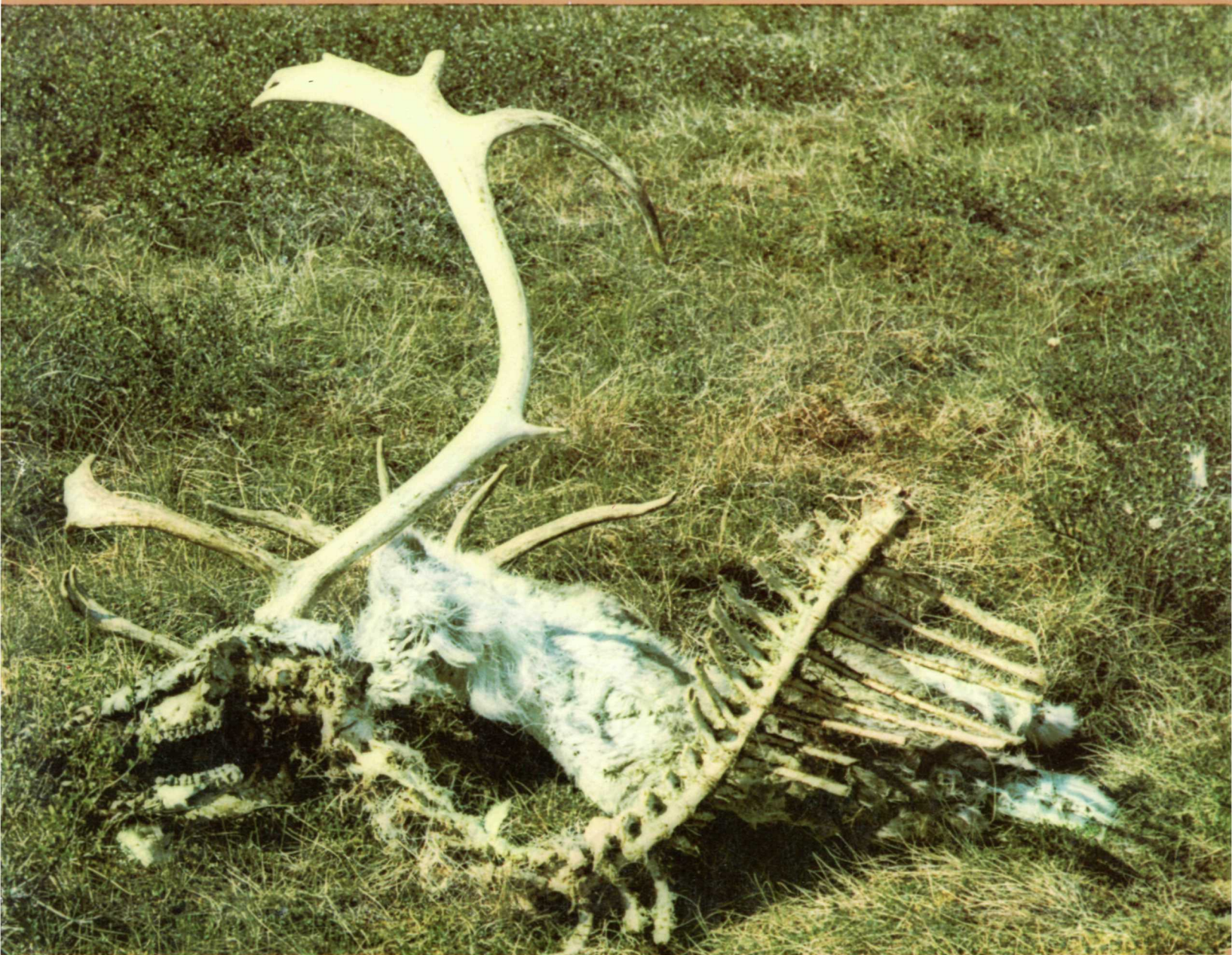


by Frank L. Miller

Biology of the Kaminuriak Population of barren-ground caribou Part 2



**Canadian
Wildlife
Service
Report Series
Number 31**



Environment Canada
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Environnement Canada
Service de la Faune

Biology of the Kaminuriak Population of barren-ground caribou

Part 2: Dentition as an indicator of age and sex; composition and socialization of the population

by Frank L. Miller

Canadian Wildlife Service
Report Series – Number 31

A series to consist of four parts:

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and seasonal distribution by G. R. Parker

Part 2:

Dentition as an indicator of sex and age;
composition and socialization of the population
by F. L. Miller

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The author

Frank L. Miller is a research scientist with the Canadian Wildlife Service in Ottawa. A graduate in wildlife management of the University of Connecticut (B.Sc.) and Oregon State University (M.Sc.), he has been with the CWS since 1965. Following completion of his phase of the study of the Kaminuriak Population of barren-ground caribou, he embarked, in 1971, on studies of Peary caribou and muskoxen on Melville and adjacent islands in the Canadian High Arctic.

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Perspective

Barren-ground caribou numbers in northern Canada were estimated at three million up to the 19th century. The introduction of firearms to Indians and Eskimos, the arrival of whalers in the mid 19th century, and the demand for northern furs in the early 20th century were followed by a rapid increase in the annual kill of caribou. Reductions probably did not occur on the range as a whole before 1900, but were reported locally as early as the mid 1800's. The caribou range in northern Canada was first surveyed from the air in 1948–1949, and an alarmingly low estimate of 670,000 caribou was made. Various studies throughout the 1950's and early 1960's indicated a decline in numbers which reached an all-time low about 1957. This decline apparently ended in that year, and the population has since undergone little change.

The early studies are now regarded as pioneers in caribou research. They successfully monitored the trend in total numbers and identified many factors responsible for the decline in caribou populations. They contributed a great deal to knowledge of caribou ecology but were inconclusive, because of limitations on their duration and the size of the areas covered.

In the early 1960's many conservation agencies recognized the need for intensive study of a particular barren-ground caribou population to provide information on population dynamics, human utilization and range condition. The Canadian Wildlife Service began such a study, lasting 2½ years, in spring 1966. It chose the Kaminuriak Population mainly because it was accessible and its range limits were relatively confined. One biologist was responsible for each segment of the study: total numbers, mortality, recruitment and seasonal distribution; sex and age composition; seasonal physical and reproductive condition; winter range evaluation. The study

was designed and carried out by the CWS, but the game agencies of Manitoba, Saskatchewan, Alberta and the Northwest Territories all contributed personnel at various stages.

The results of the research program were first reported to the Administrative and Technical Committees for Caribou Preservation in 1970. The recommendations arising from these reports were subsequently made available to the game agencies of Manitoba, Saskatchewan, Alberta and the Northwest Territories. This report is the second of four publications on the barren-ground caribou study, to be published in the CWS Report Series.

Abstract

Canadian Wildlife Service biologists collected a total of 999 barren-ground caribou (*Rangifer tarandus groenlandicus*) during four periods of each year from March 1966 to July 1968. Nine hundred and forty-three caribou were from the Kaminuriak Population which ranges over an area of about 282,000 km² in northern Manitoba, northeastern Saskatchewan, and the southeastern District of Keewatin, Northwest Territories, and 56 were from the Beverly Population, which ranges west of the Kaminuriak Population. Collections were taken so as to obtain animals during the major life history phases of the annual cycle. Males totalled 436 and females 563. The adult segment, 46 months of age or over, comprised 178 males and 306 females.

The age composition of the Kaminuriak Population was estimated from tooth eruption and replacement, by linear dental measurements, and by microscopic examination of annuli in the cementum of mandibular teeth, prepared histologically.

The age data were used to determine the effects of natality and mortality on the population and the sexes and ages of animals grouping together at different times of the year.

The degree of segregation and associated socialization was measured by classifying the groups from which the collec-

tions were made and by observing group structuring throughout the study period. The high degree of segregation in the caribou bands and direct observations of groups, particularly in the spring, lead to the conclusion that caribou are socially cohesive.

I postulate that the primary function of postcalving aggregations is socialization; such aggregations provide favourable situations for the regrouping of former winter bands. I believe that such regrouping is necessary because (1) the core of the wintertime cow-juvenile band is formed by a matriarchal bloodline which may be supplemented from time to time by neighbouring caribou; and (2) the bull band, the basic male social unit, maintains from year to year a distribution of breeding bulls that will ensure, under natural conditions, a supply of breeders.

The large base of juvenile and sub-adult animals in the collection indicates that the population has the potential to increase rapidly. Prime animals 4 to 6 years old were well represented, suggesting an expanding, or at least stable, population. High representation of males and females in the adult segment continued until the 9th year. Once they reached their prime, however, males apparently had a higher rate of death than females. It is suggested that the rate of birth for males and females is about equal and mortality for males and females is constant until the prime of life.

Differential mortality between cohorts, however, could have considerable impact on the total size of the population, and on subsequent numbers of breeding females. The evidence suggests that in cohorts subjected to higher mortality the female segment suffers greater losses. Consequently the female segment in such cohorts may be particularly small. This intra-cohort mortality would be even more important if an excessive rate of death occurred within two or three successive cohorts, especially while the population was being heavily harvested.

Résumé

De mars 1966 à juillet 1968, au cours de quatre périodes comprises dans chacune des années, des biologistes du Service canadien de la Faune ont capturé un total de 999 caribous des toundras (*Rangifer tarandus groenlandicus*). De ces caribous, 943 appartenaient à la population de Kaminuriak dont l'aire de distribution couvre une superficie d'environ 282,000 km², dans le nord du Manitoba, le nord-est de la Saskatchewan et le sud-est du district de Keewatin (Territoires du Nord-Ouest). Les 56 autres provenaient de la population de Beverly dont l'aire s'étend à l'ouest de celle de la population de Kaminuriak. La méthode de rassemblement des spécimens a prévu l'obtention des animaux au moment des principales phases de leur cycle annuel. Le nombre des mâles s'est élevé à 436 et celui des femelles à 563. Le segment des adultes (animaux âgés de 46 mois ou plus) était formé de 178 mâles et de 306 femelles.

L'estimation de la répartition de la population de Kaminuriak selon l'âge s'est faite par l'étude des modes d'éruption et de remplacement des dents, le mesurage linéaire des dents et l'examen des anneaux de croissance annuelle des coupes histologiques du ciment des dents de la mandibule.

Les données sur l'âge ont servi à déterminer les effets de la natalité et de la mortalité sur la population ainsi que le sexe et l'âge des animaux qui se rassemblent à différentes époques de l'année.

On a mesuré le degré d'isolement et celui du groupement correspondant en classifiant les groupes à partir desquels l'échantillon avait été prélevé et en observant la structuration des groupes tout au long de la période d'étude. Le degré élevé d'isolement dans les hardes de caribous et les observations directes des groupes, particulièrement au printemps, permettent de conclure que ces animaux forment une entité sociale unie.

Je pose comme postulat que la fonction première des rassemblements après la période de mise bas est de permettre aux individus de socialiser; ces rassemblements

créent des situations favorables au regroupement d'anciennes hardes hivernales. J'estime que ce regroupement est nécessaire pour les deux raisons suivantes: (1) le noyau du groupe hivernal femelles-jeunes est formé d'une famille matriarcale à laquelle peuvent de temps en temps venir s'ajouter des caribous du voisinage; (2) le groupe des mâles, élément social de base chez les mâles, maintient d'année en année une lignée de reproducteurs qui assurera, dans des conditions naturelles, une population de géniteurs.

L'importante base de jeunes et d'animaux presque adultes de l'échantillon indique que la population peut augmenter rapidement. Les animaux dans la force de l'âge étaient bien représentés, ce qui dénote une population croissante ou, du moins stable. Il y avait, jusqu'à la neuvième année, un fort pourcentage de mâles et de femelles dans le segment adulte. Une fois arrivés à la force de l'âge cependant, les mâles ont apparemment connu un taux de mortalité plus élevé que celui des femelles. Les données permettent de croire que la natalité chez les mâles et les femelles est à peu près égale; par ailleurs, la mortalité dans les deux groupes reste constante jusqu'à ce que les animaux atteignent la force de l'âge.

Le taux de décès différentiel entre générations peut avoir beaucoup de conséquences sur l'importance numérique de la population et sur le nombre ultérieur de femelles reproductrices. En effet, tout porte à croire que, dans les générations frappées d'une forte mortalité ce sont les femelles qui sont les plus durement touchées. Par conséquent, le segment des femelles dans ces générations peut être particulièrement petit. Cette mortalité intra-génération pourrait être plus importante encore si un taux de mortalité excessif frappait deux ou trois générations consécutives, spécialement si la population faisait alors l'objet d'une chasse intense.

Резюме

Канадские биологи службы живой природы собрали на бесплодных землях в общей сложности 999 карibu.

Во время четырех периодов каждого года с марта 1966 по июль 1968 г.г. Девятьсот сорок три карibu были из популяции «камшурьяк», населяющей территорию свыше 282 000 км² в северной Манитобе, северо-восточном Саскачеване и юго-восточном районе Кьюэтина в Северо-Западных Территориях; 56 было из популяции «бевебли», находящейся западнее популяции «камшурьяк». Коллекция животных производилась с целью наблюдения за ними во время основных исторических жизненных фаз годового цикла. Всего самцов было 436, а самок 563. Из этого числа во взрослый сектор в возрасте 46 месяцев и выше, входило 178 самцов и 306 самок.

Возрастной состав популяции определялся путем наблюдения прорезания зубов и замены новыми, линейного измерения зубов и путем микроскопического анализа, проведенного гистологически.

Данные о возрасте использовались для определения воздействия рождаемости и смертности на популяцию, а также для определения пола и возраста группировок животных в разные времена года.

Степень отделения и соответствующее общественное поведение была измерена путем классификации групп, из которых отбирались коллекции, и путем наблюдения за структурой группы на протяжении всего периода. Высокая степень отделения в стадах карibu и прямые наблюдения за группами, в частности весной, привели к заключению, что карibu общественно спяны.

Я считаю, что первичной функцией послеотеловых объединений является общественное поведение; такие объединения создают хорошие условия для

перегруппировок бывших зимних стад. Я считаю, что такие перегруппировки необходимы, так как:

а) стержень зимнего стада самок-подростков составляется из животных, родственных по материнской линии, которые время от времени могут заменяться соседними карibu;

б) стадо, состоящее из самцов, основная общественная единица, из года в год поддерживает распределение племенных самцов, которое в природных условиях обеспечивает поставку производителей.

Большой процент подростков и молодых самцов в коллекции указывает на наличие потенциала быстрого роста популяции. Хорошо были представлены в коллекции животные в расцвете жизненных сил, в возрасте от 4 до 6 лет, что обещает в будущем увеличение или по крайней мере устойчивость популяции.

Высокий процент самцов и самок во взрослом секторе продолжался до девятого года. Однако, когда они достигли расцвета жизненных сил, у самцов, очевидно, была более высокая смертность, чем у самок. Предполагается, что процент рождаемости самцов и самок почти одинаков, а смертность самок постоянна вплоть до расцвета жизненных сил.

Разница в смертности когорты, однако, может оказать значительное влияние на общий размер популяции и на последующее число племенных самок. Данные показывают, что в когортах, подверженных более высокой смертности, сектор самок несет большие потери.

Следовательно, сектор самок в таких когортах может быть совсем небольшим. Такая смертность внутри когорты была бы более серьезной, если бы высокий процент смертности возникал в двух или трех последующих когортах, особенно когда размер популяции значительно уменьшается вследствие охоты.

Introduction

The numbers of barren-ground caribou (*Rangifer tarandus groenlandicus*) in northern Canada before the 19th century were estimated at several million (Anderson, 1924; Clark, 1940). Alarming decreases in numbers, since about the 1850's, were probably caused by the whalers who wintered along the arctic coast during the latter half of the 19th and the early 20th centuries. The CWS, therefore, began a long series of investigations in 1948. In the first comprehensive report, Banfield (1954) estimated the mainland population at about 668,000 and presented evidence for the decrease and its causes.

The 1948 study led to further research into the factors responsible for the drastic decrease. Meanwhile the decline continued until, by 1957, the mainland populations were at an alarmingly low 200,000 (Kelsall, 1960). Indians and Eskimos annually killed far more than the annual recruitment; and forest fires were destroying much of the prime winter range. The caribou was placed on the endangered species list; conservation practices were introduced to the Indians and Eskimos; and an extensive wolf control program was initiated in an attempt to reduce total mortality. Limited aerial surveys and reports from many sources suggest that the decline in caribou populations ended around 1960. The caribou populations were then said to be increasing at an alarming rate but such reports were not based on up-to-date information. A range-wide survey conducted in spring 1967 resulted in a total estimate of about 400,000 mainland caribou (Thomas, 1967). But a critical analysis of the interpretation of raw data derived from surveys made in 1967 and earlier suggests that total numbers changed little from 1957 to 1967 (Parker, 1971).

In 1966, the CWS began an intensive study of the Kaminuriak Population of northern Manitoba, northeastern Saskatchewan and the southern District of Keewatin, Northwest Territories (NWT). The main objective was to obtain detailed information on caribou biology, human utiliza-

tion and range conditions by study of a particular population for about 2½ years. All mainland caribou populations were assumed to be subject to similar environmental problems. The Kaminuriak Population was chosen because it presented fewer logistic problems than others and its study would be less expensive.

The program combined the efforts of four biologists, working as a team whenever possible but generally pursuing a particular field of research, according to the objectives of the project. The goals were as follows:

- a. To determine the size of the population, to record seasonal movements, and to relate population size to range capacity, annual mortality, and natality.
- b. To determine the sex and age composition from large representative samples of the population.
- c. To obtain detailed information on reproductive rate, growth, physical (nutritional) condition, mortality (from hunting and natural causes), and the pathological conditions of the caribou.
- d. To determine the relationship of forage use on the taiga winter range to forage abundance, distribution and availability.

Nine hundred and forty-three caribou were collected from the Kaminuriak Population to determine its sex and age composition. The animals' sex was self evident, but I also tested the accuracy of determining sex from mandibular or diastema lengths, and found them to be reliable. I estimated the age of caribou from eruption and replacement patterns, by linear dental measurements, and by counting annuli in histological sections of dental cementum of mandibular teeth. In addition, 56 specimens were taken from the Beverly Population which ranges west of the Kaminuriak Population. The data on reproduction, growth and physical conditions collected by Dauphiné (in prep.) were related to age data collected in the present study. In the present report the age data will be used for determining the effects of natality and mortality on the population and group composition at different times of the year.

