THE STATUS OF APPLIED MOOSE AGING TECHNOLOGY

W. J. Dalton,[1] G. D. Francis,[2]
[1]Ministry of Natural Resources, Fort Frances, Ontario P9A 1J4;
[2]Ministry of Natural Resources, Box 5080, Kenora, Ontario, P9N 3X9

ABSTRACT: A survey of North American jurisdictions is the basis of a report on applied moose ageing methodology. The literature was reviewed with respect to progress in aging technology, and validity of applied techniques. Eighteen jurisdictions, of 21 with moose harvests, age moose for management purposes. Sixteen agencies base ages on counts of cementum annuli. Many jurisdictions do not use the maximum technology available: histological sectioning and staining. All current techniques suffer from subjective counting criteria, and inadequate verification. Image enhancement holds promise for near term advances toward objective counting of cementum annuli.

ALCES VOL. 24 (1988) pp.69-77

Sergeant and Pimlott's (1959) cementum annuli count technique for moose (*Alces Alces*) aging superceded, in accuracy and precision, the wear class technique of Passmore, Peterson, and Cringan (1955) (Sergeant and Pimlott 1959 - Table 1, Simkin 1967, Dzieciolowski 1976). Similar trends were seen in other ungulates: elk (*Cervus elaphus*) (see Keiss1969), mule deer (*Odocoileus hemionus*) (see Low and Cowan 1963, Erickson *et al.* 1970), white-tailed deer (*Odocoileus virginianus*) (see Ryel *et al.* 1961, Gilbert and Stolt 1970, Boozer 1969, LaPierre 1976).

Sergeant and Pimlott (1959) cautioned that the cementum annuli technique for aging moose required accuracy validation through checks against known age specimens. They suggested the precision of counts for younger animals would be plus or minus 1 year due to variation in the deposition of the first layer. Further, they suggested that the precision of counts for older moose would be plus or minus 2 years because later annuli are too small to count accurately. Although the method was widely adopted, the accuracy and precision of moose first incisor (I_1) annuli counts was not reported on until 1978 (Gasaway*et al.* 1978, Cumming and Evans 1987).

Gasaway, *et al.* (1978) assessed annuli counts with known age moose teeth. Five 0.3 mm cross sections were cut from first incisors ($I_{1's}$) with a lapidary saw, or a single thin longitudinal (sagittal) section was obtained by grinding alternate sides of the tooth. For moose 2 - 11 years old, 56 percent of cross sections (n=36) and 51 percent of sagittal sections (n=40) were correctly aged. Two "observers agreed on 57 and 64 percent of the longitudinal and cross sections, respectively."

Gasaway *et al.* (1978) identified cementum layers with low contrast, and to a greater extent the presence of extra lines as the sources of error. Lockard (1972) and Rice (1980) have studied the occurrence of anomalies in white-tailed and mule deer cementum annuli. Up to 50% of teeth examined showed irregularity, but the rate of error was low when personnel were familiar with the anomalies. Lockard (1972) found a tendency to overage deer due to a 3X preponderance of false or split annuli, over compound annuli. Gasaway *et al.* (1978) noted this would lead to underestimates of the growth rate of populations, a serious error.

Cumming and Evans (1978) reported on three repeatability tests of moose annuli counts. A half-tooth sagittal face was prepared, by grinding or cutting (no polishing), for dissecting microscope examination under reflected light. With one exception only, the agreement between any two observers (n=3,4,4), or the same observer tested a second time (n=1,0,1), was less than 50 percent. Unanimous agrement was obtained for only 8 of 50, 11 of 150, and 3 of 50 individual teeth for the three tests respectively.

The methods of incisor preparation used by Gasaway *et. al.* (1978) and Cumming and

Evans (1978) differed substantially. The poorer results obtained in Cumming and Evans (1978) tests may reflect the difference in methodology, or it may be attributed to geographic variability in seasonality of cementum growth.

