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CEMENTAL DEPOSITION, TOOTH SUCCESSION, AND HORN DEVELOPMENT AS CRITERIA OF AGE IN DALL SHEEP

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Abstract: Patterns of cementum, tooth succession, and external and internal horn annuli were studied in 129 specimens of Dall sheep (*Ovis dalli*). Fluoromicroscopy of annually produced cemental layers may be used to estimate age of all sheep older than 1 year. During the first 4 years of life age can be determined from the sequence of incisor replacement. Counts of annual horn increments provide a means of estimating age, but may be difficult to distinguish in older animals, particularly females.

The purpose of this study was to find reliable methods for estimating the age of Dall sheep.

I have investigated growth patterns of horns, replacement and attrition of teeth, pattern of deposition of dental cementum, and have compared age-related characteristics of bighorn sheep (*Ovis canadensis*) and Dall sheep.

The validity of horn-segment counts as indicators of age in bighorn sheep was established by Geist (1966).

The sequence of eruption and replacement of teeth in Dall sheep has not been described, except in a very general way by Murie (1944).

Techniques for the study of annual increments in cementum were first described by Laws (1952, 1953). Similar methods have been applied to North American cervids by Sergeant and Pimlott (1959), McEwan (1963), Low and Cowan (1963), Gilbert (1966), Ransom (1966), and to bovids by Armstrong (1965), and Novakowski (1965). These earlier studies have shown that cementum is deposited on the roots of the teeth in the form of alternating layers, of which one translucent and one opaque layer represent 1 year's deposit.

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couragement, especially for donating the bulk of the specimen material used during this study, and for his critical review of the manuscript. P. L. Wright, R. S. Hoffmann, and W. B. Rowan, Department of Zoology, University of Montana, offered many helpful suggestions during the research and preparation of the manuscript. R. Baker, Stella Duncan Institute, University of Montana, assisted in fluoromicroscopy and photomicrography. Radiograms were prepared by B. Cerino, Health Service, University of Montana. Several specimens were provided by biologists of the Alaska Department of Fish and Game, and the University of Alberta. To these persons, as well as to others not individually named, I express my sincere thanks.

MATERIALS AND METHODS

All but 11 of the specimens utilized were obtained from Nunamiut Eskimo hunters from the central Brooks Range, Arctic Alaska. The skulls or mandibles and horns from 118 Dall sheep harvested for food were saved and carefully labeled as to sex, date, and location between 1950 and 1966, an average of 7 per year. Dall sheep do not play an important role in the economy of the Nunamiut, but they are hunted when caribou are scarce (Rausch 1951). Ten more specimens, including one of known-age, from various locations in south central Alaska were provided by biologists of the

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Alaska Department of Fish and Game, and the skull of a 5-day-old lamb was obtained from the University of Alberta. Bones were cleaned by means of dermestid beetles and bleached in hydrogen peroxide. After cleaning, all bones and horns were dried thoroughly before being measured.

Published birth dates for Dall sheep fall between 5 May and 28 June (Sheldon 1930: 366, Dixon 1938:216, Murie 1944:89, Rausch 1951:193). Since the frequency distribution of births is not known, the median date, 1 June was used.

Horns

The horns of 89 Dall sheep (37 ♂♂, 52 ♀♀) were utilized in this phase of the study. Counts of external horn segments were made as described by Geist (1966). The accuracy of counts of the annual rings was checked in a series of horns which had been sawn lengthwise, as suggested by Rausch (1951) and Taylor (1962). In such sections, the limits of successive annual increments of horn are readily visible. Counts of annual horn rings were used to check the reliability of other methods of estimating age.

Replacement of Teeth

The dental terminology of Riney (1951) and of Sisson and Grossmann (1953) has been followed in the present work. Symbols for deciduous teeth are preceded by "D." The sequence of replacement of teeth was determined by direct examination of cheek-teeth and incisors. A tooth was considered to be erupting if any portion was visible above the level of the alveolus in the cleaned mandible. Radiograms proved useful in determining the state of development of permanent teeth within the alveoli. Fifty of the 129 specimens showed evidence of eruption and were used to study tooth succession. By comparing specimens of un-

known age with two specimens of known age, and by counting annual rings in the horns, it was possible to estimate age within ± 1 month, when date of death was known.