Study area and migration

Figure 1
Overall summer and winter ranges of Kaminuriak caribou. Caribou do not commonly use the area in its entirety in any one year but do so at various times through a series of years

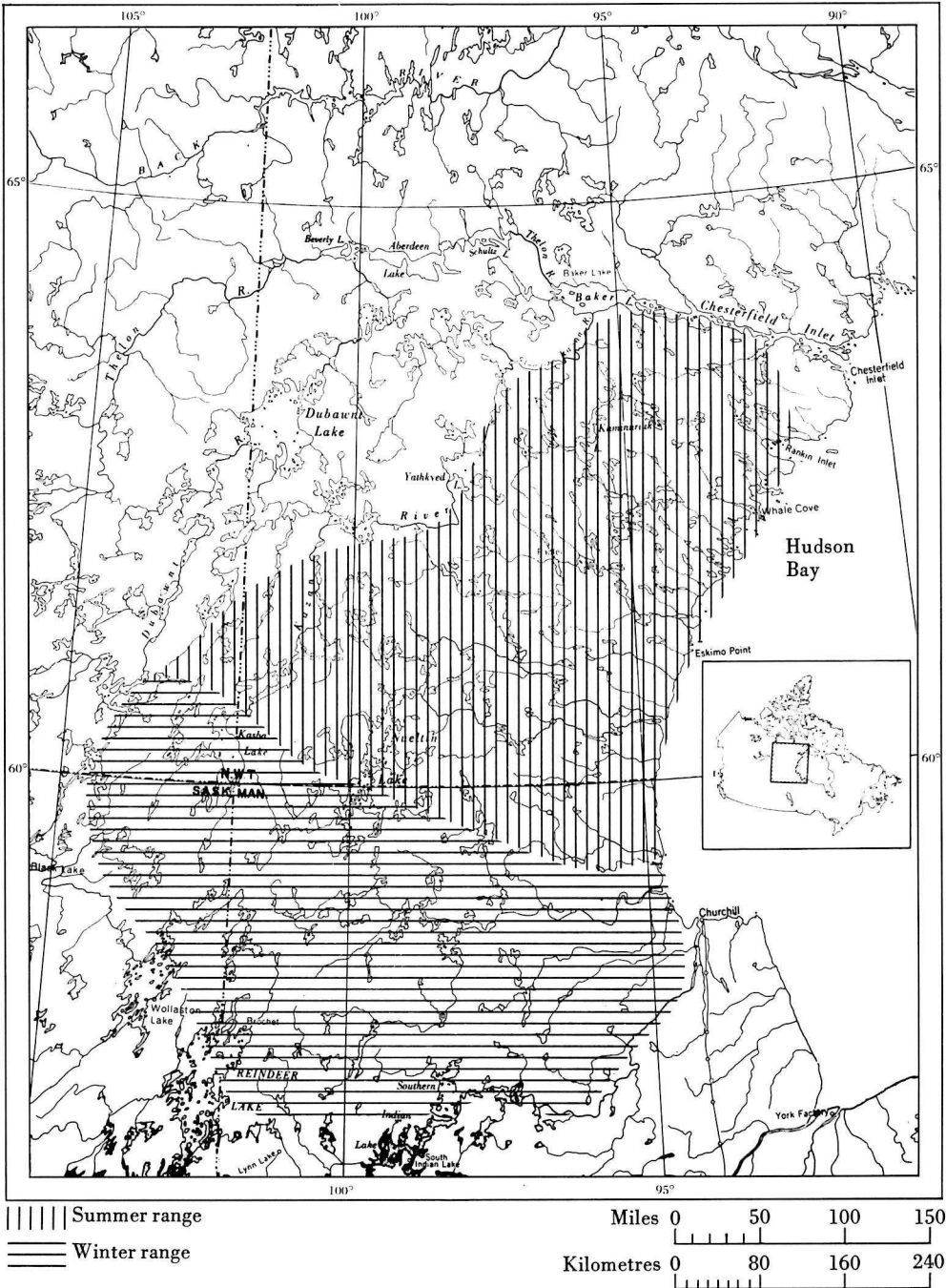
1. Study area

Kelsall (1968) has described the barren-ground caribou range on mainland Canada. Beckel (1958a and 1958b), Rowe (1959) and Miller (in prep.) have described portions of the study area in detail. The study area (Fig. 1) encompasses the entire range of the Kaminuriak Population. About 282,000 km², it is bordered on the east by Hudson Bay. From Chesterfield Inlet, its northern boundary, the perimeter of the range extends westward to Baker Lake, then southwest to Selwyn Lake on the Saskatchewan – NWT border. To the south, the perimeter follows the Churchill River to the west shore of Southern Indian Lake, then extends northwest across the northern ends of Reindeer and Wollaston Lakes to Selwyn Lake.

The summer range on the tundra covers about 160,500 km². It lies north of a line extending westward from the mouth of the Caribou River, north of Caribou Lake, through Nueltin Lake, to about the north end of Snowbird Lake in the District of Mackenzie, NWT. The winter range in the open boreal forest, south of the summer range covers about 121,500 km² (Fig. 1). During field work, however, most of the caribou wintered on the western half of the range. Some caribou winter on the coastal lowland tundra, west of Eskimo Point and Rankin Inlet, but their numbers are usually low and vary considerably from year to year.

The study area is geographically divided into the coastal lowlands extending inland about 137 km from Hudson Bay, the interior plateau west of the lowlands, and the hill and mountain regions (Robinson, 1968). The lowlands are characterized by numerous elongated drumlins and linear eskers. Drainage is poor, with many streams meandering from one depression to another, sometimes forming into long, narrow lakes when rock ridges or moraines block their outlets (Robinson, 1968). The interior plateau generally has an elevation of less than 150 m. Rock outcrops are more prevalent here than on the lowlands, and

Figure 1



drumlins and eskers are characteristic formations (Robinson, 1968). The westernmost section of the study area comes within the interior hill subregion where bare rock hills and ridges are predominant features (Robinson, 1968). The elevation is generally from 350 to 450 m; the maximum elevation is about 550 m.

The study area is divided into the following floristic types: Tundra, Forest-tundra, and Northwestern Transition sections of the boreal forest (Rowe, 1959). The term *tundra* is synonymous with *barren-ground*. It is carpeted with mosses, lichens, sedges, grasses, dwarfed woody plant species and herbaceous flowering plants. Vegetation is lush in the lower areas, scanty in higher drier areas (Kelsall, 1968). Dwarfed black spruce (*Picea mariana*), white spruce (*P. glauca*), tamarack (*Larix laricina*), jack pine (*Pinus banksiana*), birches (*Betula* spp.), aspen (*Populus tremuloides*), poplar (*P. balsamifera*), alders (*Alnus* spp.) and willows (*Salix* spp.) grow on the forest-tundra. The forested portion of the study area, corresponding generally with the winter range, is open boreal forest, with black spruce mostly dominant inland. White spruce dominate sites with better soils or drainage, tamarack is often dominant on the more northern sites, jack pine on burned or sandy sites. Birches, aspen, poplar, alders and willows occur in varying degrees and are sometimes locally dominant. Extensive bogs and muskegs occur throughout the study area and much of the land mass is covered with water.

The winters are severe and prolonged, springs cool and wet, summers relatively dry and moderate. Winter temperatures are consistently below -29°C and often dip to -40°C . The mean annual minimum temperature is -46°C , and the lowest recorded temperature is -51°C (Kelsall, 1968). The mean annual maximum temperature is 27°C . Mean annual precipitation is 30–41 cm on the winter range and 15–30 cm on the summer range (Kelsall, 1968). The mean annual total snowfall on the winter range is 102–127 cm, the mean annual

maximum depth of snow is 51–76 cm (Kelsall, 1968).

2. Migration patterns

Caribou of the Kaminuriak Population usually begin their spring migration in April, with local, often multi-directional movements. They are well on their way to the tundra by May, usually arriving on the calving ground by the end of the month. Calving takes place, for the most part, during the first three weeks of June; and large post-calving groups begin to form by late June and early July. The caribou meander over the tundra for the first part of July, then begin their midsummer migration southward to the forest-tundra or taiga in late July or early August. The extent to which the animals penetrate the taiga varies from year to year. Many migrating animals have returned to the tundra by late August and early September. Rutting takes place in October, mainly along the northern edge of the forest-tundra, and may continue at a low level in early November, when the autumn migration begins. In November or early December, the caribou arrive in the open boreal forest for the winter. Throughout that season there is usually much movement; the mature bulls leave the other caribou and go further south. The advanced signs of spring initiate the annual migration cycle again. Parker (1972) describes these movements in details.

Methods

We shot the caribou (Table 1) and hauled the carcasses to processing sites, where we took measurements and specimens.

Each caribou was decapitated. The mandible was dissected, fleshed, dried and shipped to the laboratory for examination of the teeth. The standard terminology for deer teeth (Riney, 1951) was used in this study. I took the nomenclature for tooth morphology from Loomis (1925), Frick (1937), and Banfield (1961).

We soaked the mandibles in hot water for several days, to loosen any soft tissue and foreign matter, scrubbed them with stiff-bristle brushes to remove the tissue and to clean the teeth, and air-dried them thoroughly. We then took the following data:

- Height of the first incisor (i1) and of all molariform teeth, second premolar (p2), third premolar (p3), fourth premolar (p4), first molar (m1), second molar (m2), and third molar (m3) on the buccal side;
- Heights of the anterior and posterior cusps on the m1, m2 and m3;
- Maximum width of enamel and dentine on the anterior cusp of the m1;
- Length of the right and left dentaries;
- Length of the right and left tooth row;
- Length of the right and left diastema;
- Types of teeth present: deciduous (milk), erupting, or permanent. In addition, we recorded the following data for all molars of the right mandibular bone: weight, lingual and buccal width, antero-posteriad length, and stages of growth (open or closed) for the apices of the roots.

All tooth heights were measured from the lowest point of the stained gum line to the highest point of the buccal ridge. A tooth was considered as erupting if it had not fully erupted but a portion of its crown was stained. The length of the mandible was measured ventrally from the posterior rim of the ramus to the anteriormost portion of the alveolar bone below the i1. The length of the diastema was measured dorsally from the junction of the anterior surface of the p2 and the alveolus to the anteriormost

Table 1

Summary of collection periods, aircraft and methods used in collecting 999 caribou in northern Canada, April 1966–July 1968

Collection period	Location	Aircraft	Methods
1966			
Apr. 7–28	NW Manitoba	Otter	Aerial search, shooting on lake ice
June 5–Jul. 5	SE District of Keewatin, NWT	Beaver	Ground spotting, stalking and interception
Sept. 17–24	S Central District of Keewatin	Otter	Aerial spotting, ground stalking
Nov. 21–Dec. 1	NW Manitoba	Otter	Aerial search, shooting on lake ice
1967			
Apr. 10–20	NW Manitoba, NE Sask., SE District of Mackenzie, NWT	Otter	Aerial search, shooting on lake ice
May 25–June 13	SE District of Keewatin	Otter, G2-A helicopter	Aerial spotting and shooting, ground stalking and interception
Sept. 15–21	SE District of Keewatin	Otter, G2-A helicopter	Aerial spotting and shooting, shooting from next to helicopter
Nov. 28–Dec. 12	NW Manitoba	Otter	Aerial search, shooting on lake ice
1968			
Apr. 12–24	NW Manitoba	Otter	Aerial search, shooting on lake ice
June 12–16	SE District of Keewatin	Beaver, G4-A helicopter	Aerial spotting and shooting
July 12–16	Central District of Keewatin	Beachcraft	Ground spotting, stalking and interception
July 14–17	SE District of Keewatin	Beachcraft	Aerial spotting, ground stalking and interception

portion of the alveolar bone posterior to the crown of the i1.

The mandibles were forced apart at the mandibular symphysis between the left and right i1, and all incisiform teeth were removed by hand. The molariform teeth of the right mandibular process were removed with tooth extractors. The teeth were stored in 5 per cent formalin. The left dentaries were air-dried, then the infundibula of the molariform teeth were cleaned out with a dissecting needle. The left dentaries were then sprayed with clear plastic coating, dried, and subsequently mounted on jaw boards by sex and age classes.

During the experimental phase of the work decalcifying solutions and time requirements, dehydration, mounting media, types of microtomes, stains, staining time and processes were varied to determine the

most reliable procedures. The most effective histological procedures are given in Table 2, labour requirements in Table 3.

The teeth were rinsed in running tap water for 24 hours, placed in labelled, perforated, stainless steel capsules and submerged in nitric acid decalcifying solution (Table 2) at the rate of one molar or two incisors per 150 ml of solution. Incisiform teeth from caribou younger than 34 months were decalcified for 18–24 hours and from older individuals for 24–36 hours. Molariform teeth from all caribou were decalcified for 48–72 hours.

Termination of decalcification was determined subjectively. When the root portion was flexible under slight pressure, the tooth was removed from the decalcifying solution, rinsed in running tap water for 24 hours, and stored in distilled water.

Table 2
Histological techniques and reagents used in processing caribou teeth

Steps	Techniques and reagents
Decalcification	Commercial nitric acid
	67.18% nitric acid, 7.5 ml
	Distilled water, 92.5 ml
Mounting for sectioning	Ames Tissue-Tek O.C.T. mounting compound
Sectioning	Ames Tissue-Tek cryostat microtome at -30°C
Mounting for staining	Albuminized slides
Staining	Harris haematoxylin and Eosin Y
	Harris haematoxylin, 5–30 min
	Distilled water, 2 min
	Distilled water, 5 min
	Eosin Y, 30 sec
	Distilled water, 2 min
	0.5% sulphuric acid in 70% ethanol, 3–5 sec
	10% sodium bicarbonate solution, 5 min
	Distilled water, 2 min
	70% ethanol, 4 min
	95% ethanol, 4 min
	100% (absolute) ethanol, 2 min
	Xylene, 2 min
	Mounting
	Fisher's Permunt
Mounting and reading	Glycerin diluted 1:1 with H_2O
	Reading
	Bausch and Lomb zoom microscope $35\times - 860\times$
	Most readable between $100\times$ and $400\times$
	$20\times - 80\times$ dissection scope to check staining and gross structures

The crown of the tooth was removed with a scalpel. The root portion was mounted on a pre-cooled metal mount in Ames Tissue-Tek O. C. T. mounting compound so as to allow the blade to pass through the buccal and lingual surfaces. The teeth were cut on an Ames Tissue-Tek cryostat (freezing) microtome at approximately -30°C , in sections 12–15 microns thick.

The incisiform tooth was sliced away until the pulp area, from the neck of the

Table 3
Time requirements for preparing slides of caribou tooth sections

Procedure	Minutes
Locate tooth, transfer to capsule, rinse in running tap water	5
Place in nitric acid decalcifying solution	1
Rinse in running tap water	1
Transfer to distilled water	1
Prepare label, mount tooth on microtome	2
Section tooth	10–20
Mount tooth on slides, label, place on drier	10–30
Staining	35–65
Mount in Fisher's Permunt, place on drier	5–10
Range of time required	70–135

crown to the apex of the root, could be seen through the dentine. The sectioning was continued and 10 longitudinal sections — Nos. 15, 25, 30, 33, 36, 39, 42, 45, 55 and 65 — were kept for mounting. Eight longitudinal sections were retained from each molariform tooth. The first two sections were taken before the pulp cavity was reached. The remaining six sections were taken from the pulp cavity region, one for every 5 to 10 slices made. The sections were placed in distilled water in compartmentalized plastic petri dishes in order of cutting. The slides were layered 24 hours in advance with fresh egg white. Five and four sections from incisiform and molariform teeth respectively were placed on each slide, in order of cutting, with their apices pointing in one direction. Each slide was coated with water to prevent the sections from curling and to facilitate the mounting process. Excess water was removed, and the slides dried overnight on a slide warmer at 40°C . The sections were stained with Harris haematoxylin and Eosin Y by the procedure shown in Table 2. After a minimal staining time each slide was checked with a dissection microscope to determine the need for additional staining. A cover slip was then applied to each slide with Fisher's Permunt and the slides were dried

on slide warmers at 40°C for at least 48 hours. The sections were scanned at $100\times$ to $200\times$ with a Bausch and Lomb zoom microscope. The thinner cemental layers on the upper portion of roots were often read at $400\times$. Each slide was read at least four times with considerable lapses of time between each reading.

The ages in months were established by histological examinations of the il or ml. The following assumptions were made: an annulus (winter rest line) is apposed each year; all annuli can be recognized from supernumerary lines; all caribou were born in June.

All the information obtained was put on data preparation forms for punch card processing and subsequent compilation on computer tape. A review of related literature on age determinations is given in Appendix 1, and references listed by author and date for species investigated are listed in Appendix 2.

Dentition as an indicator of age and sex

1. Morphology of the mandibular dentition

Barren-ground caribou are heterodonts, having a dentition composed of incisors, canines, premolars and molars

$$\left(\frac{I_0}{I_3} \frac{C_1}{C_1} \frac{P_3}{P_3} \frac{M_3}{M_3} \times 2 = 34 \right) \text{ (Banfield, 1961).}$$

The mandibular dentition of the newborn consists of 14 deciduous teeth: 8 incisiform (i1, i2, i3, c1) and 6 molariform (p2, p3, p4). The deciduous teeth are smaller versions of their permanent counterparts (Fig. 2 and Plate A) except for the deciduous p4 which is sextitubercular, an additional pair of cusps making it longer than its permanent counterpart (Plates A and B).

The permanent mandibular dentition is subhypodont, selenodont (Banfield, 1961) and consists of 20 teeth: 8 incisiform (i1, i2, i3, c1) and 12 molariform (p2, p3, p4, m1, m2, m3). The eight incisiform teeth have chisel-like crowns and single roots set loosely in the alveoli for flexibility. The incisors are small: the i1 is the largest and most functional (Fig. 2) and receives the greatest attrition with age; the i3 is the smallest.

The deciduous and permanent p2 are often lophodont-like, but many exhibit the selenodont pattern of the p3 and p4. The lophodont p2 has a more complete longitudinal ridge, usually with two isolated transverse ridges extending buccally from what would be the anterior and posterior crescents. In the selenodont p2 the anterior crest has fused with the posterior crescent (Loomis, 1925), giving the tooth a more crescentic outline.