Sergeant and Pimlott (1959) prepared both ground sagittal thin sections and polished sagittal faces. They did not discuss the merits of either with respect to the quality of results.

Three sources of variability have been identified. Two are due to variable experimental units: quality of annuli zonation, and variation in deposition of the first cementum layer. The third source of error is the experimental error due to methods. The errors are not compensating (Gasaway *et al.* 1978, Rice 1980), and no model for correction has been attempted.

Essentially two methods have been employed to age ungulate teeth by cementum annuli. The first involves preparing a thin section or the face of a bisected tooth through sawing, and/or grinding, and polishing in some cases (Sergeant and Pimlott 1959, McEwan 1963, Low and Cowan 1963, Ransom 1966, Mitchell 1967, Simkin 1967, Wolfe 1969, Douglas 1970, Ouellet 1977, Gasaway *et al.* 1978, Cumming and Evans 1978). The second technique, again with many variations, attempts to enhance the readability of annuli by preparing stained histological sections (McEwan 1963, Low and Cowan 1963, Gilbert 1966, Reimers and Nordby 1968, Lockard 1972, Miller 1974, Turner 1977, Leader-Williams 1979, Rice 1980). In some instances sawn and/or ground thin sections have been stained (Lockard 1972), or decalcified and stained (Keiss 1969, McCutchen 1969, Cumming and Evans 1978), and cross section faces were scorched and polished (Ouellet 1977).

Lockard (1972) compared specific variations of the two methods using incisors of white-tailed deer. Annuli were not consistently apparent in stained ground sections, but they were in histologically prepared incisor sections. Low and Cowan (1963) rejected both ground thin sections and half tooth polished surfaces (faces) as giving unsatisfactory results for mule deer. They settled on a histological technique.

There has been some experiments which varied one or more aspects of histological tooth section preparation. Thomas (1977) and Stone *et al.* (1975) evaluated different stains from those in standard use at the time. Each found alternatives which had virtues above and beyond hematoxylin or hematoxylin and eosin. Miller (1974) experimented with decalcifying solutions, time limits, dehydration methods, mounting media, types of microtome, stains, and staining time.

Much of the work to refine techniques was done on white-tailed deer, mule deer, and caribou (*Rangifer tarandus*). Cementum annuli in these species are narrow and enhancement seemed a necessary and often obligatory measure. Moose annuli are large by comparison and in many teeth the zonation is obvious. One of us, (Dalton, unpubl.), having worked with teeth prepared in two jurisdictions, suspected this had led to a lack of rigor in moose aging programs. The reasons for greater rigor in the preparation of smaller ungulate teeth are also evident in moose at unacceptable levels (Gasaway *et. al.* 1978, Cumming and Evans 1978).

In addition to wear classification and I_1 annuli counts, a number of other aging methods have been tested: annuli in cementum pads (moose, Wolfe 1969; red deer (*Cervus elaphus*), Mitchell 1967), eye lens weight (Simkin 1967), insoluble lens proteins (white-tailed deer, Ludwig and Dapson 1977), and layers in incisor secondary dentine (moose, Haagenrud 1978). None has proved a practical substitute for cementum annuli counts of moose I_1 teeth, due either to overhead in methodology or more often to lower accuracy.

An attempt was made to do three things in this report: survey the moose aging technology currently applied in North American jurisdictions, compare this level of applied technology against what has been published, and to seek avenues to advance current or potential technologies. This paper does not address strategies for aging structures collection or the use of ages as a management tool.

METHODS

North American jurisdictions with moose management programs were polled by telephone in April 1988. The questions were directed to technical staff if possible. Only the methods being applied to ascertain the ages of moose for management purposes were included. Research branches or institutions were not surveyed.

Questions determined whether or not a management program was in place, what parts of the animal (aging structures) were collected and which general method was applied. Where annuli counts were carried out, the technical details were recorded. Respondents were asked about the level of effort in the counting process, and whether or not there was quality control.