Cemental Layers

The first incisor (I_1) was chosen as the tooth most suitable for study of the cementum. This tooth is easily removed and it is the first of the replacement dentition to erupt. Techniques utilizing the third molar (M_3) from sheep, as described by Armstrong (1965), could not be applied because the coronal cementum on many specimens was damaged or lost. In museum specimens which could not be mutilated, the tooth was removed by soaking, after which the lower half of the root was cut off and the remainder of the tooth was then replaced and glued in position. Several techniques were investigated to determine the best method for detecting the annual layers in the cementum. In all cases the individual teeth were first imbedded in plaster of Paris to facilitate handling, and to prevent unnecessary chipping during sectioning. Sections were cut with a 1-inch dental diamond wheel attached to a Dremel Moto-tool (Pfungst and Co., Inc., 62 Cooper Square, New York 3, N. Y.). The specimens were water-cooled during sectioning. Sections from 1–2 mm thick were obtained and reduced to a thickness of 50–75 μ by the Frost technique (Frost 1958:274–276). Sections 50 μ thick may be produced in less than 10 minutes by this method.

Since the thickness of the cemental layer differs from place to place on the root of the tooth, sagittal sections of the entire root proved to be most satisfactory. Sections decalcified and stained by standard techniques did not produce satisfactory results when examined by transmitted or polarized light. Similar results were reported by Arm-

strong (1965) who discovered that stained sections from incisors of bighorn sheep were not suitable for determination of age. One of the major problems is that cementum of the incisiform teeth is very thin and the annuli are crowded together. I found that even most careful staining procedures result in blending of annual layers making delineation of annuli nearly impossible.

After further experimentation, a new procedure was devised which did not require staining or decalcification: sections were washed by shaking in a vial of distilled water to which several drops of liquid detergent had been added, and then were rinsed in distilled water; after dehydration in 70 percent and absolute ethanol (5 min in each), the sections were dipped in xylene and mounted in Permount (Fisher Scientific Co., Fairlawn, New Jersey). The slides were examined by means of a Zeiss Standard GFL fluorescence microscope equipped as follows: Osram high-pressure mercury lamp; exciter filter III with barrier filters 53/47. Optimum magnification was 160 \times .

RESULTS AND DISCUSSION

Determination of Age from Horns

Annual increments in horns of wild sheep are sometimes difficult to count. Murie (1944) reported that the growth-rings fall very close together in horns of old Dall sheep ewes, making it difficult to determine accurately the age of some individuals. In the present study also, external horn-rings were difficult or impossible to count in very old animals, and in some cases the horns of females had been broken to within a few centimeters of the base.

Careful study of one known-age ewe, with well developed horns, revealed that the first horn-ring forms during the first winter of life and one is formed each win-

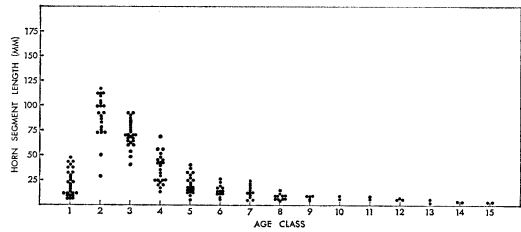


Fig. 1. Length of annual horn increments in Dall sheep ewes.

ter thereafter. The chronological arrangement of horn-rings in Dall sheep is the same as that reported for bighorn sheep by Geist (1966). I found that the horns of Dall sheep begin to develop when lambs are about 4 months old. The sex of lambs cannot be determined from the horns, but after the first year, the horns of males have larger bases than those of females which are also more slender. The corneous sheath continues to grow throughout the life of the individual, but it acquires the greater part of its length during the second and third summers (Figs. 1 and 2). The basal circumference and the length of horns of Dall sheep rams increase at essentially the same rate (Fig. 3).

The annual ring is a result of interrupted growth during the winter. Little, if any, growth was taking place in the horns of animals killed from October through January. In a sample of 18 sheep killed in February, the horns of one had a new annual ring. By May, new growth was evident in all horns. Growth appears to be most rapid during early summer, and by the end of September has essentially ceased. If a birth date of June 1 is assumed, it is obvious that after the first year, new growth begins annually as much as 3 months before that date. Thus, an animal not yet 5 years old may show 5 horn-rings and 6 increments, the last of which is incomplete. In late fall, such an

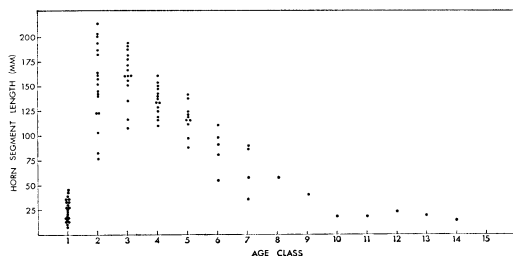


Fig. 2. Length of annual horn increments in Dall sheep rams.

animal would have 6 complete annual increments at an age of 5½ years.