The selenodont origin of p3 and p4 is somewhat masked by the inferior condition of the posterior crest and crescent. An entire primary cusp is formed by the fusion of the anterior crest and the posterior crescent. The posterior crest and, to a lesser degree, the anterior crescent are isolated. The anterior crescent often fuses medially on the lingual side of the posterior crescent. It is the most complex column, triangular in outline, resulting from the formation of a mediolingual conulid. The premolars are

Figure 2

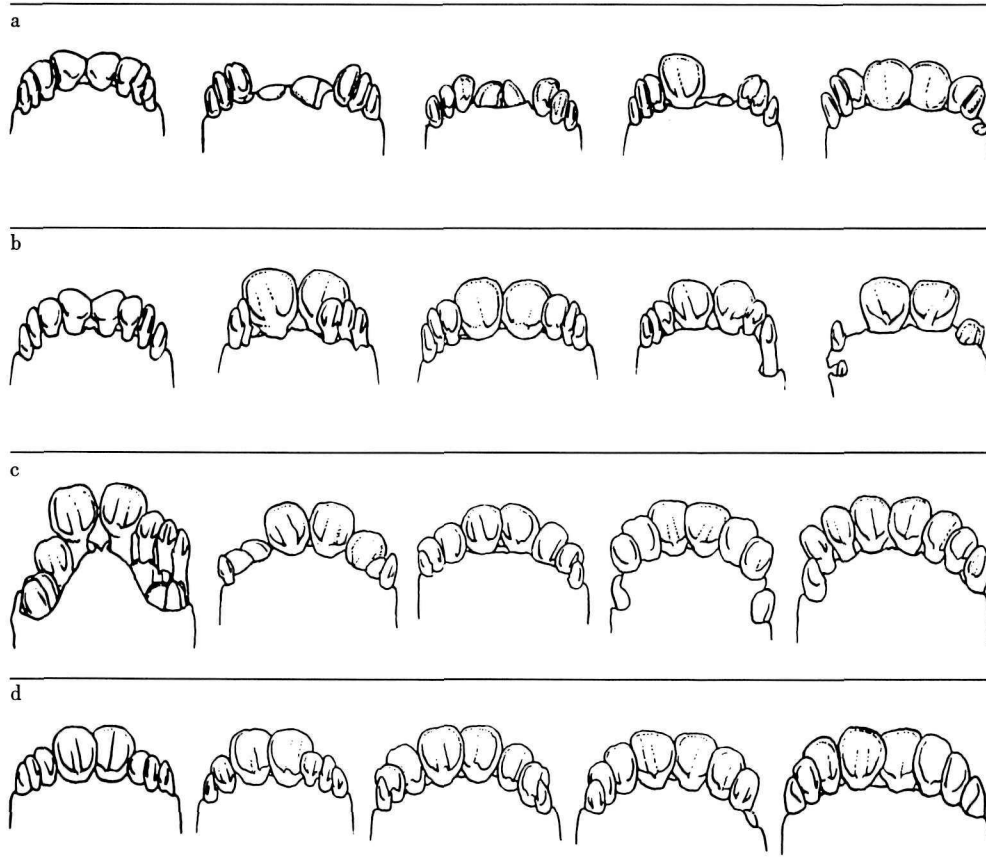


Figure 2

Dorsal view of eruption patterns for the incisiform teeth of caribou (a) 10 months, (b and c) 12 months, showing possible variations, (d) 13 months

Figure 3

Five parts of a selenodont tooth, buccal side of a left p4

almost or as large as the molars. The primary parts of the premolar teeth and of the molar counterparts are illustrated in Figure 3.

The m1, m2 and m3 are selenodont. The first two are quadritubercular, while the third has an additional, single, distal cusp. The anterior crescent becomes the metaconid, the anterior crest the protoconid, the posterior crescent the entoconid, and the posterior crest the hypoconid (Fig. 4). These cusps are separate columns in the newly erupted tooth (Frick, 1937), but by the time the animal has a complete permanent dentition, at 24 to 29 months (Plate A), attrition of the occlusal surfaces of m1

Figure 3

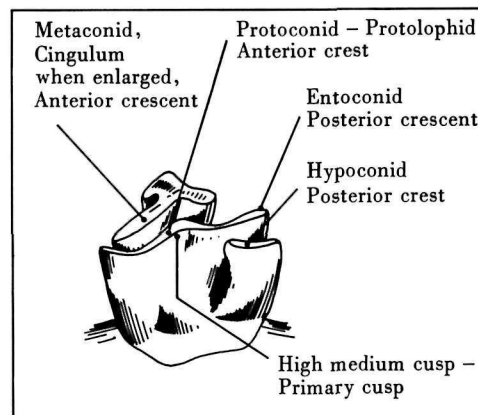


Table 4

Percentage frequency of occurrence of stages of eruption of teeth of Kaminuriak caribou according to age during first 29 months of life

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*D — milk tooth.

†E — erupting tooth. An erupting tooth has a stained portion but has not migrated to its position of permanent orientation.

‡A — absent tooth (permanent tooth not yet erupted).

§P — permanent tooth.

^{||}Numerical values — frequency of occurrence,

in percentages, of each type of tooth. When no values are given, occurrence is 100 per cent. Incisors and premolars equal D E P, molars equal A E P.

and m2 produces the cross-over pattern of the protolophid and the entoconid. Most often the dentine line of the metaconid merges with the ridge of the protolophid. The hypoconid is usually a separate column in all molars. The four other columns of the m3 are also separate.

The caribou's relatively small, long-crowned, selenodont molars are believed by Flerov (1952) to be an adaptation to feeding on soft vegetation, such as lichens.

Kelsall (1968) and Skoog (1968) believe that the incisors are well suited for grazing lichens and sedges, which do not

require any particular strength, but not for cutting hard woody plants. The incisors are essential for any grazing or browsing, and Miller (in prep.) has reported that the Kaminuriak caribou browse hardwood species heavily, as do the woodland caribou (*R. t. caribou*) which have similar dentition (Cringan, 1957; Simkin, 1965; Bergerud and Nolan, 1970). It is likely that the incisors are well suited for browsing as well as grazing; readily broken or malformed incisors would be detrimental to the species.

The main difference in how the incisors function in browsing and grazing

could be behavioural, as indicated by variations in wear patterns of these teeth in caribou from forested and tundra areas. In the former, attrition of the incisors is horizontal; in the latter, it is sharply vertical and mostly on the labial surface. These variations suggest that barren-ground caribou graze with a forward head motion that results in the bulk of the wear occurring along the anterior surface of the vertical plane of the first incisor. The strengths of incisors of different cervid species should be compared quantitatively when fresh dental material is available.

Table 5

Closure patterns for the apices of permanent, mandibular molariform tooth roots in Kaminuriak caribou at various ages (n = 374). A = absent from tooth row, E = erupting tooth, P = permanent tooth, U = open apex, C = closed apex, numerical value = frequency of occurrence in percentages, no value = 100 per cent occurrence

Age, mon.	Permanent tooth					
	p2	p3	p4	m1	m2	m3
5	A	A	A	EU	A	A
10	A	A	A	PU-47 PC-53	EU	A
12	A	A	A	PU-44 PC-56	PU	A
13	A	A	A	PU-43 PC-57	PU	A
15	A	A	A	PU-17 PC-83	PU-67 PC-33	EU
17	A	A	A	PU-18 PC-82	PU-77 PC-23	EU
22	EU	EU	EU	PC	PU-21 PC-79	EU*
24	PU	PU	PU	PU-12 PC-88	PU-21 PC-79	PU
25	PU-88 PC-12	PU-94 PC-6	PU	PC	PU-11 PC-89	PU
27	PU-63 PC-37	PU-69 PC-31	PU-63 PC-37	PC	PC	PU-53 PC-47
29	PU-53 PC-47	PU-56 PC-44	PU-56 PC-44	PC	PC	PU-69 PC-31
34	PC	PU-3 PC-97	PU-7 PC-93	PC	PC	PU-12 PC-88
36	PC	PC	PC	PC	PC	PC†

*m3 is considered erupting in most individuals through 27 mon. of age.

†One m3 had an enlarged distal root which remained opened at 36 mon.

2. Eruption and wear of the mandibular teeth

Table 4 shows the eruption patterns for the mandibular teeth of Kaminuriak caribou for each age class. The closure patterns of the apices of permanent molariform mandibular tooth roots in the specimens studied (Table 5) allow an investigator to distinguish between 24-month-old caribou with full permanent dentition and 36-month-old caribou. At 24 months, the apices of p4 and m3 are open, at 36 months they are closed. There is slightly better than a 50 per cent chance that the apices of

the roots of these teeth will be open at 27 to 29 months of age, but the apices of all molariform tooth roots are closed at 36 or more months.

Table 6 compares approximate ages of permanent mandibular tooth eruption in *Rangifer*: Canada (this study; Bergerud, 1970; Banfield, 1954), Alaska (Skoog, 1968), Lapland (Bromée-Skuncke, 1952) and the USSR (Sokolov, 1937). Agreement between my findings and those of Bergerud, Skoog, Bromée-Skuncke, and Sokolov is close, with slight deviations for individual teeth. Banfield and I differ: he places erup-

tion of the permanent dentition including premolars at 18 months, I place it between 24 and 29 months; he reports eruption of m3 as occurring a full year earlier than I do. McEwan (1963), also working with mainland barren-ground caribou in Canada, found deciduous premolars in seven of eight caribou aged 23 to 24 months, and evidence of wear on permanent premolars at 25 to 27 months. Bergerud (1970) found that premolars erupted between 24 to 27½ months in Newfoundland caribou.

Kelsall's (1968:25) statement "that dates of tooth eruption may vary," is an apparent attempt to reconcile the difference between the reports of Banfield (1954) and McEwan (1963). However, nowhere in the literature on the teeth of cervids does one find documentation to support such wide variations in the time of eruption for teeth of the same species from approximately the same locations.

At birth, the newborn calves examined had eight deciduous incisiform teeth and six erupting premolars (Plate A), slightly more erupted than those examined by Skoog (1968) and Banfield (1954). By the second week, the calf is grazing and the infundibula of its premolars are compacted with vegetation. A tartar stain has appeared and the crests and crescents of the premolars have a fine dentine line. At 1 to 2 months, the incisors and canines show no wear and deciduous p2 shows little or no wear. The maximum width of the dentine on the deciduous p2 and the anterior cusp of the deciduous p3 is about equal to the width of the adjacent enamel, but the dentine line on the medial and posterior crests and crescents of the deciduous p3 is narrower than the surrounding enamel.

Three-month-old caribou have a complete set of 14 deciduous mandibular teeth (Plates A and B) and the permanent m1 has started to erupt, as observed earlier by Banfield (1954) and Skoog (1968). The permanent m1 shows little or no wear on its anterior cusps (Plate B). After the beginning of the 3rd month the dentine area has broadened on all crests and crescents of

Table 6

Approximate ages in months at which permanent teeth become fully erupted in *Rangifer* mandibles according to this study, Bergerud (1970), Skoog (1968), Banfield (1954), Bromée-Skuncke (1952), and Sokolov (1937)

Permanent tooth	Kaminuriak caribou			Nfld. caribou (Bergerud 1970)	Alaskan caribou (Skoog 1958)			Canadian caribou (Banfield 1954)	Lapland reindeer (Bromée-Skuncke 1952)	U.S.S.R. reindeer (Sokolov 1937)
	Begins	Completed 50%	Completed 100%		Begins	Earliest	Completed average			
i1	9	11	13		10	10	11	10	12	10
i2	11	13	15		10	11	12	10	12-14*	12†
i3	11	13	15		11	11	12	10	12-14*	12†
c1	11	14	16		11	11	12	11-15	12-14*	15‡
p2	21	25	28	24-27½	21	22	24	18	30	29‡
p3	21	25	28	24-27½	21	22	24	18	30	29‡
p4	21	25	28	24-27½	21	22	24	18	28	29‡
m1	3	4	5	3	3	4	4	3	4	3-3½
m2	10	13	15	13	5	11	13	10	15	15
m3	15	26	28	25-27½	15	22	25	17	28	29§
Full set			29	27½		22	25	18	30	29

*Fully usable by 16 mon.

†Functional by 17 mon.

‡Fully usable at 36 mon.

§Shows signs of wearing at 36 mon.

^{||}Earliest full set 24 mon.

the deciduous p2 and p3 and usually exceeds the maximum width of adjacent enamel (Plate A). After 3 months some wear is noticeable on the i1, but the other incisi-form teeth show none. The permanent m1 erupts during the 4th month and was present in all the 5-month-old caribou collected (Plate B). At 5 months, the incisi-form teeth are little changed from 3 months. Wear on the deciduous p2 varies from very slight to moderate, revealing areas of dentine as wide as adjacent enamel. All crests and crescents of the deciduous p2 and p3 show dentine areas as wide as or wider than surrounding enamel. Dentine on the permanent m1 may not be exposed at all or it may be almost equal in width to the adjacent enamel. Dentine exposure on the posterior cusps is less than on the anterior cusps. Between 5 and 10 months, little additional dentine is exposed. The only significant change in the mandibular dentition is the initial eruption of the permanent i1 in some individuals (Fig. 2). The m2 has migrated above the alveolar bone, but is not above the gum in most animals

(Plate A). The anterior cusps of m1 have perforated the gingivae in a few of the specimens.

By 12 months, the permanent i2, i3 and c1 are erupting (Fig. 2). Wear on the deciduous premolars has accelerated and the maximum width of the dentine on the deciduous p3 is more than twice the width of adjacent enamel. The posterior cusps of the m2 have erupted on some caribou, but show no attrition (Plate A). At 13 months, all i1 are permanent (Fig. 2). At 15 months, all eight incisi-form teeth, the m1 and m2 are permanent, and the m3 has begun to erupt (Plate A). The maximum width of dentine areas exceeds the maximum width of adjacent enamel on all deciduous p3 and p4 and on most p2. The width of dentine on the permanent m1 is usually equal to or slightly more than that of the enamel, and the dentine line on the m2 is narrower than its surrounding enamel. The p2, p3 and p4 are deciduous until after 17 months (Plate A). Attrition at 17 months is similar to that at 15 months. The dentine has widened slightly and on some individuals the

anterior cusps of the m3 have erupted and may show a faint dentine line.

At 22 months the permanent premolars are erupting (Plate A). At that stage, the deciduous premolars may be entire, well-rooted teeth or they may be milk caps with absorbed roots adhering to the crowns of the erupting permanent premolars. The m3 may have partly erupted and dentine on the m1 is wider than the surrounding enamel.

At 24 months, premolars may be deciduous, or they may be permanent, lightly stained and easily recognizable. In the permanent p3 and p4 the crests and crescents are worn only slightly. Eruption in the m3 is considerably advanced; its anterior and, to a lesser degree, the medial cusps may show wearing. At 25 months eruption and wear are slightly advanced, but comparable to that at 24 months. The anterior and medial cusps of the m3 have erupted in nearly 90 per cent of the specimens.

At 27 months, most premolars and the m3 are permanent. Wear on the newly erupted permanent premolars varies: it sel-

dom occurs in the p2, but dentine lines are worn to a width almost equal to that of adjacent enamel in the p3 and p4. The dentine on the m1 and m2 is equal to or greater than that of adjacent enamel. The dentine on the m3 may range from a mere trace, on the medial and distal cusps, to a width just about equal to that of the surrounding enamel on the anterior cusps and on some medial cusps, especially on the buccal side.

At 29 months, full permanent dentition occurs (Plates A and B). Many newly erupted permanent premolars, easily recognizable as such, are faintly stained. The p2 shows little or no wear, and the dentine of the permanent p3 and p4 is narrower than the adjacent enamel. The maximum width of the dentine on the m1 is greater than the maximum width of the enamel. The dentine of the m1 is usually wider than the enamel on the buccal side, but narrower on the lingual side. The lingual cusps of the m3 may or may not show wear; the dentine on buccal cusps is exposed to a width equal to or slightly less than that of adjacent enamel.

The full permanent dentition is subject to less attrition during winter than in summer. In winter, vegetation is relatively free of abrasive materials largely because the roots are frozen in the earth and the caribou do not ingest that abrasive-laden portion of the plants.

The degree of individual variation in the attrition patterns of the mandibular teeth within age-classes is great enough to limit the value of assigning age from tooth wear. However, categorization of wear patterns serves as a basic management tool. Descriptions have been made for Alaskan caribou by Chatelain (1954), Watson and Keough (1954) and Skoog (1956, 1968). Chatelain developed age-class groupings of 1, 2, 3, 4-6, 7-9 and 10+ years. Skoog (1968) reported groupings of calves, 1, 2, 3-5, 6-8, and 10+ years. Watson and Keough produced a key to age based on subjective evaluation of eruption and wear of the mandibular teeth and on quantitative measurements.

In this section I will present only a cursory descriptive account of the mandibular molariform teeth from 3 to 10+ years of age. Age determination will be discussed in detail in the section, "Estimating age and sex by dental measurement." As subjective descriptions do not warrant a seasonal consideration after 39 months and because autumn is the time when most caribou would be hunted for sport, I will describe the premolars and molars of caribou 39 to 123+ months old, collected in September of the year. The following descriptions are based on average wear patterns of the specimens at each age.

2.1. 39 months

The 3-year-old class had fully developed mandibular tooth rows and wear was becoming noticeable. The distal cusp of the m3 had moderate to no wear. The gum line around the distal cusp had not retracted sufficiently to expose the full height of the cusp, because the jaw was not completely elongated (Watson and Keough, 1954). The posterior occlusal surface of the p2 was worn and a definite line of dentine, narrower than the adjacent enamel, was evident in some specimens while in others the p2's were not at all worn. The dentine lines on the occlusal surfaces of the p3 and p4 were usually about as wide as the adjacent enamel. In some specimens, mostly males, the dentine on the posterior crest was wider than the adjacent enamel. Dentine surfaces on the molars were usually equal to or slightly greater in width than the adjacent enamel. In some specimens, the buccal cusps of the m3 showed little wear, with dentine lines narrower than the adjacent enamel.

2.2. 51 months

In the 4-year-old class, wear had advanced on the occlusal surfaces of the premolars and molars to a point at which the dentine was wider than the adjacent enamel on all teeth except the p2. Wear on the p2 was restricted to the posterior surfaces of the tooth and varied from slight to

moderate. On the m1, the maximum width of dentine exceeded that of the adjacent enamel. The distal cusp of the m3 showed moderate wear with the dentine usually as wide as or slightly wider than the adjacent enamel.