The tabulated telephone survey results were sent to the respondents for confirmation.

RESULTS

Aging Structure Collections

It was determined that 21 North American jurisdictions have moose hunting seasons (Table 1). Eight agencies (including Alaska) request that hunters provide them whole or half-jaws. Eleven agencies (including Alaska) request that only the first incisors, or the incisor row, be submitted.

Aging Methods In Use

Of the 18 jurisdictions who collected material for aging, 16 do cementum annuli counts of moose incisors ($I_{1's}$) (4 of these also employ the wear class method), and 2 wear age only (Table 1). Two agencies collecting whole or half jaws limit aging to annuli counts of $I_{1's}$.

Three agencies do not at present have aging programs. Colorado has a very low harvest, 3-5 moose, and classifies kills as adult, yearling, or calf. Idaho terminated their moose aging program in 1986. The Yukon Territory did have an aging program but has lost it due to budget constraint.

Teeth Preparation and Reading

Incisors were prepared for annuli counts (Table 2) by sawing or grinding a tooth face in 5 jurisdictions (including Ontario). Seven agencies cut thin sections, ±100 microns, with saws or grindstones (including Ontario). Three of five agencies using histologically prepared sections (< 20 microns) employed a commercial laboratory (in all cases Matson's Laboratory, Milltown, Montana which uses a paraffin embedding technique).

The binocular dissecting microscope (field microscope) was used to read the annuli of tooth faces, and most thin sections (Table 2). New Brunswick and two Ontario labs used compound microscopes to read the latter. With one exception histological sections were read with compound microscopes; Utah used a fish scale projection machine.

Quality Control

Two agencies (excluding 1 Ontario lab) routinely age two teeth per moose (Table 2). Three agencies, including one of the former (Manitoba), routinely count each tooth prepared more than once (Table 3). Seven other agencies (including Alaska) mount more than one section per tooth (Table 2) on the same slide. Thus 11 jurisdictions have some type of systematic redundancy built into their systems to detect aging errors. We did not ascertain whether any of the agencies established independence between estimates from the same animal. In the case of multiple sections on single slides this would not be the case unless unusual measures were taken.

A number of other labs take some precau-

Table 1. Moose aging structures collected and aging techniques applied by management agencies, with moose hunting seasons, in North American jurisdictions.

		AGING METHOD			
JURISDICTION	AGE STRUCTURES COLLECTED	WEAR	ANNULI	AVERAGE HARVEST	AVERAGE # AGED
Alaska					
Fairbanks	$I_{1'S}$	-	YES	-	200
Anchorage	HALF JAW, ANTLERS	YES	YES	4,300	475[a]
Alberta	INCISOR ROW	-	YES	-	600
British Columbia[b]					
Cranbrooke	ONE I_1, ANTLERS	-	YES	450	110[c]
Kamloops	$I_{1'S}$	-	YES	-	228
Prince George	$I_{1'S}$	-	YES	1,200	1,200
Colorado	NONE (CLASSIFY A,Y,C)	-	-	-	4
Idaho	NONE (JAW UNTIL 1986)	(NO)	(YES)	-	-
Maine	$I_{1'S}$ FROM CARCASS	NO	YES	850	625
Manitoba	HALF JAW	NO	YES	-	800+
Minnesota	$I_{1'S}$	-	YES	1,000[d]	950
Montana	HALF JAW	YES	NO[e]	484	90
New Brunswick	JAW FROM CARCASS	YES	YES	-	40
Newfoundland	WHOLE JAW	YES	YES	6,500	2,000[f]
North Dakota	INCISOR ROW	-	YES	125	100
N.W.T					
Inuvik Region	WHOLE JAW	NO	YES	175	40
Southern Region	NONE	-	-		
Nova Scotia	HALF JAW	YES	NO	< 200	< 200
Ontario - Regions					
Algonquin	WHOLE JAW	YES	YES	900	300
North Central	WHOLE JAW	YES	YES	2,844	1,000
Northeastern	WHOLE JAW	YES	YES	2,025	850
Northern	WHOLE JAW	YES	YES	1,400	1,150[f]
Northwestern	WHOLE JAW	YES	YES	1,953	600
Quebec	$I_{1'S}$	-	YES	11,000	2,250
Saskatchewan	$I_{1'S}$	-	YES	3,500	1,200
Utah	$I_{1'S}$	-	YES	-	-
Washington	$I_{1'S}$	-	YES	-	5
Wyoming	$I_{1'S}$	-	YES	1,500	500+
Yukon	NONE, (IN PAST $I_{1'S}$)	-	(YES)		

