repeatability of moose (*Alces alces*) age as estimated from dental cement layers. European Journal of Wildlife Research 54:6–14.
Sauer, P. R. 1973. Seasonal variation in physiology of white-tailed deer in relation to cementum annulus formation. Dissertation, State University of New York, Albany, USA.
Scheffer, V. B. 1950. Growth layers on the teeth of pinnipedia as an indication of age. Science 112:309–311.
Sergeant, D. E., and D. H. Pimlott. 1959. Age determination in moose from sectioned incisor teeth. Journal of Wildlife Management 23:315–321.
Solberg, E. J., A. Loison, J. M. Gaillard, and M. Heim. 2004. Lasting effects of conditions at birth on moose body mass. Ecography 27:677–687.
Wolfe, M. L. 1969. Age determination in moose from cemental layers of molar teeth. Journal of Wildlife Management 33:428–431.
Zeileis, A., C. Kleiber, and S. Jackman. 2008. Regression models for count data in R. Journal of Statistical Software 27:1–25.

Associate Editor: Rominger.