2.3. 63 months

In the 5-year-old class, the attrition was not distinct from that in the 4-year-old class and separation by subjective evaluation would be subject to considerable error. Some specimens in the 5-year-old class had slightly more wear on the posterior half of the p2, the anterior and posterior buccal cusps of m1 and the distal cusp of m3.

2.4. 75 months

In the 6-year-old class, wear on the p2 was still restricted to the posterior half of the occlusal surface. The raised pointed appearance of the lingual side of the p3 and p4 was somewhat reduced, but still present in many specimens. The molars first showed a horizontally inclined buccal-lingual plane. The single distal cusp and two posterior cusps of the m3 were considerably worn in some individuals.

2.5. 87 months

In the 7-year-old class, attrition on the mandibular teeth of some animals overlapped that of 6- and 8-year-old classes. Assignment of age by year was subject to considerable error. Wear on the p2 was usually restricted to the posterior half of the occlusal surface. The raised pointed appearance of the anterior and posterior crescents of the p3 and p4 was lost in most specimens. The plane between the buccal and lingual cusps of the molars was horizontally inclined. The single distal cusp and two posterior cusps of the m3 were worn almost horizontal in some individuals.

2.6. 99 months

Attrition in the 8-year-old class was only slightly greater than in the 7-year-old class. The most noticeable difference was

in the p2, on which both the anterior and the posterior portions were worn. The posterior crest of the p4 showed slightly more attrition than in the 7-year-old class and the dentine surface joining the anterior and posterior cusps was more concave. The distal cusp of the third molar showed additional wear in some specimens, but separating 7-year-old from 8-year-old caribou on the basis of wear patterns would be subject to considerable error.

2.7. 111 months

In the 9-year-old class, the occlusal surface of most molariform teeth approached a buccal-lingual horizontal plane. The most distinctive characteristics were the flattening of all occlusal surfaces of the p2 and m3, the nearly equal height of all m3 cusps, and the extensive attrition of the m1.

2.8. 123+ months

In the 10+-year-old class all molariform teeth were very worn: they were on a more or less even plane, and the buccal-lingual plane was nearly horizontal. The infundibulum between the anterior cusps of the m1 was nearly obliterated or absent in some specimens.

There are many reasons for the individual variations in the wear patterns of the molariform teeth of individual caribou. Three primary causes of variation are malocclusion from misalignment of the maxillary and mandibular tooth rows, variations in the curvatures of the rami, and variations in the primary and secondary axes of the mandibular blades. Minimal wear on the lingual crests of molariform teeth, resulting from malocclusions, leads to underestimation of age. Excessive wear on the premolars, resulting from variations in the curvatures of the rami or from variations in the secondary axes of the mandibular blades, leads to overestimation of age.

A further complication in estimating ages of caribou by visual examination of the molariform mandibular tooth rows is the variation in the observer's ability to

evaluate the wear patterns. The possibility of error on the observer's part may require lumping of animals into age groups of 2 to 4 years in length. A good approach to the use of jaw boards would be to estimate the caribou's age by age-class (1-10+ years), then place the individuals in age groups: 1, 2, 3, 4-5, 6-9, and 10+ years. These categories would provide sufficient data on trends for use in management.

Much of the variation in wear of teeth likely results from differences in total intake of forage and individual preferences for food species. In general, those caribou 5 years of age or younger which show the most wear on their mandibular teeth are the heaviest within the particular age-class.

Some caribou, however, show extreme variations in the wear patterns of their teeth resulting from missing teeth and abnormal alignment of the mandibular or maxillary tooth rows. Extreme cases of these conditions are shown in Figs. 4, 5, and 6. Irregularities of the types illustrated would cause variations in wear patterns that would confound age determinations by visual examination or by measurements of tooth heights.

Figure 4 shows the malocclusion of the tooth rows of a 75-month old male. No attrition occurred on the p2 and the posterior cusps of the m3 because of the offset along the primary axes of the maxillary and mandibular tooth rows.

Figure 5 shows irregular wear of an upper P4, resulting from the absence of an opposing lower p4, in a 97-month-old female. Also the lower p2 and p3 were less worn than normal because the opposing upper teeth were missing.

Figure 6 illustrates the teeth of a 94-month-old female in which the P3 and P4 were missing from the maxilla. The adjacent M1 was reduced by decay to a point below the gum line. Deterioration of the maxillary tooth row reduced the wear of the medio-posteriad portion of the lower p4 and the anterior cusps of the lower m1. The upper P2 had migrated posteriorly, and the lower p2 consequently suffered no attrition.

Figure 4

Buccal view of dental malocclusion, in a 75-month-old male caribou, resulting from misalignment of the primary axes of the maxillary and mandibular tooth rows

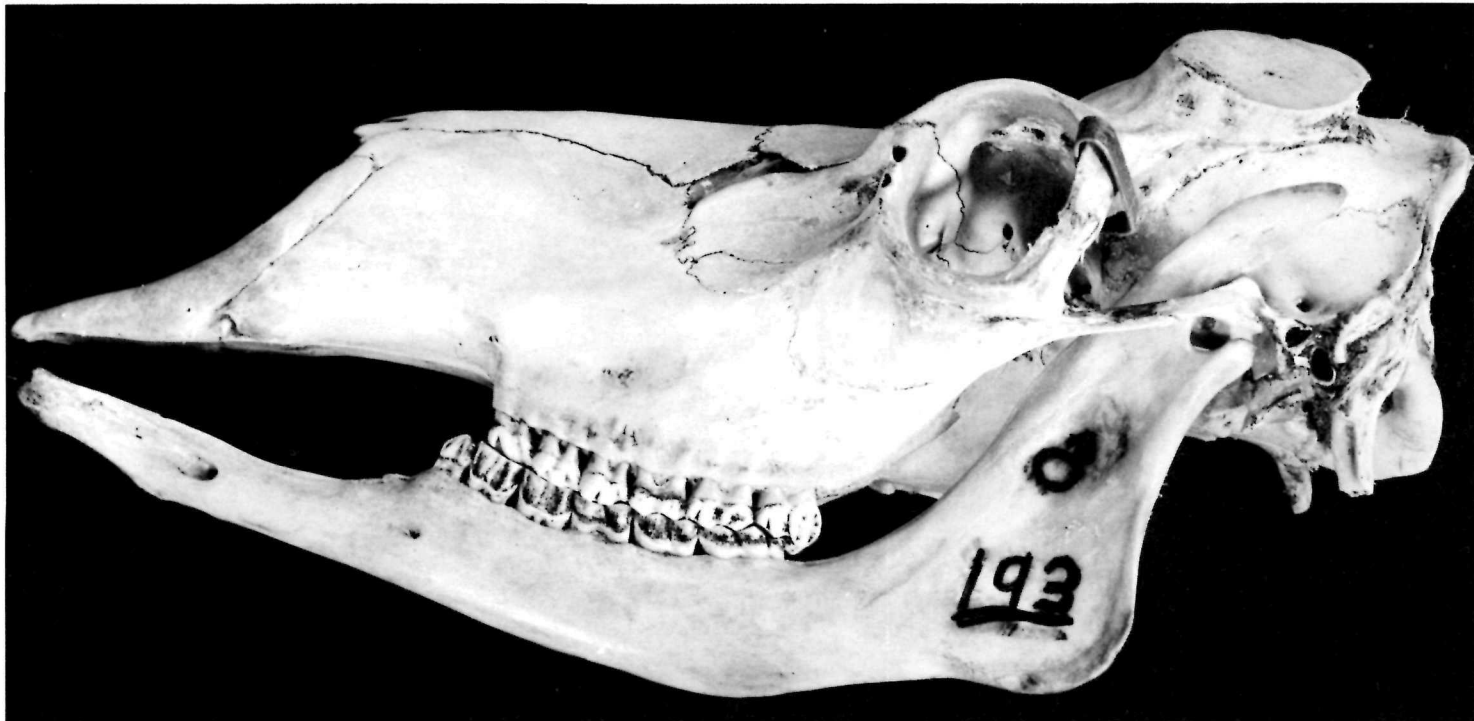


Figure 5
Buccal view of dental malocclusion, in a 97-month-old female caribou, resulting from the absence of opposing molariform teeth



Figure 6
Buccal view of dental malocclusion, in a 94-month-old female caribou, resulting from the loss of molariform teeth and tooth decay

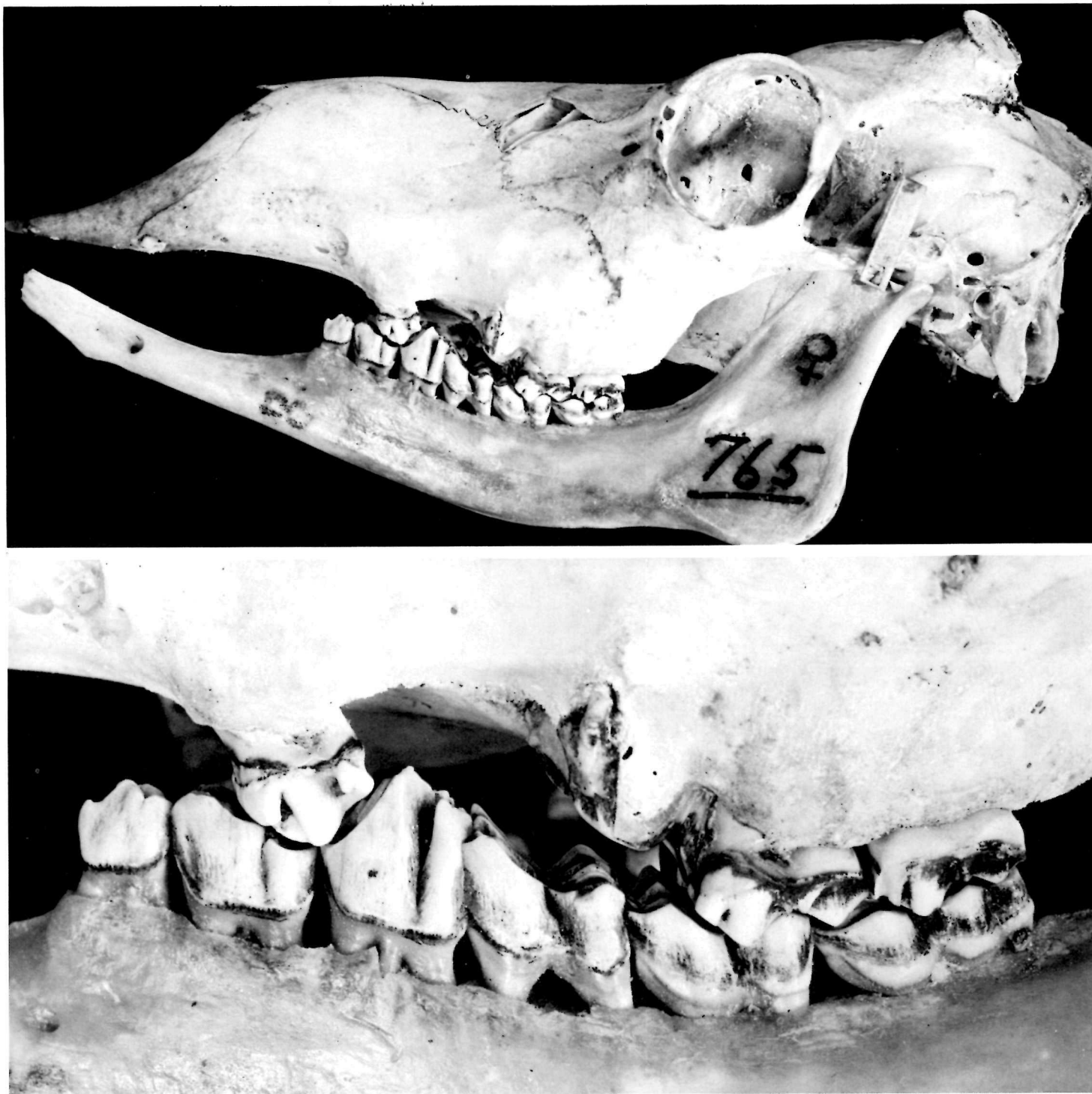
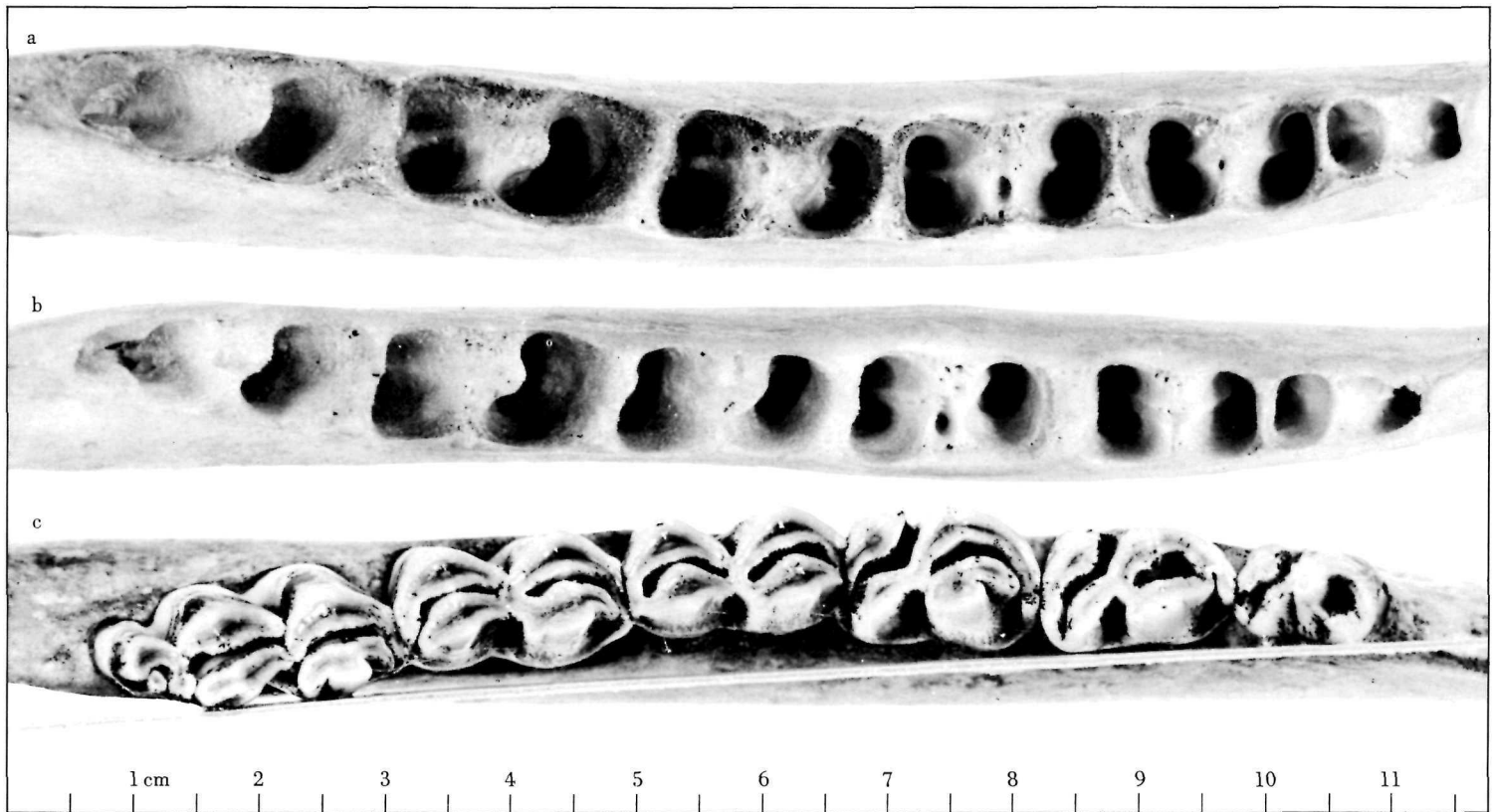


Figure 7
Caribou mandibles showing occlusal view of
(a) the alveoli of a 29-month-old female, (b)
the alveoli of a 41-month-old male, (c) the
buccal-lingual curvature in the primary axis of
a 37-month-old male

Figure 7



This condition suggests that the maxillary tooth row was damaged before the animal's second summer when the permanent upper and lower second premolars had not yet erupted.

Wearing of the molariform teeth of caribou is sometimes greatly influenced by the orientation of teeth in their sockets, and the curvature of the primary and secondary axes of the ramus. The curvature of the primary axis might be distorted either buccal-lingually or anterior-posteriorly and the secondary axis might be distorted dorso-ventrally. Figure 7 illustrates the normal curvature of the primary and secondary axes, and variation in socket formation and alignment.

Races of *Odocoileus hemionus* on the volcanic areas of the Cascade Mountains

and the high desert areas of the Great Basin, and of *O. virginianus* on the Sonoran Desert areas of the Southwest, the sandy Gulf Coast, the east coast of Florida, the Pine Barrens of New Jersey, and the sand dune areas of Cape Cod live in habitats which provide as much or more abrasive materials in food than do caribou habitats. Furthermore, Severinghaus and Cheatum (1956) report that deer from the sandy offshore islands of Massachusetts and a dry, dusty area of Texas had a tooth wear rate approximately double that of deer from upper New York State. None of the caribou from the Kaminuriak and Beverly populations showed any great deviation from the norm in dental attrition caused by eating highly abrasive food. From my empirical experiences in estimating the ages of car-

ibou, black-tailed deer (*O. h. columbianus*) and white-tailed deer by tooth eruption and wear, I believe that the molariform teeth of most 5- to 10-year-old Kaminuriak caribou show relatively less wear on the average than other deer of similar ages. I therefore differ from Kelsall (1968:28) in his statement that "caribou pick up more sand and other abrasive material with their food than deer." Furthermore, his statement that "some caribou are apparently more selective in choosing clean food than others," (Kelsall, 1968:28) is equally unsupported. Much of the forage on the summer feeding areas is subject to considerable wind action with consequent deposition of microscopic abrasives over much of the vegetation.

3. Age determination by dental annuli

Initially, teeth were decalcified using formic acid with formaldehyde, sectioned, dehydrated in alcohol, and stained with Harris haematoxylin. As less than 25 per cent of the slides thus prepared were readable, a series of trials was made in an effort to improve the technique. Different concentrations of the decalcifying agents formic acid, nitric acid and citric acid were tested singly and in combination.