[a] Age structures from permit hunts only. (Approx. 5% of other hunters submit jaws.)
[b] Labs at Fort St. John and Williams Lake not surveyed.
[c] Plus 200 sectioned and aged for other offices in Province.
[d] Every other year.
[e] Montana occasionally has annuli counts done.
[f] Includes calves and yearlings which are wear aged only.

tion by double checking some teeth, or getting second opinions either internally or from Matson's (Table 3). These were not generally systematic or permanent features of the programs.

DISCUSSION

Age Model

One aspect of aging technology which is crucial to accuracy is the interpretation of the sequence of annuli deposition. The moose literature is contradictory in this regard. The Gasaway *et al.* (1978) model for moose ages was based on wide opaque zones being deposited in the winter, at odds with Sergeant and Pimlott's (1959) finding that these zones were probably laid down in the summer. Wolfe (1969) used the latter definition. Mitchell (1967) and Douglas (1970) studied the problem closely in red deer. The wide opaque, cementocyte rich, zone was clearly deposited in the summer and fall. This is also the case with white-tailed deer (Lockard 1972, Gilbert 1966), caribou (Miller 1974), reindeer (Reimers and Nordby 1968), and pronghorn (*Antilocapra americana*) (McCutchen 1969).

The photo in Gasaway *et al.* (1978) Figure 1 shows a known age 4.5 year old moose. It shows an opaque outermost layer as would be expected by Mitchell (1967). If opaque material is laid down in the summer and fall, the first wide opaque band in this tooth must have been laid down in the second summer of life. Apparently the first winter translucent line is poorly developed and is adjacent to the dentine-cementum interface. One of us (Dalton, unpub.) observed that 4% (n=50) of moose from the Northwestern Ontario Region did not have calf summer/fall opaque material, in the region of the tooth normally aged, on one of two $I_{1's}$, while an additional 4% had no calf summer opaque on either I_1. This condition can be detected because the first year opaque cementum does not exceed the tip of the dentine, while second year

Table 2. Procedures used to prepare and age moose incisors.