Some experience is required to distinguish annual rings from other corrugations on the horns, especially in females and older males. The unique character of the annual ring is that it forms a deep, continuous groove with loosened edges, whereas the other corrugations consist of smoothly rounded ridges and grooves. In horns sawed lengthwise, the location and number of annuli are obvious. In such sections the horn appears to consist of a series of stacked cones, each of which represents an annual increment.

The horn-tips of Dall sheep are rarely "broomed," but they may show considerable wear in animals more than 5 years old. In some cases, the first year's growth may be almost completely worn away, but the first annual ring was not visible in only 13 of 47 specimens in the 5–17-year-classes. For these, I concluded that the most distal annual ring was that which separated the second and third annual increments. In most cases, however, even if the loosened edges of the first annual ring have worn away, its location is marked by a noticeable swelling in the horn. In no case was the second ring worn away. A count of horn rings provides an index of age to the nearest year. If the date of death is known, and a median birth date is assumed, the age of the individual animal can be estimated to ± 1 month.

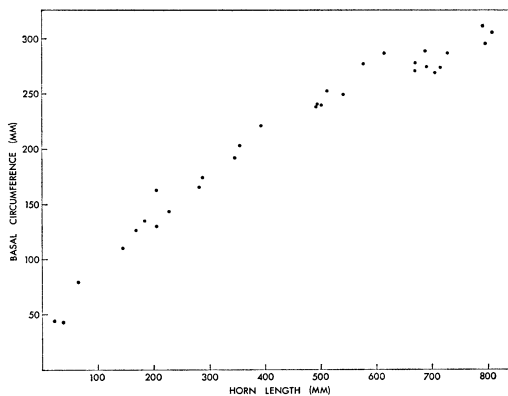


Fig. 3. Growth patterns in the horns of Dall sheep rams.

Determination of Age from the Sequence of Tooth Eruption

The deciduous dentition of Dall sheep is essentially complete at birth. The formula for this dentition is DI 0/3, DC 0/1, DP 3/3. The deciduous incisors and incisiform canines are much smaller than their permanent successors and have a distinct neck at the junction of the crown and root. The canines persist longer than any of the other deciduous mandibular teeth.

Permanent premolars were counted in 63 specimens. Mandibles with damaged tooth rows, those of immature animals with incomplete permanent dentition, and those of aged animals in which secondary loss of teeth had occurred were excluded. The P_2 was absent from 5 of the 63 specimens.

The DP_2 and DP_3 have 2 roots, and DP_4 has 3 roots; premolars P_2 and P_3 have a single root, and P_4 has a double root. The DP_4 may easily be distinguished from P_4 by the presence of 3 cusps, whereas the permanent tooth has only 2 cusps. This character allows immediate recognition of animals 2½ years old or younger. During the respective periods of eruption of M_1 , M_2 , and M_3 , there is noticeable inflation of the

buccal surface of the mandible adjacent to the alveolus.

Boyd et al. (1964) reported considerable variation in the timing of eruption of permanent incisors of domestic sheep in Europe, which they attributed to annual changes in available food. The specimens used in the present study were collected over a period of 16 years and in each case the timing of the replacement of deciduous teeth was sufficiently consistent to indicate the age of Dall sheep in their first 4 years of life (Table 1). For such animals killed in the fall, 1-, 2-, and 3-year-olds will have one, two, and three pairs of permanent incisors. No differences in the sequence of tooth eruption between rams and ewes was observed.

Study of wear of the teeth, within each year-class, revealed such great individual variation that this technique had little value for determination of age.

The sequence of tooth replacement in Dall sheep differs from that of bighorn sheep. Eruption of P_2 and P_3 precedes that of I_2 in bighorn sheep (Taber 1963), but follows that of I_2 in Dall sheep. In bighorn sheep, P_4 is the last of the premolars to erupt, while P_2 is the last to erupt in Dall sheep.

Determination of Age from Cemental Increments

The deposition of cementum of Dall sheep begins approximately when the tooth emerges from the alveolus. One year's deposit includes one fluorescing and one dark band. The fluorescing part of the cementum appears pale green and bright against a dark background. The timing of formation of cemental increments corresponds to the formation of annual segments and annual rings in the horns. Growth of the dark zone begins in the fall, before the rut, and

Table 1. The periods of eruption of the teeth as determined from the mandibles of 50 Dall sheep.