Decalcification with formic acid as described by Low and Cowan (1963:467) for mule deer, by McEwan (1963:111–112) for barren-ground caribou, and by Gilbert (1966:200) for white-tailed deer gave unsatisfactory results. The annulations revealed by subsequent staining were usually only partly readable and there was often much sloughing of the cementum at the dentino-cemental interface.

Formic acid with sodium citrate and Jenkin's fluid were costly and time consuming to use, and the sections were mostly unacceptable for age determination.

Decalcification with 0.1 N nitric acid at first gave good results when combined with the use of a cryostat microtome, although it took three times longer than with formic acid. Later, this method proved variable and thus unsatisfactory, as the stained sections were often barely readable.

Sixty-seven per cent commercial nitric acid finally proved to be the best concentration for decalcifying the teeth. Reimers and Nordby (1968:958) used this agent on reindeer teeth but with a decalcification time of only 24 hours as compared to generally 36 hours for first incisors in the present study.

I now believe that many of our problems with formic acid, especially the sloughing of the cementum, were due to prolonged storage of the teeth in a dried condition. I ran comparative decalcification tests between 25 per cent (5 per cent by volume) formic acid and 67 per cent nitric acid. The teeth used in these tests were pulled shortly after they were obtained, and

stored in 5 per cent formalin until decalcified. All teeth were subsequently treated in the same way after decalcification. The sections obtained from teeth decalcified in formic acid were better than those earlier produced by the same technique, and there was no sloughing of the cementum layers. But 67 per cent nitric acid still produced sections superior to any decalcified in formic acid.

Dehydration of the tooth sections with ethyl alcohol was necessary when sectioning teeth in wax blocks with the conventional microtome used in the early stages of the histological work. Later, the use of a cryostat freezing microtome eliminated the dehydration step. It is likely that much of the separation of the cementum from the dentine at the dentino-cemental interface was caused by dehydration. Possibly, varying rates of expansion and contraction, and cutting with a dull microtome blade led to the breakage of connective fibres at the dentino-cemental interface and subsequent sloughing of the cementum.

Teeth were processed using the histological technique presented in Table 2. I was able to use only 5 per cent of 3,000 microscope slides produced before the final method was developed compared to about 75 per cent of the 2,400 slides later produced. All the retained tooth sections were read at least four times, with several days between each reading to decrease the chance of error that would result from remembering an earlier estimate.

The type of section which allows one to count the number of annuli correctly is debatable. Sergeant and Pimlott (1959:317–318) preferred longitudinal sections to transverse sections of moose (*Alces alces*) teeth; they thought that the full sequence of growth layers is exhibited only in localized thickenings of cementum. Similarly, Olson (1967:16) favoured longitudinal sections through the entire length of the boss area of teeth from white-tailed deer and moose as such sections expose the maximum number of annuli. I agree with those authors. The longitudinal section allows

the observer to determine more accurately the origins of annuli and the splitting, merging or phasing out of an annulus along the course of the cementum. It is possible to miss such changes in an annulus when transverse sections are used.

Erickson and Seliger (1969:385) wrote that the most distinct area of cemental annuli is always included in the transverse sections of mule deer teeth but is often missed in longitudinal or sagittal sections. I think that their choice of transverse tooth sections was primarily influenced by technical considerations. From detailed discussions of plastic mounting techniques with Erickson, I have concluded that it is much more difficult to orient incisor teeth in a plastic mould for longitudinal than for transverse sectioning. Obtaining successful sagittal sections with a Gillings-Bronwill thin-sectioning diamond saw such as they used is sporadic, at best, and time consuming. Orienting a tooth in a wax block for sectioning with a conventional microtome poses similar difficulties. As the tooth is not visible in the wax and shifts as the wax cools, it is only by chance that the correct angle for sagittal sectioning is obtained. A tooth can often be correctly aligned by trial and error, but this takes a lot of time and is not practical when working with a large number of teeth. When a cryostat microtome is used, the tooth can be exactly positioned, then frozen onto the metal plate before sectioning.

In caribou, the longitudinal section from il is especially valuable for detecting the dentino-cemental interface and the first annulus, which may be close to the interface or may be obscured by staining. The first cemental annulus in the il can be traced into the apex of the root where it phases out; all other annuli continue around the apex and thus are distinguishable from the first annulus. This condition could be missed on a transverse section if the first annulus and the maximum or correct number of annuli were not distinct on the same section. This contribution is undoubtedly species-specific.

Figure 8

Longitudinal section through the il of a 16-year-old caribou showing alternating dark and narrow, light and wide layers in the cementum (500 \times). D, dentine; S, separation caused by processing; C, cementum; P, peridental membrane

I generally used sections from the boss area of the posterior concave face of the il since, like Sergeant and Pimlott (1959:317), I found the cementum was thickest there. The greatest apposition of cementum in the ml was on the pad between the roots, as reported for red deer (*Cervus elaphus*) by Mitchell (1963:350), but the annuli were usually too indistinct to count. I used sections from the lingual and buccal faces of the ml roots where the annuli were clearer though closer together.

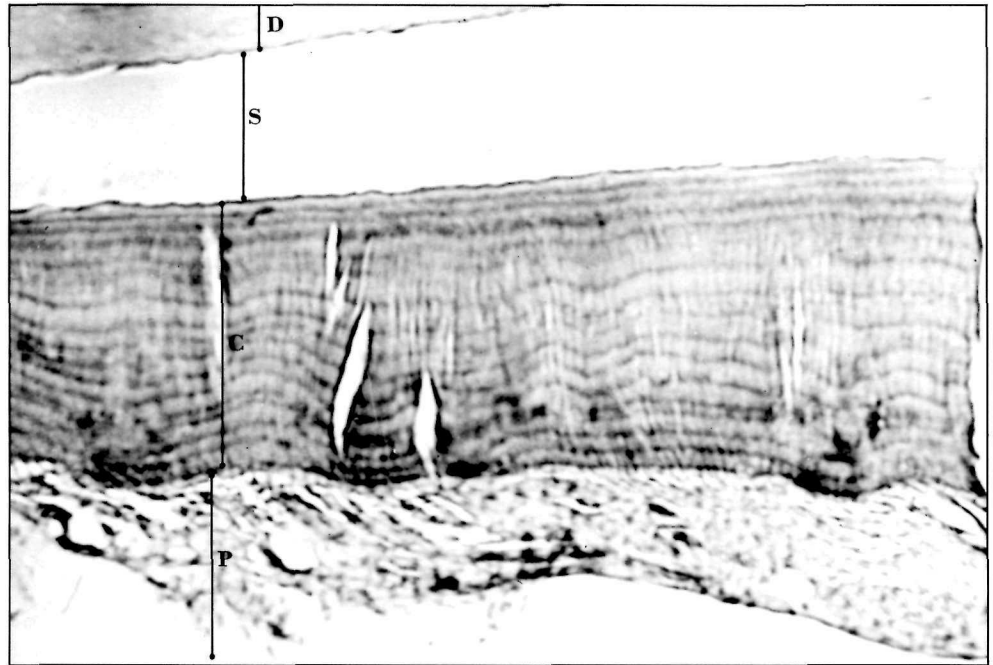
Egg white used as an albumen adhesive for microscope slides must be fresh because stale egg albumen clouds the annuli and results in a great loss of detail. Slides should not be layered with egg albumen more than 24 hours before mounting the tooth sections.

Mayer's acid haemalum, as used by Reimers and Nordby (1968:958), proved to be an unsatisfactory stain; it was often weak, and many annuli could not be accurately traced. Wright Stain No. 16 used alone produced a few excellent stains but most sections so stained were unacceptable. It was also unsatisfactory when used with Eosin Y. Many workers have obtained satisfactory staining results using haematoxylin alone, but the additional contrast obtained from a combination of Harris haematoxylin and Eosin Y significantly improved the readability of most slides.

If a permanent record of aged material is not required, heated gelatin-glycerol (Reimers and Nordby, 1958:958) could be used as a mounting agent. I used Fisher's Permunt but never solved the problem of the distortion which often results when a cover slip is applied to make a permanent mount. Furthermore, the use of Fisher's Permunt adds considerable time, and thus cost, to the mounting procedure.

Scanning of sections was best done at 100 \times to 200 \times higher magnifications than those used by other workers on sections from other species. To completely evaluate many of the tooth sections, magnifications of 200 \times to 400 \times were also used. The root of il in the boss area, first

Figure 8



described by Low and Cowan (1963:468), contained the most distinct cemental layers and yielded sections in which the annuli could best be counted. I was often able, and found it necessary, to confirm the reading by examining the relatively close layering of cementum on the upper portion of the root and the diffuse annuli in the root apex.

The dental cementum of the il is acellular except in the apex of the root, as described by McEwan (1963:112) and Reimers and Nordby (1968:958). The cementum in the root apex is cellular and similar to the structure described for moose by Sergeant and Pimlott (1959:319), for Indiana white-tailed deer and Isle Royale moose by Olson (1967:29), and for Norwegian reindeer by Reimers and Nordby (1968:958). The cementum consists of a pattern of broad, lightly-stained layers and narrow, darkly-stained bands or winter rest lines (McEwan, 1963:112).

Teeth from animals collected in April, May, June, September, November and December were examined to determine the chronological sequence of the two types of cemental layering. The sequence suggests that the broad, lightly-stained layers were apposed during the annual rapid growth periods of July–September and July–December, for males and females respectively; and that the winter rest lines were apposed during the period of little or no growth after December and before April of the following year (Figs. 8, 9).

To determine when apposition or cementum began and when the first winter rest line was formed, I examined sections of unerupted, permanent il from the mandibles of 5- and 10-month-old caribou. It was evident that the apposition of cementum had started by the 5th month of life.

A thin layer of dental cementum was present on the upper one-third to one-half of the root exterior. Sections from the per-

Figure 9a

Longitudinal section through the il of a 101-month-old caribou (125 \times). Box indicates detailed area shown in Figure 9b

Figure 9b

Longitudinal section through the il of a 101-month-old caribou (500 \times). Note light area of cementum beyond eighth annulus deposited during ninth summer of life. D, dentine; I, dentino-cementum interface; C, cementum; P, peridental membrane; 1 - 8, annuli

Figure 9a

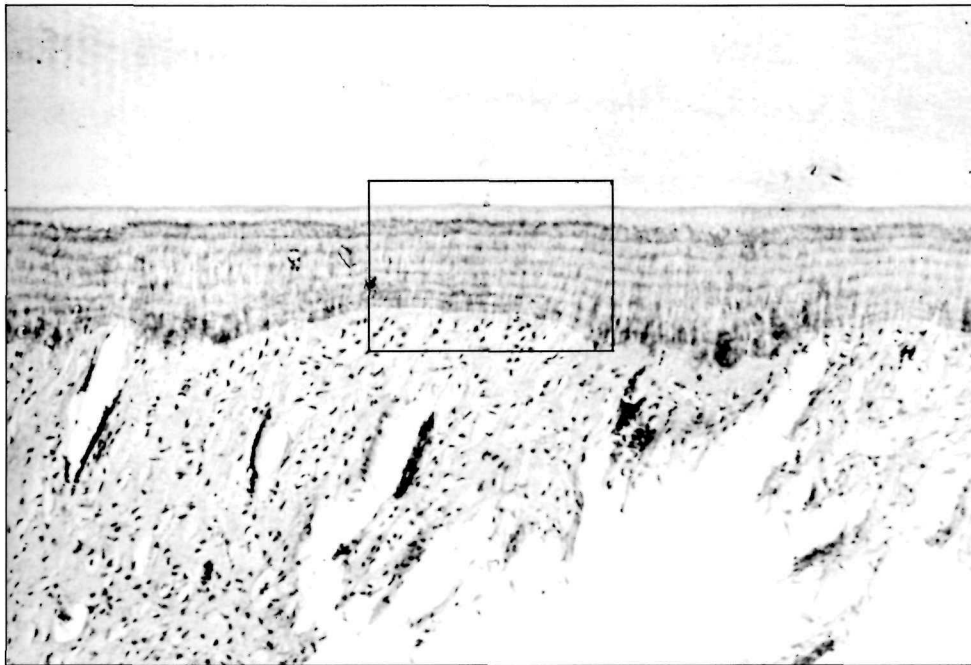


Figure 9b

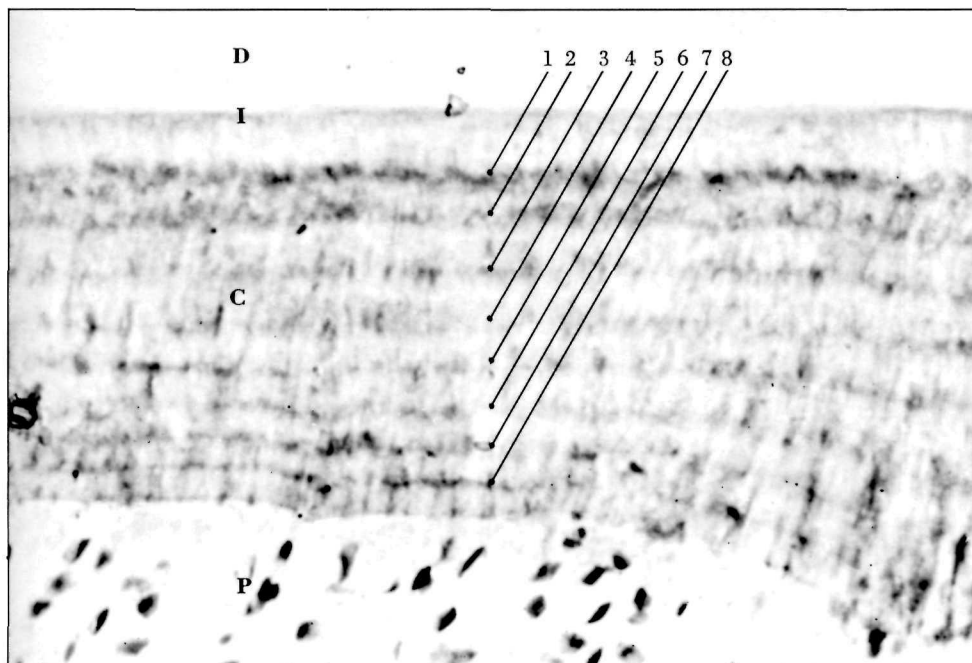


Figure 10a

Longitudinal section through the il of a 12-month-old caribou (125 \times). Box indicates detailed area shown in Figure 10b

Figure 10b

Longitudinal section through the il of a 12-month-old caribou (500 \times). D, dentine; I, dentino-cementum interface; C, cementum; A₁, first annulus; P, peridontal membrane

Figure 10a

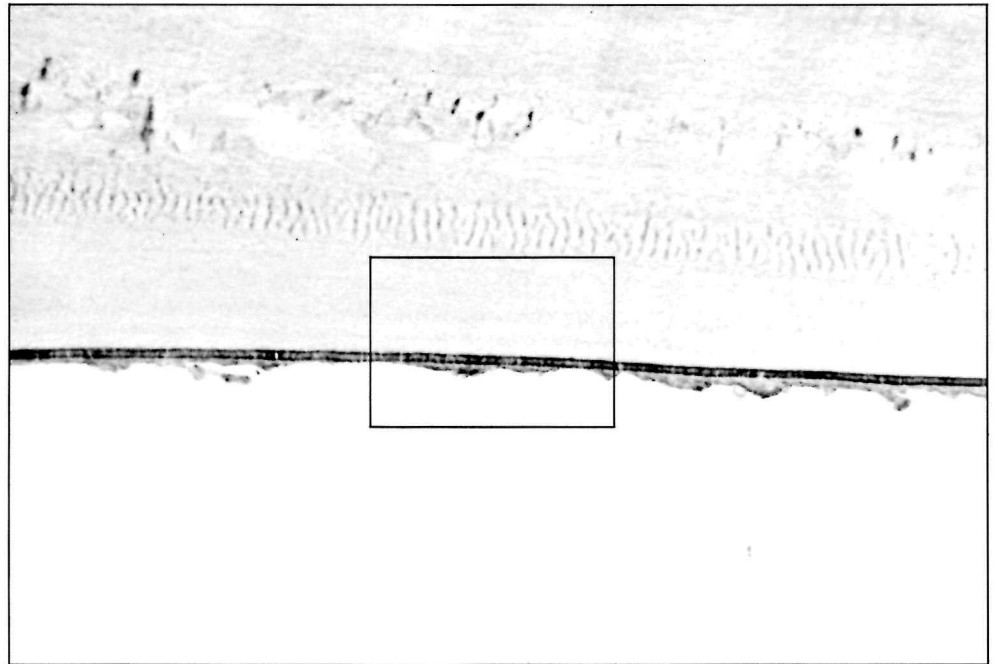


Figure 10b

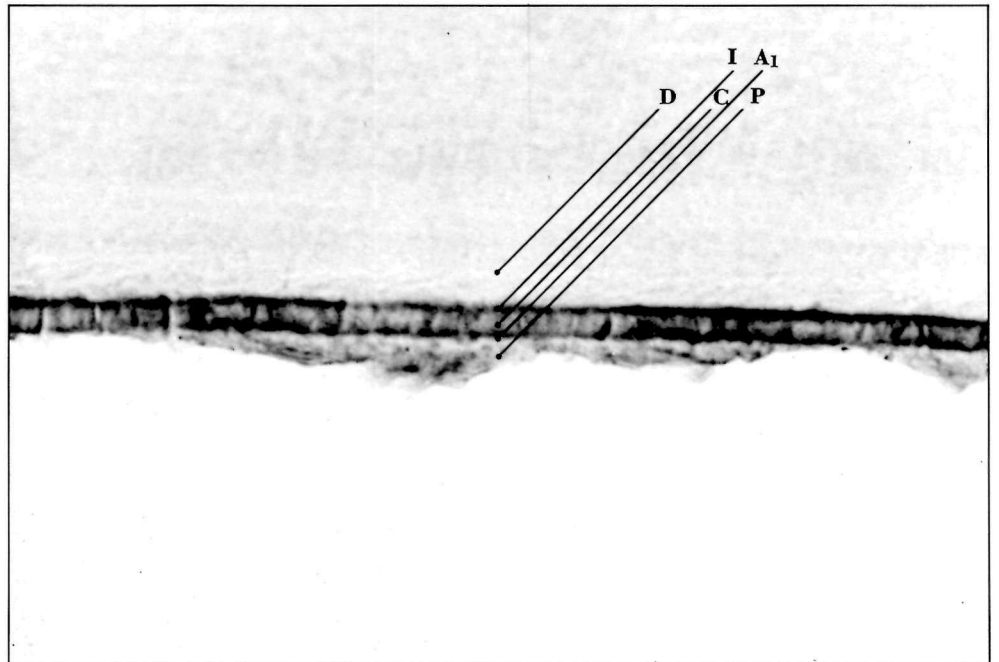


Figure 11a
Longitudinal section through the il of a 15-month-old caribou (125 \times). Box indicates detailed area shown in Figure 11b