JURISDICTION	SECTIONING PROCESS	SECTION TYPE	# OF TEETH	MICROSCOPE TYPE	TYPE OF LIGHTING	MOUNT TYPE[a]	PRESENTATION
Alaska							
Fairbanks	SAW THIN	CROSS	1	DISSECTION	TRANSMITTED	SLIDE >1	WET
Anchorage	GRIND THIN	SAGITTAL	1	DISSECTION	TRANSMITTED	SLIDE	WET
Alberta	HISTOLOGICAL[b]	SAGITTAL	1	COMPOUND	TRANSMITTED	SLIDE >1	PERMANENT
British Columbia							
Cranbrooke	GRIND THIN	SAGITTAL	1	DISSECTION	T (AND R)	HAND HELD	WET
Kamloops	GRIND THIN	SAGITTAL	1	DISSECTION	REFLECTED	HAND HELD	DRY
Prince George	GRIND THIN	SAGITTAL	1	DISSECTION	TRANSMITTED	HAND HELD	WET
Maine	SAW THIN	CROSS	1	DISSECTION	R and T	SLIDE >1	WET
Manitoba	GRIND THIN	SAGITTAL	2	DISSECTION	R and T	HAND HELD	DRY
Minnesota	SAW FACE	SAGITTAL	2	DISSECTION	REFLECTED	HAND HELD	WET
New Brunswick	GRIND THIN	SAGITTAL	1	COMPOUND	R and T	-	WET
Newfoundland	GRIND FACE	SAGITTAL	1	DISSECTION	REFLECTED	PLASTICINE	WET
North Dakota	HISTOLOGICAL[b]	SAGITTAL	1	COMPOUND	TRANSMITTED	SLIDE >1	PERMANENT
N.W.T.	GRIND FACE	SAGITTAL	1	DISSECTION	REFLECTED	HAND HELD	WET
Ontario Regions							
Algonquin	SAW THIN	SAGITTAL	1	COMPOUND	TRANSMITTED	SLIDE	PERMANENT
North Central	SAW FACE	SAGITTAL	1	DISSECTION	REFLECTED	PLASTICINE	WET
Northeastern	SAW THIN	SAGITTAL	1(2)	COMPOUND	TRANSMITTED	SLIDE	WET
Northern	SAW THIN	SAGITTAL	2	DISSECTION	REFLECTED	SLIDE	PERMANENT
Northwestern	SAW THIN	SAGITTAL	1	DISSECTION	R and T	SLIDE	PERMANENT
Quebec	SAW FACE	CROSS	1	DISSECTION	REFLECTED	PLASTICINE	DRY
Saskatchewan	GRIND THIN	SAGITTAL	1	DISSECTION	TRANSMITTED	HAND HELD	DRY
Utah	HISTOLOGICAL	SAGITTAL	1	FISH SCALE	TRANSMITTED	SLIDE >1	DRY
Washington	HISTOLOGICAL[b]	SAGITTAL	1	COMPOUND	TRANSMITTED	SLIDE >1	PERMANENT
Wyoming	HISTOLOGICAL[c]	SAGITTAL	1	COMPOUND	TRANSMITTED	SLIDE >1	PERMANENT

[a] Where >1 appears, more than one section was mounted per tooth.
[b] Matson's Laboratory, P.O. Box 308, Milltown, Montana 59851
[c] Use Matson's procedure, with different stain.

Table 3. Effort and quality control brought to bear while aging moose incisors.

JURISDICTION	COUNT ROUTINELY > 1 TIME	TIME TO COUNT ANNULI	COST PER TOOTH	ACCURACY CHECK, (AC) DOUBLE CHECK, (DC) SECOND OPINIONS, (SO)
Alaska				
Fairbanks	NO	1 - 4 minutes	UNKNOWN	SO IN HOUSE, AC GASAWAY *et al.* 1978
Anchorage	NO	30 - 60 seconds	UNKNOWN	SO IN HOUSE, DC SOME
Alberta	NO	1 - 2 minutes	$1.90 U.S.	AC SOME
British Columbia				
Cranbrooke	NO	5 seconds	UNKNOWN	(DC & SO IN PAST)
Kamloops	NO	5 - 30 seconds	UNKNOWN	DC 10%
Prince George	NO	< 1 minute	UNKNOWN	SO MATSON'S•
Maine	NO	30 - 60 seconds	UNKNOWN	DC 20%
Manitoba	YES	1 minute	UNKNOWN	DC ALL, AC i.e. 2 TEETH/MOOSE
Minnesota	NO	1 - 4 minutes	$1.90	AC i.e. 2 TEETH/MOOSE
New Brunswick	NO	Varies with clarity	$4.50	SO MATSON'Sa
Newfoundland	NO	10 - 60 seconds	UNKNOWN	AC INTERNAL, DC SOME, SO MATSON'S•
N.W.T.	YES	1 minute	UNKNOWN	SO IN HOUSE, AC IN HOUSE
Ontario - Regions				
Algonquin	NO	20 - 60 seconds	$4.00	(DC SOME IN PAST)
North Central	NO	approx. 1 minute	UNKNOWN	DC SOME
Northeastern	NO	30 - 60 seconds	UNKNOWN	(SO ALL IN HOUSE TO 1986 75%+ AGREE)
Northern	NO	< 1 minute if clear	UNKNOWN	SO RESEARCH LAB, AC (2 TEETH/MOOSE)
Northwestern	NO	1 - 2 minutes	$3.50	SO RESEARCH LAB
Quebec	YES	1 - 2 minutes	$1.95	DC ALL
Saskatchewan	NO	< 30 seconds	UNKNOWN	INFREQUENT SO IN HOUSE
Utah	NO	1 minute	$2.20	-
Wyoming	NO	1 - 2 minutes	$3.00	DC SOME, SO MATSON'S•