TEETH	DECIDUOUS	PERMANENT
I_1	At birth or first week	13-16 months
I_2	At birth or first week	25-28 months
I_3	At birth or first week	33-36 months
C	At birth or first week	45-48 months
P_2	At birth or first week	27-32 months
P_3	At birth or first week	25-30 months
P_4	At birth or first week	25-30 months
M_1	1- 4 months
M_2	8-13 months
M_3	22-40 months

ceases the following spring, during the lambing period. A count of the dark zones proved most satisfactory for estimating age, since such zones are analogous to annual rings of the horns. One year must be added to the age obtained from I_1 because this tooth does not erupt until the animal is approximately 13 months old. To compensate for this, the dentino-cemental interface was chosen to represent the first year's increment. By counting each dark zone, including the dentino-cemental interface, the age in years is determined. If the date of death is known, age can be estimated to the nearest month.

Figure 4, a tooth section from an animal estimated to be 52 months old, illustrates zones of cemental growth during successive years. The first summer is represented by Zone A and subsequent summers by Zones B-D. The dentino-cemental interface is labeled 1, and Zones 2-4 represent winter growth. The narrow white layer surrounding the tooth is the periodontal membrane. The area inside the dentino-cemental interface is dentine (X). In this specimen, Zone 5 is just beginning to form and is represented by the thin dark line just inside the periodontal membrane. If the date of death were not known, its age would be estimated at between $4\frac{1}{2}$ and 5 years.

Occasionally lamellae may be seen within

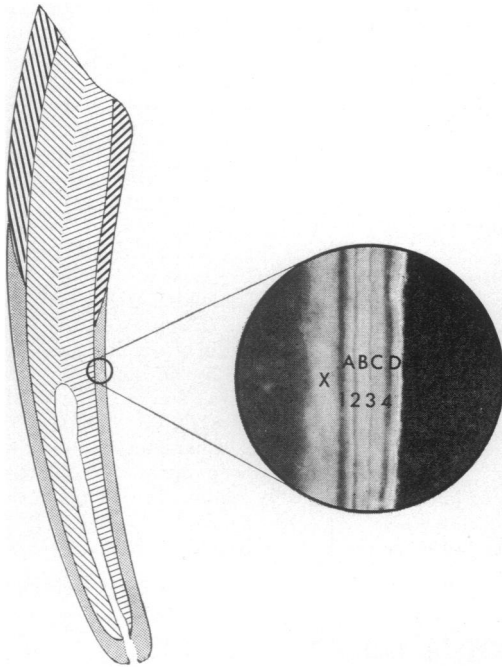


Fig. 4. Internal anatomy of the first incisor and fine structure of the dental cementum. Bold diagonals represent enamel, the narrow diagonals dentine, the stippled area cementum, and the clear area pulp cavity. Fluorescence photomicrograph shows cementum layer. Zones A-D represent summer growth and Zones 2-4 represent winter growth. Zone 1 is the dentino-cemental interface. The dentine is indicated by X.

the light zones but the difference between the lamellae and the dark zones is readily apparent. Nishiwaki et al. (1958), Low and Cowan (1963), Gilbert (1966), and McCutchen (1966) described similar lamellae in teeth of the sperm whale (*Physeter catodon*), mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), and pronghorn antelope (*Antilocapra americana*), respectively.

One specimen was found which showed one less cemental increment than was revealed by a count of the annual rings of the horns. Bloom and Fawcett (1962) reported that if the periodontal membrane is damaged or destroyed, cementum may be re-

sorbed. An injury or other abnormality may have resulted in the loss of one annual increment in this specimen. However, I found that annual increments of the cementum are well defined, for example, 17 distinct annuli were counted in two specimens, which is close to the ultimate age in wild sheep.

The amount of cementum which is deposited annually in Dall sheep tends to decrease with age, but the dark and light zones may always be identified, even in the oldest animals, by means of fluoromicroscopy.

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REPRODUCTIVE BIOLOGY OF THE WHITE-TAILED JACK RABBIT IN NORTH DAKOTA¹

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Abstract: Reproductive characteristics of the white-tailed jackrabbit (*Lepus townsendii campanius*) were determined from 836 animals collected between April, 1964, and December, 1965. A synchronous breeding pattern, with four well-defined peaks of annual activity, was apparent. The breeding season was 148 days in length, and extended from late February through mid-July. A definite annual cycle of sperm production was found. Weights of the testes and the epididymides varied directly with this cycle. The number of ova shed decreased steadily as the breeding season progressed. Females produced an average of 3.29 litters annually. Litter size ranged from one to nine, with an average of 4.6. Combined pre-implantation and intra-uterine losses were 21 percent, and appeared to be more prevalent in older females.

The white-tailed jackrabbit is prevalent throughout the northern prairies of North America. However, this species has received very little attention, and there is a paucity of information concerning its ecology and

life history. The desirability of extensive investigations concerning the biology of the jackrabbit was evident following recent declines in rabbit populations in North Dakota. An inquiry into the reproductive biology of this species was conducted from April, 1964, through December, 1965.

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