Figure 11b
Longitudinal section through the il of a 15-month-old caribou (500 \times). D, dentine; I, dentino-cementum interface; C, cementum; A₁, first annulus; P, peridontal membrane

Figure 11a

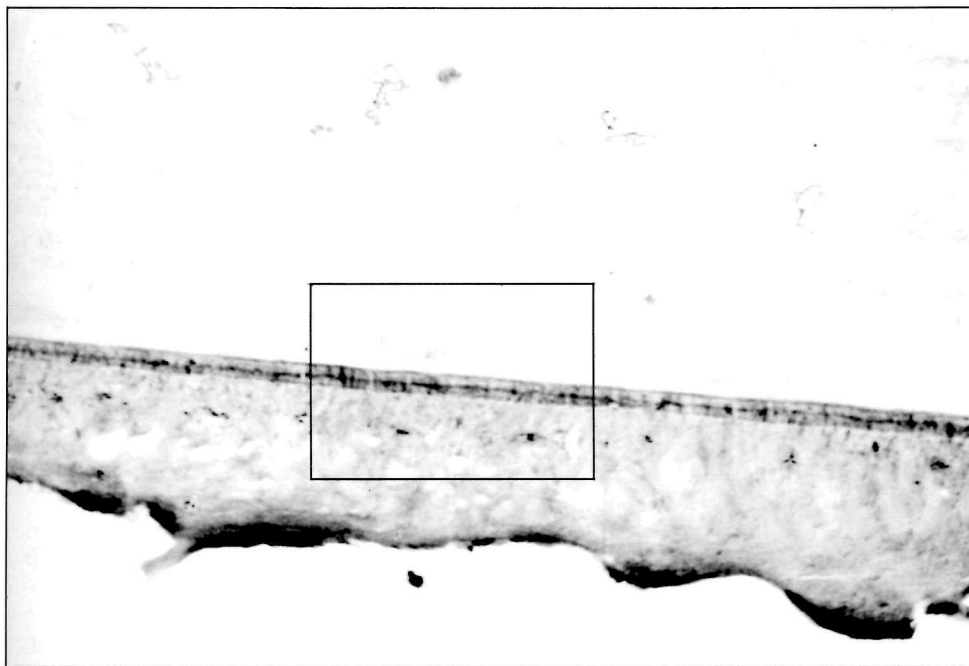
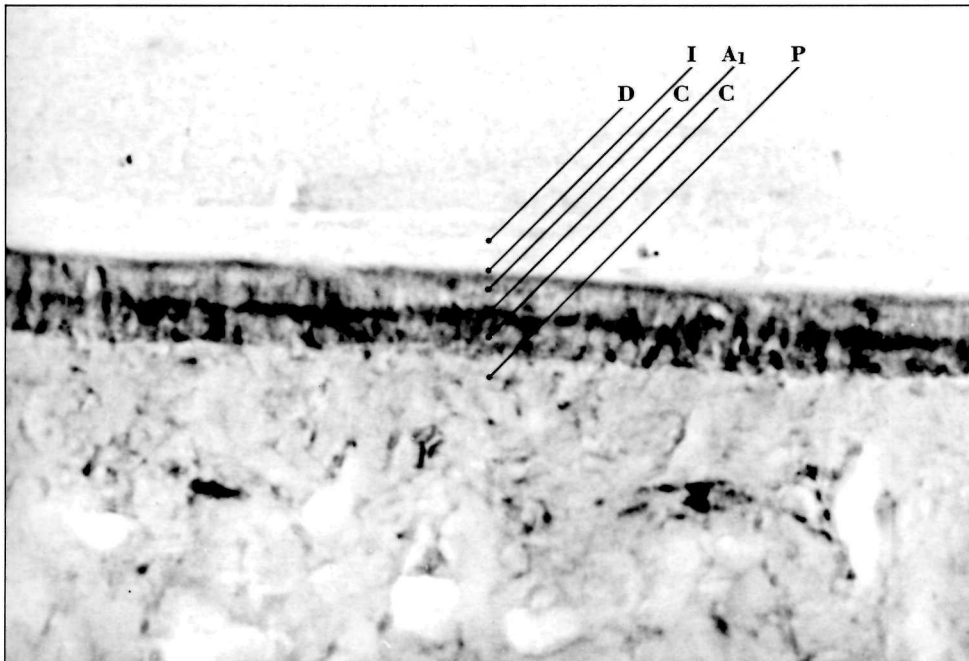


Figure 11b



manent il of 10-month-old animals had a broad, lightly-stained layer of cementum terminating almost at the open apex of the root. The open apex helps the observer to identify the first winter rest line which, at 10 to 12 months, is on the exterior of the cementum.

At 12 months the first winter rest line is against the peridontal membrane and there is little or no proliferation of the cementoblasts that form areas of lightly-stained cementum (Fig. 10). At 12 or 13 months, some sections have the fibres of the peridontal membrane aligned at 90° to the margin of the cementum, and cementum is often deposited in pockets along the course of the root at the cemento-peridontal membrane interface, especially in the apical cemental area.

At 15 months the sections show three layers; two broad, lightly-stained ones separated by a winter rest line (Fig. 11). The outer, light area of cementum begins to form during the second summer of life, probably continuing well into the second autumn. I could not detect any sex-linked difference in the initiation of the true winter rest line, although rutting male caribou lose body weight and fat reserves from October to December and female caribou continue to gain weight and store fat during that period. Neither could I detect current rest lines in the teeth of caribou collected during November and December; in most cases winter rest lines did not exist at the cemento-peridontal membrane interface.

At 22 months, sections show a current winter rest line against the peridontal membrane (Fig. 12). This condition also occurred in most older caribou collected in April and is evidence of the annual formation of the winter rest line before April. No lightly-stained cementum was visible outside the last winter rest line in tooth sections from adult Norwegian reindeer killed in May (Reimers and Nordby, 1968:959). The conditions described lead to the assumption that cementum is laid down each year in alternating bands — light and broad, dark and narrow — forming an an-

Figure 12a

Longitudinal section through the il of a 22-month-old caribou (125 \times). Box indicates detailed area shown in Figure 12b

Figure 12b

Longitudinal section through the il of a 22-month-old caribou (500 \times). D, dentine; I, dentino-cementum interface; C, cementum; A₁, first annulus; A₂, second annulus; P, peridental membrane

Figure 12 a

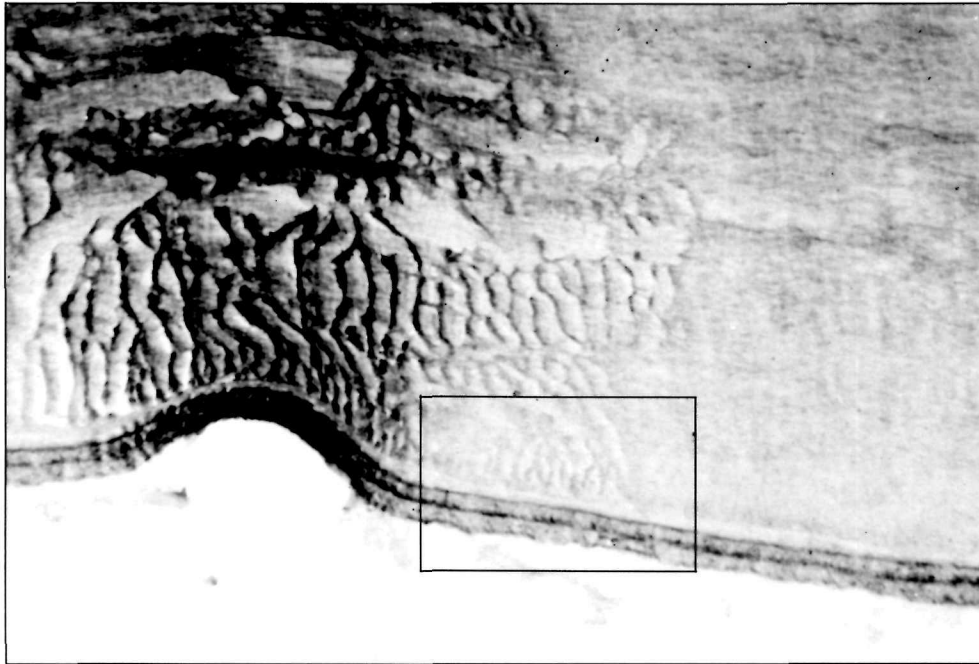
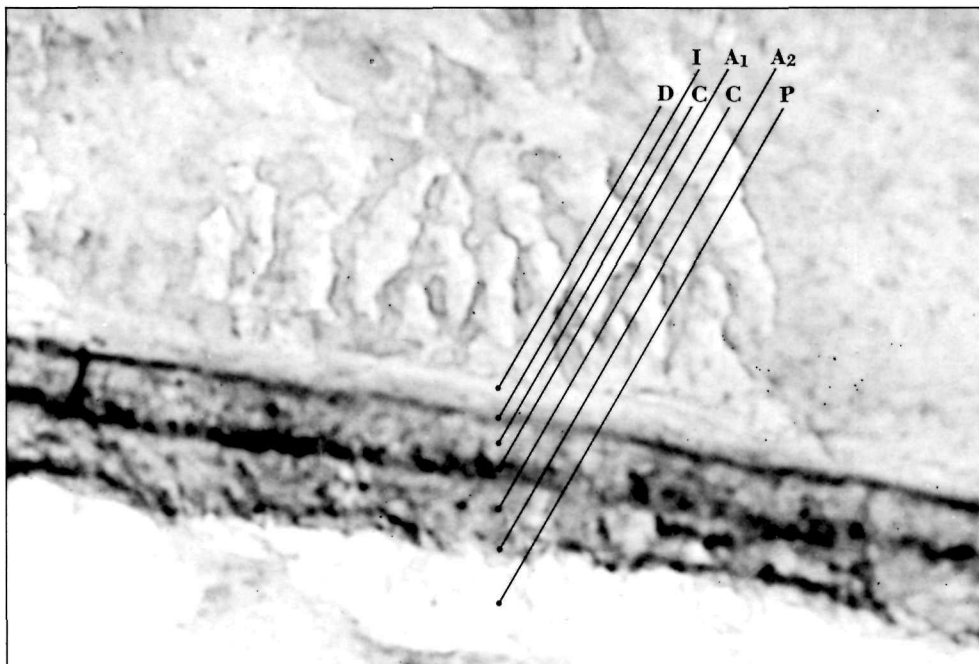


Figure 12 b



nulus, and the regularity with which this is done allows us to count the annuli to determine the age of caribou.

I found that cementum had been deposited on the roots of the permanent il and ml before crown eruption. However, McEwan (1963:111) reported that in his study of caribou, cemental deposition did not occur until eruption of the permanent il. Within and among species, reported times of first deposition of cementum are variable:

- Moose — before eruption (Sergeant and Pimlott, 1959:319) and after (Wolfe, 1969:430);
- White-tailed deer — il, before eruption (Gilbert, 1966:201; Olson, 1967:35);
- Mule deer — il, after eruption (Low and Cowan, 1963:469);
- Black-tailed deer — formation of dark cemental line, different in appearance from subsequent rest lines, during the first winter (D. Thomas, pers. comm.);
- Domestic sheep (*Ovis aries*) — before eruption (Saxon and Higham, 1968:634–635);
- Pinnipeds, carnivores and rodents — conflicting evidence, not directly applicable. The observed variation may reflect differences in techniques as well as species characteristics and population conditions.

Double winter rest lines, or *rut lines* as first termed by Low and Cowan (1963:469), occurred in some teeth of males and females. The secondary rest line was easy to distinguish from the true annual rest line in most cases but difficult in a few. When double rest lines occurred, they were usually present for each year of life except the first. In some cases, however, they were duplicated only for certain years. No causal pattern could be discerned. The low incidence of this condition did not justify further exploration as it did not interfere with my objectives. Reimers and Nordby (1968:959) found rut lines only in males from exceptionally good range. Whether secondary rest lines are caused by the rut or by other factors leading to variations in growth remains unanswered.

All investigators of dental cementum have found a pattern of alternating cemental layers of differing densities, produced by periodically differing rates of cemental apposition. The broad lightly-stained zones are usually associated with periods of rapid growth and the narrow, darkly-stained bands with periods of nutritional stress. In grizzly bears (*Ursus arctos*) (Mundy and Fuller, 1964:865) and black bears (*Ursus americanus*) (Stoneberg and Jonkel, 1966: 413), however, the winter rest line begins to form before the bear enters its den. This suggests that formation of the winter line is not initiated by the bear's reduced food intake. The reasons offered for the cause of alternating cemental layers are varied, and often convincing until applied as universal concepts. The explanations include rates of nutritional stress as a primary or secondary stimulus, cyclic hormonal changes and photoperiodism, and changes in cementum from the variation in friction on the roots caused by seasonal changes in overall food intake. Klevezal' and Kleinenberg (1967:7-33) discuss in detail annual cemental layers and the supposed reasons for their formation.

My finding of a first winter rest line in the teeth of 10- and 12-month-old caribou agrees with that of Reimers and Nordby (1968:958) for Norwegian reindeer; Gilbert (1966:201), Ransom (1966:198) and Olson (1967:20) for white-tailed deer; Sergeant and Pimlott (1959:319) and Wolfe (1969: 430) for moose; and Saxon and Higham (1968:634) for domestic sheep. However, McEwan (1963:112) for barren-ground caribou, Low and Cowan (1963:468) and Erickson and Seliger (1969:387) for mule deer, Mitchell (1963:351) for red deer, and Flook (1970:22-23) and Keiss (1969:177) for wapiti (*Cervus canadensis*) all found that the first full winter rest line was formed during the second winter of life. I have no explanation for this difference.

Counting the annuli is the weakest point in the technique, as many tooth sections cannot be entirely evaluated without some degree of subjectivity. Cemental an-

nuli are the best criteria available for determining the age of caribou despite their limitations.

4. Estimating age and sex by dental measurements

The following 51 dental measurements were evaluated by computer programs for possible indicators of caribou ages. The measurements given are of teeth from left and right dentaries unless specified. For example, p2R means second premolar from right dentary. Tooth height measurements were made on the labial face of i1 and the buccal sides of p2, p3, p4, m1, m2, and m3.

1. Height i1
2. Height p2
3. Height p3
4. Height p4
5. Height anterior cusp m1
6. Height posterior cusp m1
7. Width enamel, anterior cusp m1
8. Width dentine, anterior cusp m1
9. Height anterior cusp m2
10. Height posterior cusp m2
11. Height anterior cusp m3
12. Height posterior cusp m3
13. Weight p2R
14. Width p2R
15. Length p2R
16. Weight p3R
17. Width p3R
18. Length p3R
19. Weight p4R
20. Width p4R
21. Length p4R
22. Weight m1R
23. Width m1R
24. Length m1R
25. Weight m2R
26. Width m2R
27. Length m2R
28. Weight m3R
29. Width m3R
30. Length m3R
31. Average height i1
32. Average height p2
33. Average height p3
34. Average height p4
35. Average height anterior cusp m1
36. Average height posterior cusp m1

37. Average width enamel, anterior cusp m1
38. Average width dentine, anterior cusp m1
39. Average height anterior cusp m2
40. Average height posterior cusp m2
41. Average height anterior cusp m3
42. Average height posterior cusp m3
43. Length right dentary
44. Length right tooth row
45. Length right diastema
46. Length left dentary
47. Length left tooth row
48. Length left diastema
49. Average length mandible
50. Average length tooth row
51. Average length diastema

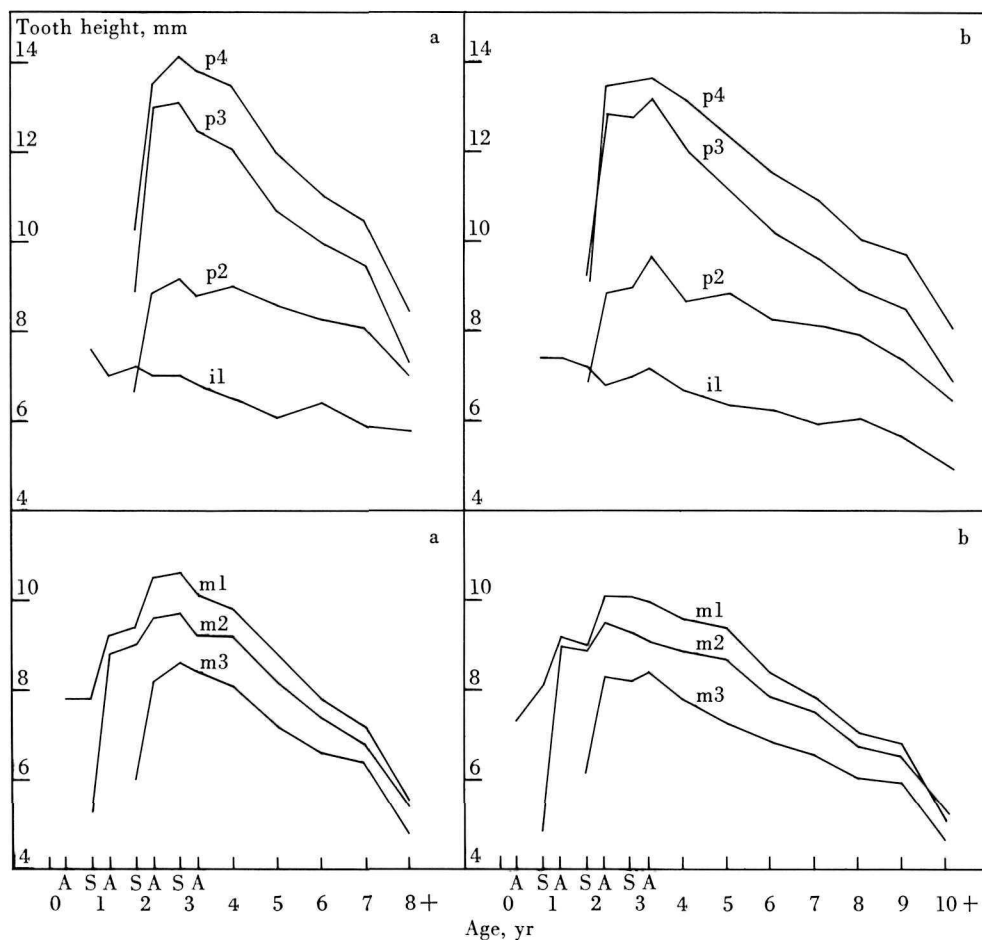
This section deals with the use of readily obtainable dental variables for assigning the age and, in some cases, the sex of individual caribou accurately enough for management purposes. While not necessarily as accurate as the histological approach, the dental measurements are simpler, quicker and more economical when dealing with large series of specimens and can be used by field personnel with minimal instruction.