• Matson's Labratory, P.O. Box 308, Milltown, Montana 59851

cementum does. The 3.5 year old known age moose from British Columbia (Sergeant and Pimlott 1959, Fig. 5) had a thick opaque layer laid down in the first summer/fall of life.

We disagree with Cumming's rules for aging moose, but note his observations of variability in early cementum layers (Cumming and Evans 1978 - Appendix I). There should not be a translucent band next to the cemento-dentine juncture unless it is formed in the first winter. The outer edge of the first translucent band counts 1 year, the second as two years. Some variability in interpretation of moose teeth can be expected across the North American range of moose (Peterson *et al.* 1983, Young and Marty 1986, see discussion above re: age models). It would assist labs everywhere if the variability was assessed and reported.

Error Reduction

It is not clear whether the majority of labs which take precautions designed to improve their level of accuracy (double counts, cross checks between teeth, and multiple sections from the same tooth), can improve the utility of their data by doing so. The efficiency of double counts or multiple sections from the same tooth for this purpose must be called into question. Characteristics of sampling units which produce errors are likely to reproduce themselves in multiple sections, multiple counts, and multiple teeth. Experimental errors due to technique will also tend to replicate within and between labs. Precision is not evidence of accuracy. Identified discrepancies may help to reduce error rates but cannot eliminate error, or identify the rate of error.

State Of The Art

Many jurisdictions are not using the maximum amount of technology which has been developed to date (histological techniques). It can be expected that there is a gradient in accuracy of the methodology corresponding to the level of technology applied. However, no effort has been expended to document these differences. Experiments using known age materials to test annuli counting methodologies against each other are called for.

Low budgets and scarce staff were mentioned a number of times by respondents in reference to the level of technology employed. However, few labs understood their costs. Are many managers complacent about the moose aging portion of management programs?

Subjective Counting

We are concerned that a cornerstone of moose management has not been cemented in place. We have identified a number of points of weakness, and suggested or implied that fixes are possible or at least desirable. These have been limited to the immediate details of current practice. What remains is the possibility of circumventing problems by new approaches. The crux of the aging problem is the subjective way annual layers of cementum deposition are counted. There must be ways to remove the subjective element. The pursuit of a definitive technique should be a primary goal of research efforts.

Research in the area of advanced histological techniques may still simplify and enhance the available methods. Indeed it cannot be said with certainty that the best combination of procedures now available are in use anywhere. However, we suspect that histological techniques carry a limited potential because of the overhead in preparatory steps. Further development of the technique will not in itself eliminate the subjective element.

Objective Counting

The ultimate technique would be simple and objective. Say, for example, where the technician inserts a clean whole incisor into a slot and obtains a reading, much as a vial is inserted into a spectrometer for elemental analysis. How closely have people working with sound waves (ultrasound), shock waves, or sonar and radars looked at this problem? A study of cementum elemental structure, using the scanning electron microscope, is called for as baseline data in the search for a suitable technique. The tooth is a physical structure and may yield to physics.