I have shown that the ages of Kaminiariak caribou can be determined by eruption and replacement of the mandibular teeth for all animals through 21 months and for many animals up to 28 months. The state of the closure of the apices of tooth roots can be used to separate 2-year-olds from 3-year-olds (Table 5): the apices of the p4 and m3, the last to mature, are open at 24 months but closed at 36 months. The roots are closed at 27-29 months and at 34 months in approximately 25 per cent and 86 per cent of specimens respectively.

Caribou with full permanent dentition and closed roots can usually be separated by subjective evaluation of dental characteristics if the animal is under 39 months. The permanent mandibular teeth do not show appreciable wear until the end of the fourth summer of life. The ridges of the premolars and the m3 of most 3-year-olds show little or no wear; the premolars are often lightly stained and the distal cusp of the m3 is usually not fully elevated. It is

Figure 13

Average heights of mandibular incisors, premolars and molars by age. (a) Male; (b) female. A, autumn (Sept. and Nov.); S, spring (Apr. and June)

Figure 13

unlikely that subjective examination of the mandibular teeth of 3-year-olds would result in underestimation of age. Any error would more likely be in an overestimation of a year.

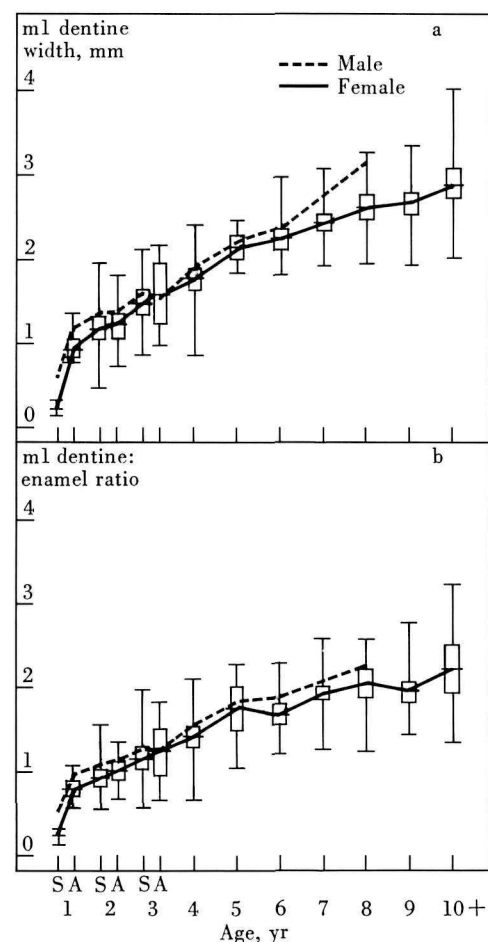
For management purposes, animals between 3 and 5 years could be classed as young breeders. Most females in that age class should be producing young, but whether males of that age have the opportunity to breed probably depends on the number of older males in the population. I suggest that the ages of the specimens in a sample be estimated to the year, but the data finally compiled only in age groups.

Quantitative dental measurements for estimating age need be applied only to caribou 39 months of age or older.

The average height from the lowest point on the stained gum line to the highest point of the buccal ridge is plotted by age for males (Fig. 13a) and females (Fig. 13b), for each of the seven permanent mandibular teeth measured (anterior cusp only for the molars because of the similarity between the anterior and posterior cusps). The period of eruption is shown for the six molariform teeth. As the animals become older, decrease in tooth height, caused by wear, continues steadily through

Figure 14

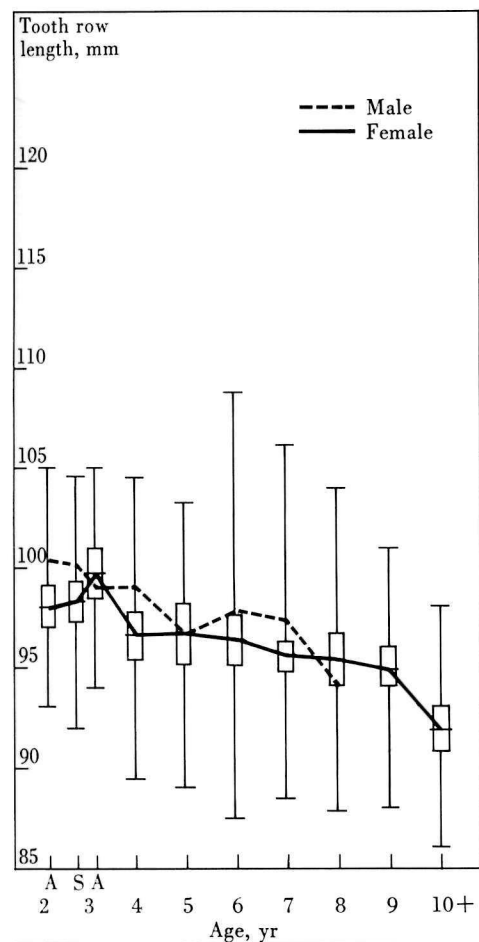
Average measurements of the m1, from specimens taken in seven collections by sex and age. (a) Dentine width; (b) dentine:enamel ratio. A, autumn (Sept. and Nov.); S, spring (Apr. and June). The brackets indicate the range, and the blocks, the 95% confidence limits around the mean for females

Figure 14

to the oldest specimens, but the older specimens were combined to shorten the graphs and increase the sample size to give estimates of variability. Thus the means for males 8 years and over and females 10 years and over are lower than would be expected at 8 and 10 years respectively. The males show consistently more wear than the females, with the means for 7-year-old males comparable with those for 8-year-old females, presumably because the former eat more food than the latter to produce and maintain a heavier body.

Figure 15
Average length of mandibular tooth row by sex and age. A, autumn (Sept. and Nov.); S, spring (Apr. and June). The brackets indicate the range, and the blocks, the 95% confidence limits around the mean for the females

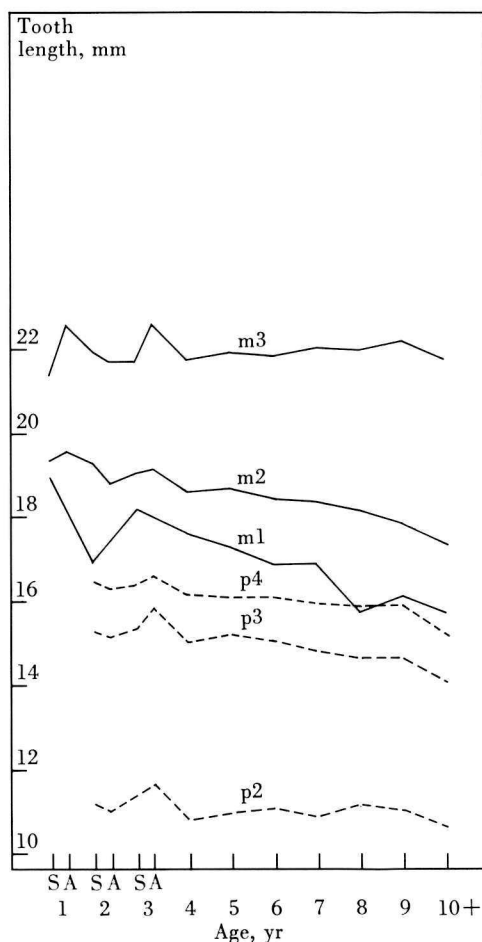
Figure 15



Enamel and dentine widths of the m1 could be used for only 7 of the 10 collections. Many readings from specimens collected in June, September and November 1966 were inconsistent with the data collected later, presumably due to errors in measurement. I concluded that it was too difficult to obtain these measurements. Figure 14 shows the width of dentine and the dentine:enamel ratio of the m1 from specimens taken in seven collections. The dentine width increases steadily with age up to about 6 years; in older females the annual increase in width is lower (Fig. 14a). The ranges and 95 per cent confidence

Figure 16
Average antero-posterior lengths of female mandibular, molariform teeth by age. A, autumn (Sept. and Nov.); S, spring (Apr. and June)

Figure 16

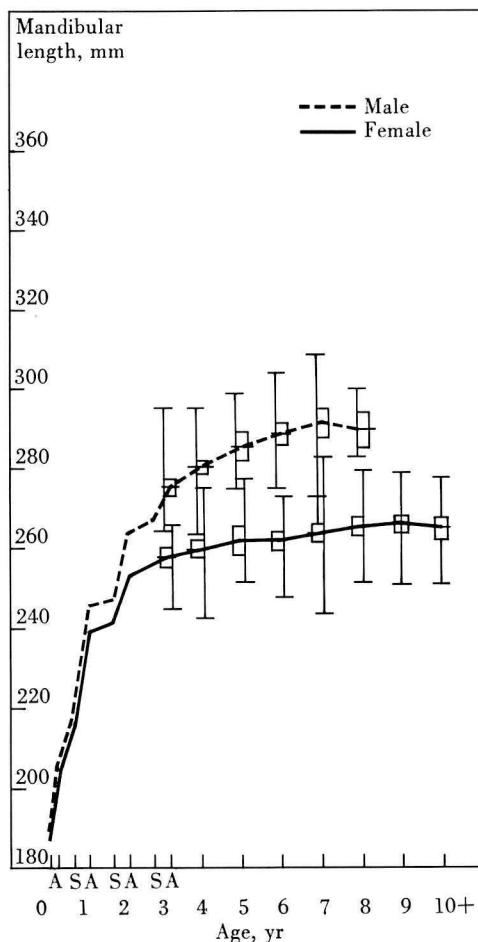


limits of the mean dentine widths for the females show that the overlap between young mature caribou and older animals is considerable (Fig. 14a). The width of enamel appears to be constant for all ages 2 years and older: the average is about 1.4 mm, the range is 0.9–1.9 mm for males and females.

Figure 14b shows the relationship of the dentine:enamel ratio to age and sex. There is a slightly greater overlap between age groups in the dentine:enamel ratio than in dentine width (Fig. 14b). By 6 years all caribou had a dentine width greater than 1.8 mm, so a rule could be used that a mea-

Figure 17
Relationship of average mandibular length to sex and age. A, autumn (Sept. and Nov.); S, spring (Apr. and June). The brackets indicate the range, and the blocks, the 95% confidence limits around the mean for both sexes

Figure 17

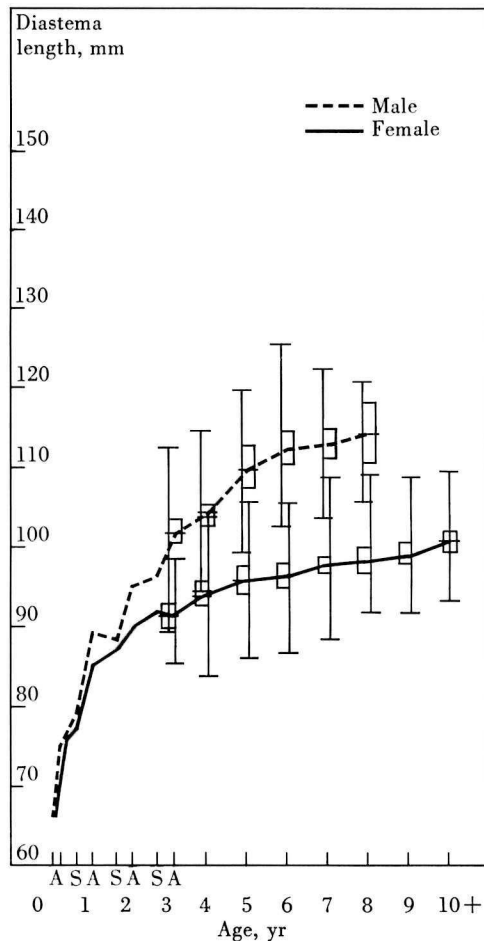


surement less than 1.8 mm indicates that a caribou is under 6 years. Other use of the relationship to estimate the ages of particular specimens is limited because of the high degree of overlap. The increased rate of wear for males is confirmed by the dentine measurements.

The relationship of tooth row length to age for both sexes, with ranges and 95 per cent confidence limits of the means for females, is plotted in Figure 15. The apparently shorter tooth row in older animals was investigated, and the average lengths of individual permanent premolars and molars are plotted in Figure 16. Females

Figure 18

Relationship of average diastema length to sex and age. A, autumn (Sept. and Nov.); S, spring (Apr. and June). The brackets indicate the range, and the blocks, the 95% confidence limits around the mean for both sexes

Figure 18

alone are plotted because of the similarity between the sexes. The means for m1 are less reliably estimated because most of these teeth were sectioned before it was decided to record the lengths and widths. The antero-posteriad length decreases with age for p3, p4, m1 and m2 but does not change for p2 and m3. The decrease was too slight and variable to be a useful criterion to age. Rees (1971) attributed the decrease in tooth row length in white-tailed deer to interstitial wear and mesial drift. As the caribou teeth taper near the gum, the wearing in height of an individual tooth would decrease its antero-posteriad length

Table 7

Results of analysis of variance of dental variables for male caribou aged 3 to 7 years

Variable	Sample n	Mean at 7 yr.	Difference with age 3-7 yr.	Avg. std. dev.		Age		Residual	
				s	df	F	df	F	df
Height, mm									
il	231	5.71	1.18	0.81	190	11.3	4†	1.5	36*
p2	239	8.06	0.99	0.94	198	7.5	4†	1.3	36
p3	238	9.42	3.55	1.08	197	74.6	4†	1.4	36
p4	241	10.47	3.63	1.18	200	66.2	4†	1.4	36
m1	237	7.13	3.28	0.90	197	85.5	4†	1.8	35†
m2	239	6.85	2.67	0.90	198	61.7	4†	1.6	36*
m3	233	6.30	2.22	1.07	193	32.2	4†	1.1	35
Length, mm									
p2	238	11.01	0.31	0.93	197	1.1	4	1.6	36*
p3	235	14.81	0.66	0.88	195	2.5	4*	1.4	35
p4	242	15.78	0.84	0.84	202	5.6	4†	1.5	35*
m1	36	17.16	1.30	1.14	26	5.0	4†	0.6	5
m2	240	18.32	1.00	0.93	199	8.9	4†	1.1	36
m3	240	22.12	0.13	1.32	199	1.5	4†	0.9	36
mandible, a	220	291.30	-21.30	7.00	180	64.5	4	2.0	35†
diastema, b	234	113.50	-15.00	4.80	193	82.1	4†	2.0	36†
tooth row, c	236	97.00	2.70	3.80	195	4.4	4†	1.5	36*
a - (b + c)	217	80.90	-9.30	4.60	177	25.9	4†	2.7	35†
Weight, g									
p2	234	1.45	-0.03	0.27	194	1.5	4	0.8	35
p3	224	3.16	0.42	0.49	184	3.9	4†	1.0	35
p4	235	3.92	0.59	0.56	195	5.6	4†	1.4	35
m1	232	3.22	0.77	0.46	194	15.1	4†	1.6	33*
m2	235	4.12	0.97	0.58	194	18.4	4†	1.3	36
m3	237	4.12	1.10	0.66	196	20.2	4†	1.2	36
Width, mm									
enamel m1	192	1.36	-0.07	0.16	160	5.4	4†	2.9	27†
dentine m1	192	2.73	-1.15	0.32	160	72.5	4†	1.1	27
p4	242	10.81	-0.06	0.58	202	0.3	4	1.4	35
m1	36	9.67	-0.32	0.44	26	2.5	4	0.7	5

*Significant at 5 per cent level.

†Significant at 1 per cent level.

and this would create a tendency for mesial drift to close the gaps.

The tooth widths showed negligible variation with age or sex. Tooth weights decreased with advancing age, particularly in males, but overlapped between age groups more than tooth heights, and thus provided a less sensitive measure of tooth wear.

The growth curves for mandibular length for both sexes are shown in Figure

17 and corresponding growth curves for diastema length are shown in Figure 18.

Values (mm) for newborn calves, males and females combined, are as follows: mandible-mean 124.0, range 108.5-138.9, 95 per cent confidence limits 121.1-126.9. Diastema-mean 38.1, range 27.9-45.3, 95 per cent confidence limits 36.6-39.7.