Or it may yield to a combination of physics and chemistry. Formic acid etching (Sohn 1967) has been found to enhance readability of annuli through differential erosion of rest lines and summer depositions. Scorching of a tooth face has also been employed (Ouellet 1977). One wonders whether coherent light (laser) diffraction patterns could be used to amplify and record the topography. Or whether the principles of radar altimeters could be applied (Befort 1988). A topographic scan with sound waves may produce similar results. The atomic force microscope (J. Kinoshita, Science and the Citizen, Scientific American, July 1988) drags a fine needle across a surface with only a billionth of a pound force, a `mirror' on the needle reflects a laser beam for measurements. A coarse analog to this machine may be what is required.

The greatest potential, for near term results, probably lies in the field of image enhancement (see Ossenbrug this issue). Simple tooth preparation methods such as cutting, grinding, and polishing may suffice. Digital images recorded at multiple light wavelengths are the key, as they are in remote sensing. Computer enhancement would present the image, and programs could probably be written to capture an age of highest probability.

Some of these ideas may be pipe dreams, one may be the idea that saves a critical aspect of a moose management program from the accountants axe. Talk someone from outside moose biology into thinking about it. What can be done in programs right now? Encourage technicians and biologists to communicate with other labs about problems and solutions. Budget for enhanced technology. Spend a day in the lab living with some of the frustration that reading teeth provides. Design experiments to teach us more about counting cementum annuli.

ACKNOWLEDGEMENTS

Funding was provided by the Canada-Ontario Forest Resources Development Agreement, and the Ontario Ministry of Natural Resources. We thank the technicians, biologists, and staff who took time to answer questions and confirm data in the tables. Two anonymous reviewers contributed heavily to the quality of the paper.

REFERENCES

BEFORT, W. 1988. Controlled-scale aerial sampling photography: Development and implications for multiresource inventory. J. Forestry 86:21-28.

BOOZER, R. B. 1969. Cementum annuli versus tooth-wear aging of the white-tailed deer of Alabama. Ph.D. Thesis Jacksonville State University, Jacksonville, Alabama.

CUMMING, H. G., AND R. EVANS. 1978. Repeatability of incisor cementum age determinations for moose. Proc. N. Am. Moose Conf. Workshop 14:68-88.

DOUGLAS, M. J. W. 1970. Dental cement layers as criteria of age for deer in New Zealand with emphasis on red deer, .*Cervus elaphus* N.Z. J. Sci. 13:352-358.

DZIECIOLOWSKI, R. 1976. Age appraisal in moose. Acta Theriologica 21(23):307-310.

ERICKSON, J. A., A. E. ANDERSON, D. E. MEDIN, and D. C. BOWDEN. 1970. Estimating ages of mule deer - an evaluation of technique accuracy. J. Wildl. Manage. 34(3): 523-531.

GASAWAY, W. C., D. B. HARKNESS, and R. A. RAUSCH. 1978. Accuracy of moose age determinations from incisor cementum layers. J. Wildl. Manage. 42(3) :558-563.

GILBERT, F. F. 1966. Aging White-tailed deer by annuli in the cementum of the first incisor. J. Wildl. Manage. 30(1):200-202.

GILBERT, F. F., and S. L. STOLT. 1970. Variability in aging Maine white-tailed deer by tooth-wear characteristics. J. Wildl. Manage. 34(3): 532-535.

HAAGENRUD, H. 1978. Layers in secondary dentine of incisors as age criteria in moose(*Alces alces*). J. Mamm. 59(4):857-858.

KEISS, R. E. 1969. Comparison of eruption-wear patterns and cementum annuli as age criteria in elk. J. Wildl. Manage. 33(1):175-180.

LAPIERRE, L. E. 1976. Comparaison entre deux méthodes d'estimation de l'âge chez le cerf de virginie (*Odocoileus virginianus*). Naturaliste can., 103:73-75.

LEADER-WILLIAMS, N. 1979. Age determination of reindeer introduced into South Georgia. J. Zool., Lond. 188:501-515.

LOCKARD, G. R. 1972. Further studies of dental annuli for aging white-tailed deer. J. Wildl. Manage. 46(1):46-55.

LOW, W. A., and I. McT. COWAN. 1963. Age determination of deer by annular structure of dental cementum. J. Wildl. Manage. 27(3):465-471.

LUDWIG, J. R., and R. W. DAPSON. 1977. Use of insoluble lens proteins to estimate age in white-tailed deer. J. Wildl. Manage. 41(2):327-329.

McCUTCHEN, H. E. 1969. Age determination of pronghorns by the incisor cementum. J. Wildl. Manage. 33:172-175.

McEWAN, E. H. 1963. Seasonal annuli in the cementum of the teeth of barren-ground caribou. Can. J. Zool. 41(1):111-113.

MILLER, F. L. 1974. Age determination of caribou by annulations in dental cementum. J. Wildl. Manage. 38(1):47-53.

MITCHELL, B. 1967. Growth layers in dental cement for determining the age of red deer (*Cervus elaphus L.*). J. Anim. Ecol. 36(2):279-293.

OUELLET, R. 1977. Une méthode améliorée dans la préparation des incisives I_1 des ongulés. Unpubl. report Ministère du Tourisme, de la Chasse et de la Pêche, Quebec.

PASSMORE, R. C., R. L. PETERSON, and A. T. CRINGAN. 1955. A study of mandibular tooth wear as an index to age of moose. Appendix "A", pp.223-238, in *North American Moose*, by Randolph L. Peterson. Toronto: Univ. of Toronto Press.

PETERSON, R. O., C. C. SCHWARTZ, and W. B. BALLARD. 1983. Eruption patterns of selected teeth in three North American moose populations. J. Wildl. Manage. 47(3): 884-888.

RANSOM, A. B. 1966. Determining age of white-tailed deer from layers in cementum of molars. J. Wildl. Manage. 30(1):197-199.

REIMERS, E., and O. NORDBY. 1968. Relationship between age and tooth cementum layers in Norwegian reindeer. J. Wildl. Manage. 32(4): 957-961.

RICE, L. A. 1980. Influences of irregular dental cementum layers on aging deer incisors. J. Wildl. Manage. 44(1): 266-268.

RYEL, L. A., L. D. FAY, and R. C. VAN ETTEN. 1961. Validity of age determination in Michigan deer. Papers of the Michigan Academy of Science, Arts, and Letters. Vol. XLVI, (1960 Meeting).

SERGEANT, D. E., and D. H. PIMLOTT. 1959. Age determination in moose from sectioned incisor teeth. J. Wildl. Manage. 23(3):315-321.

SIMKIN, D. W. 1967. A comparison of three methods used to age moose. Proc. Northeast Section of the Wildlife Society, Quebec, P.Q.

SOHN, A. J. 1967. An evaluation of the dental annuli technique for determining age of white-tailed deer in Iowa. Iowa Academy of Science 74:72-77.

STONE, W. D., A. S. CLAUSON, D. E. SLINGERLANDS, and B. L. WEBER. 1975. Use of Romanowsky stains to prepare tooth sections for aging mammals. New York Fish and Game Journal 22: 156-158.

THOMAS, D. C. 1977. Metachromatic staining of dental cementum for mammalian age determination. J. Wildl. Manage. 42(2):207-210.

TURNER, J. C. 1977. Cemental annulations as an age criterion in North American sheep. J. Wildl. Manage. 41(2):211-217.

WOLFE, M. L. 1969. Age determination in moose from cemental layers of molar teeth. J. Wildl. Manage. 33(2):428-431.

YOUNG, W. G., and T. M. MARTY. 1986. Wear and microwear on the teeth of a moose (*Alces alces*) population in Manitoba, Canada. Can. J. Zool. 64:2467-2479.