Figures 17 and 18 show that neither mandibular nor diastema lengths may be used to assign ages to mature animals, as

Table 8
Results of analysis of variance of dental variables
for female caribou aged 3 to 10 years

Variable	Sample n	Mean at 7 yr.	Difference with age		Avg. std. dev.		Age		Residual	
			3-7 yr.	7-10 yr.	s	df	F	df	F	df
Height, mm										
il	335	6.05	0.80	0.56	0.83	258	17.3	7†	1.6	69*
p2	333	8.23	0.88	1.26	1.08	255	16.7	7†	1.4	70
p3	336	9.75	3.10	1.81	1.08	258	105.9	7†	1.5	70*
p4	337	11.03	2.58	1.81	1.06	259	90.0	7†	1.5	70*
m1	337	7.95	2.12	1.72	1.06	260	63.9	7†	1.4	69
m2	334	7.61	1.67	1.62	0.99	257	48.8	7†	1.2	69
m3	330	6.73	1.47	1.33	0.93	253	39.8	7†	1.3	69
Length, mm										
p2	332	10.94	0.52	0.21	0.90	255	2.6	7*	1.4	69
p3	328	14.86	0.60	0.41	0.90	251	5.0	7†	0.9	69
p4	332	16.00	0.40	0.37	0.85	255	3.1	7†	1.2	69
m1	88	16.91	1.28	0.85	0.82	65	10.9	7†	0.9	15
m2	337	18.37	0.68	1.02	0.92	260	10.4	7†	0.9	69
m3	338	21.97	-0.06	0.11	1.30	261	0.4	7	1.0	69
mandible, a	310	263.30	-7.90	-1.20	6.60	233	13.3	7†	1.3	69
diastema, b	332	97.60	-6.10	-1.60	4.10	254	18.9	7†	1.0	70
tooth row, c	334	95.70	2.80	3.00	3.40	256	7.9	7†	1.1	70
a - (b + c)	308	69.90	-4.30	-2.40	4.60	231	9.6	7†	0.8	69
Weight, g										
p2	327	1.42	-0.05	0.06	0.26	250	1.8	7	1.0	69
p3	321	3.14	0.36	0.32	0.40	245	8.8	7†	1.7	68†
p4	324	4.01	0.40	0.46	0.50	247	10.4	7†	1.5	69*
m1	307	3.33	0.61	0.43	0.46	231	19.1	7†	1.3	68
m2	330	4.36	0.68	0.67	0.53	253	25.5	7†	1.2	69
m3	330	4.30	0.90	0.86	0.64	253	28.6	7†	1.1	69
Width, mm										
enamel m1	243	1.29	0.03	-0.09	0.17	184	1.4	7	2.0	51†
dentine m1	243	2.41	-0.92	-0.27	0.35	184	50.4	7†	0.8	51
p4	332	10.62	-0.04	-0.05	0.58	255	1.7	7	1.8	69†
m1	88	10.10	-0.53	0.51	0.47	65	1.7	7	1.3	15

*Significant at 5 per cent level.

†Significant at 1 per cent level.

the lengths differ so little. The effectiveness of mandibular and diastema lengths in determining the sex for mature animals will be discussed later.

The dental variables for males and females, shown respectively in Tables 7 and 8, were statistically tested to evaluate their use in estimating the age of individual caribou taken from the Kaminuriak population. Measurements were used only when both dentaries were available. This pre-

caution avoided the use of extreme values due to anomalies in the jaw. Males 8 years and older and females 11 years and older were not included because those samples were small.

The sample sizes differ for two reasons. Some readings were not recorded because the teeth were missing or anomalous, or the mandibles were broken. Most m1 teeth were sectioned before I decided to record their lengths and widths.

The means of dental statistics at 7 years (Tables 7, 8) were calculated so that variables related to sex could be easily picked out. The changes with age (Tables 7, 8; col. 4) indicate the magnitude of any change between 3 and 7 years and can be used to compare the rate of change for males and females. The age difference for females (Table 8; col. 5) gives the difference between 7 and 10 years and can be used for comparison to the earlier period of wear and mandible growth.

The analysis of variance was carried out as a two-factor analysis with unequal sub-class numbers (Snedecor, 1956:388) to study the variation related to age group and collection by year and season. Collection differences were not significant, although some variables gave fairly high F-ratios which were judged to be due to a few measurements rather than to consistent group effects.

The high proportion of large F-ratios for residual group differences (Tables 7, 8) is probably due to the larger variation within older, and smaller, age groups. The conclusions and comparisons will not, however, be affected by that factor, as most of the variables show very marked differences with age.

The heights of teeth, particularly the p3, p4, m1 and m2, are the variables most sensitive to differences in age, as indicated by the large F-ratios (Tables 7, 8). Length and weight differences are associated with the same wearing process but show relatively more random variation (Tables 7, 8). Rees (1971) demonstrated that tooth width was not related to the age of white-tailed deer, and my measurements of the width of the p4 and m1 confirm this for caribou (Tables 7, 8). The mandibles and diastema lengthen significantly, particularly in males (Table 7), and the m1 dentine widens (Fig. 14a) as the animal's age increases. But most of this lengthening and widening occurs before the animal reaches 5 years, so the variables are of little use in differentiating older age groups.

Table 9
Number of Kaminuriak caribou by age and tooth height for males and females with predicted age ranges (mature dentition only)

Male, n = 193						Female, n = 303									
Predicted age, yr.	p4 + m1, mm	True age, yr. *					Predicted age, yr.	p4 + m1, mm	True age, yr. *						
		3	4	5	6	7 8+			3	4	5	6	7	8	9 10+
3-4	> 25.0	13	15				3-5	> 25.0	5	5	3				
3-5	22.0-24.9	22	35	7	1		3-7	22.0-24.9	11	21	5	9	6	1	
3-6	20.0-21.9	5	18	7	8	2 1	3-7	21.0-21.9	3	8	11	8	19	2	2
5-7	18.0-19.9	1	2	8	12	11	5-9	18.0-19.9	3	3	16	25	11	6	1
6+	16.0-17.9		1	3	10		6-9	16.0-17.9	1		7	20	11	19	2
6+	14.0-15.9			2	1	2	7+	14.0-15.9			6	7	10	13	
7+	12.0-13.9				1	3	8+	12.0-13.9				3	3	7	
8+	10.0-11.9					2	9+	10.0-11.9						1	4
							10+	7.0-9.9							5

*Determined by annulations in the dental cementum.

Table 10
Percentage distribution of mandibular and diastematic lengths according to sex and age, showing incorrect prediction of sex in italics

Age, yr.		Sample size	Mandibular length, mm				Diastema length, mm			
			F	PF*	PM*	M	F	PF*	PM*	M
5+	Male	77	0	5	17	78	0	9	26	65
	Female	235	82	14	4	0	54	38	8	0
4	Male	69	4	29	26	41	16	43	30	11
	Female	37	92	8	0	0	89	11	0	0
3	Male	41	32	27	29	12	27	34	37	2
	Female	19	100	0	0	0	100	0	0	0
2	Male	63	79	16	5	0	71	26	3	0
	Female	71	100	0	0	0	97	3	0	0

*PF and PM equal probable female and probable male.

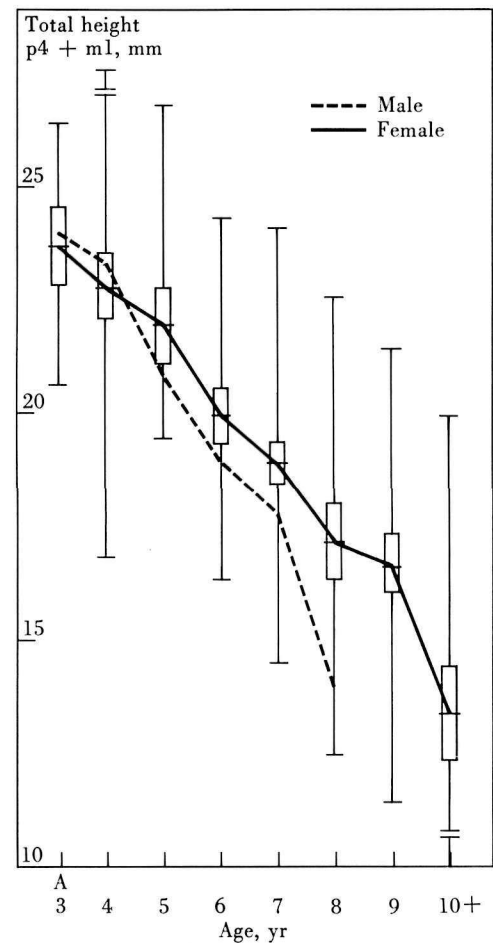
Multiple regression techniques were used to select the best combination of variables to be included in an equation to determine age. The height of the p3, with the height of the p4 a close second, was the best single indicator (Tables 7, 8). Adding the height of m1 to the heights of p3 or p4 significantly increased predictive power. Adding variables, such as mandibular length and dentine width, significantly increased the accuracy of age determinations for younger animals but decreased the accuracy for old animals. As these variables increased accuracy by only a fraction of a year they were not used.

As the p4 was used as a diagnostic tooth for age determination of caribou with incomplete dentition, its height—not the p3's—was combined with that of the m1 in the following equation.
Age = a + b₁ (Ht p4) b₂ (Ht m1)

Because of the large random variation in tooth height, the equation given by the least-squares process underestimated the slopes, thereby consistently predicting older ages for young animals and younger ages for old animals. The main function of the m1 height was to moderate the effect of individual variations. Therefore, a sum of the heights of the p4 and m1 (p4 + m1)

Figure 19
Relationship of average p4 + m1 heights to sex and age. A, autumn (Sept. and Nov.). The brackets indicate the range, and the blocks, the 95% confidence limits around the mean for females

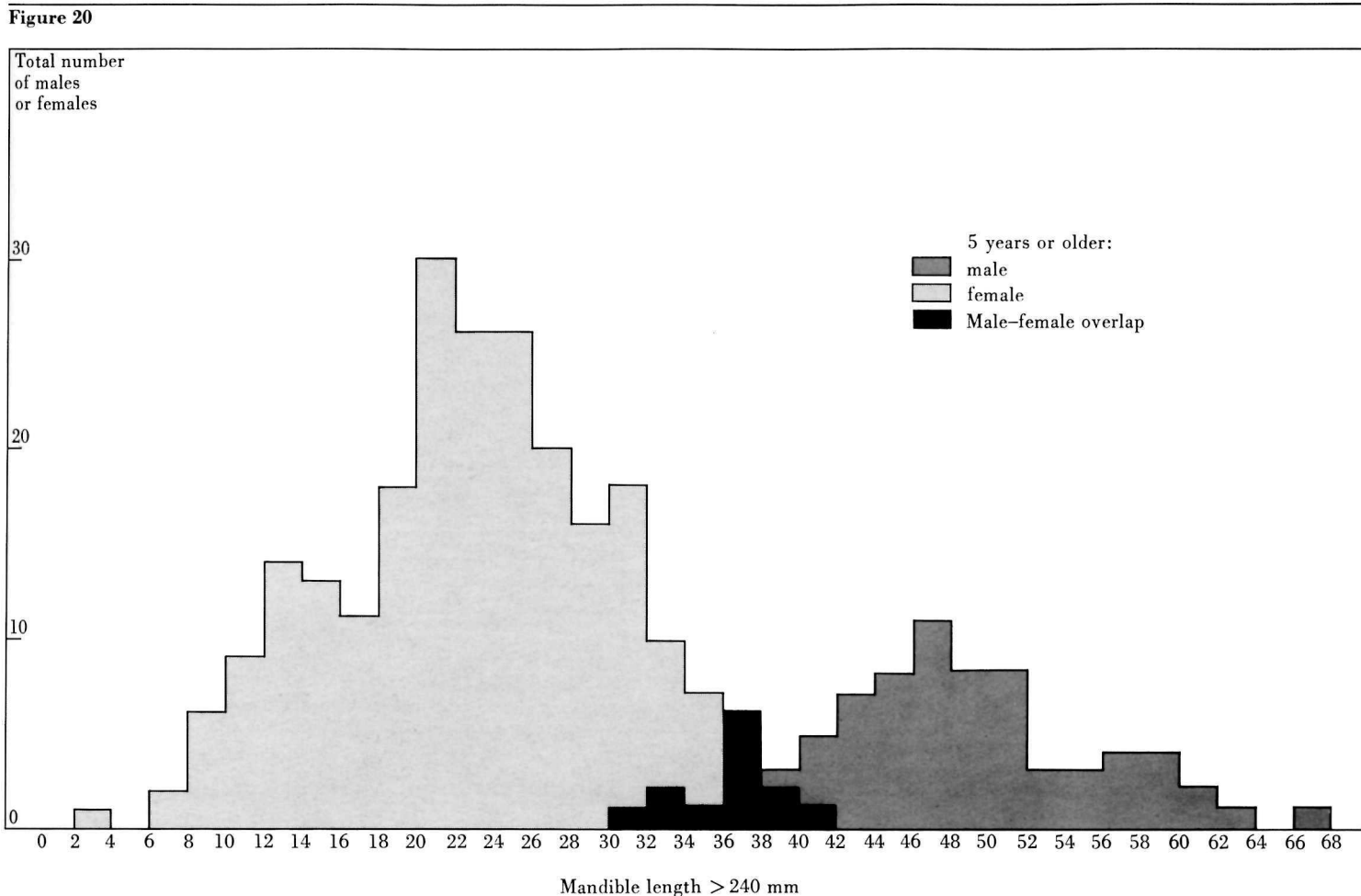
Figure 19



was tested and found effective in age separation (Fig. 19). The difference between the two heights should be checked for an anomalous difference in attrition before the sum is used. Normal specimens with appreciable wear had differences averaging 3.0 mm and ranging from 1.5 to 5.0 mm.

The age of an individual specimen can be estimated by reading off the age corresponding to the observed p4 + m1 in Figure 19. Table 9 shows the distribution of animals by age and tooth height and gives predicted age ranges. Application of Figure 19 or Table 9 requires knowledge of the

Figure 20
Frequency distribution of male and female
mandibular lengths for age classes 5+ years



sex, if the animal is 5 years or older, if the assignment of age is to be accurate.

The mandibular length reliably indicated the sex of animals 5 years of age and older but overlap in mandibular length less reliably indicated the sex of younger animals (Table 10 and Fig. 20). This differs from Bergerud's (1964) conclusion regarding Newfoundland caribou that the sex could be successfully determined from mandibular length when the animal was as young as 4 years. As Bergerud's sample was collected in the autumn, his 3-year-olds included specimens 39 to 41 months old. The 2-year-olds included 27- to 29-month speci-

mens. Bergerud achieved an accuracy of 84 per cent ($n = 19$) for males, using a mandibular length of 285 mm as the cut-off point. I obtained an accuracy of 41 per cent ($n = 41$) for 3-year-old males using a mandibular length of 277 mm. If the growth curve is assumed to be similar for the two populations, the discrepancy in the mandibular lengths indicates that the ages assigned by Bergerud, using Skoog's (1956) tooth-wear key, were somewhat low. This is reinforced by the fact that Skoog (1968) does not attempt to distinguish 3-year-olds from 4- and 5-year-olds in his summary of mandibular length.

For individuals under 5 years our sample (Table 10) was taken specifically for population study and the sex and age distribution is different from that in Bergerud's (1964: Fig. 3) sample which was obtained from hunters. His sample contained more adult males, those being the animals that hunters aim for. The sex and age distribution in the Kaminuriak sample more nearly represented that of the population.

Average mandibular measurements of the various populations studied are given in Table 11. Skoog's (1968) measurements from the Nelchina herd are consistently the highest for all age classes, mine from

Table 11
Mandibular and diastematic lengths in millimetres,
by sex and age for four populations of *Rangifer*

Age, yr.	Sex	Alaska*											
		Kaminuriak			Arctic			Nelchina			Newfoundland†		
		\bar{x}	Range	n	\bar{x}	Range	n	\bar{x}	Range	n	\bar{x}	Range	n
Mandible													
2	Male	265	248–281	63	262	244–283	51	272	255–289	207	268	258–283	9
	Female	254	255–270	71	253	237–269	66	261	248–280	87	250	244–257	7
3–5	Male	279	262–298	131	287	258–314	338	298	272–322	487	295	280–319	43
	Female	259	242–277	78	263	241–291	236	274	251–292	336	268	252–284	30
6–9	Male	289	272–308	55	301	276–321	87	315	299–335	157	307	287–328	32
	Female	264	243–282	182	267	250–290	83	282	267–294	128	272	261–286	12
10+	Male	286	286	1	300	282–310	9	319	295–346	23	306	293–325	13
	Female	264	250–277	31	267	254–277	16	283	277–296	31	275	275–276	3
Diastema													
2	Male	96	83–107	65	95	85–107	50	98	83–113	260	102	95–108	12
	Female	91	83–104	72	90	81–105	76	93	78–107	110	94	90–98	11
3–5	Male	104	89–120	132	109	90–130	338	113	95–128	784	117	94–136	51
	Female	94	84–106	78	96	83–113	279	100	85–119	418	103	94–114	37
6–9	Male	113	102–125	58	118	98–135	87	125	115–143	221	127	115–138	49
	Female	98	86–109	186	99	89–113	103	105	95–118	155	108	102–115	14
10+	Male	115	115	1	121	110–128	9	131	115–145	32	129	124–134	16
	Female	100	93–110	32	100	95–107	19	108	90–126	36	110	110–111	4

*From Skoog (1968).

†From Bergerud as quoted by Skoog (1968) with age-classes 3–6 and 7–9 yr. instead of 3–5 and 6–9 yr. for the other populations.

the Kaminuriak Population are the lowest except in 2-year-olds. The four caribou populations are discrete, and the recorded values should reflect true population differences and not just variations in techniques.

Designating mandibles of length greater than or equal to 277 mm as males is correct for 94 per cent (73 of 77) of the 5+-year-old males and 57 per cent of the 3- and 4-year-olds. It can also be shown that, for 39 months or older, mandibular lengths less than 264 mm indicate female specimens (Table 12). This leaves the sex undetermined for mandibles 264–276 mm long (Table 12), which are usually from males 3 or 4 years old or females 5 years or older.

Figure 19 shows that few specimens younger than 5 years had p4 + m1 less than 20.0 mm (only 1 of 46 males and 1 of 13 females with mandibular length between

264 and 276 mm). The 20.0 mm level was used to distinguish females at least 5 years old from younger males and females. The sex is then correctly predicted for 73 per cent of the males and 84 per cent of the females, with incorrect predictions for only 3 per cent of males and 3 per cent of females (Table 12).

The diastema length is highly correlated with mandibular length and the relationship of the two variables is the same for both sexes, so no independent information on the sex of a specimen can be obtained. However, the diastema length can be substituted if the mandible is damaged. Table 13 shows that, in animals at least 5 years old, when a diastema length of 105 mm or longer is taken as indicating that they are males, the sex determination is 91 per cent correct (95 per cent using mandibular length). However, while the range of

Table 12

Percentage distribution of Kaminuriak caribou in mandible length classes according to sex and age, assigned from cemental layers

Mandibular length, mm	p4 + ml, mm	Males, yr.			Females, yr.			Predicted sex
		3 +	3-4	5 +	3 +	3-4	5 +	
≥ 277		72	57	94	3*	0	4	Male
264-276	≥ 20.0	25	41	3	13	21	11	Undetermined
264-276	< 20.0	2*	1	3	30	2	36	Female
> 264		1*	1	0	54	77	49	Female
Sample size		187	110	77	291	56	235	

*Incorrect sex predicted.

Table 13

Percentage distribution of Kaminuriak caribou in diastematic length classes according to sex and age, assigned from cemental layers

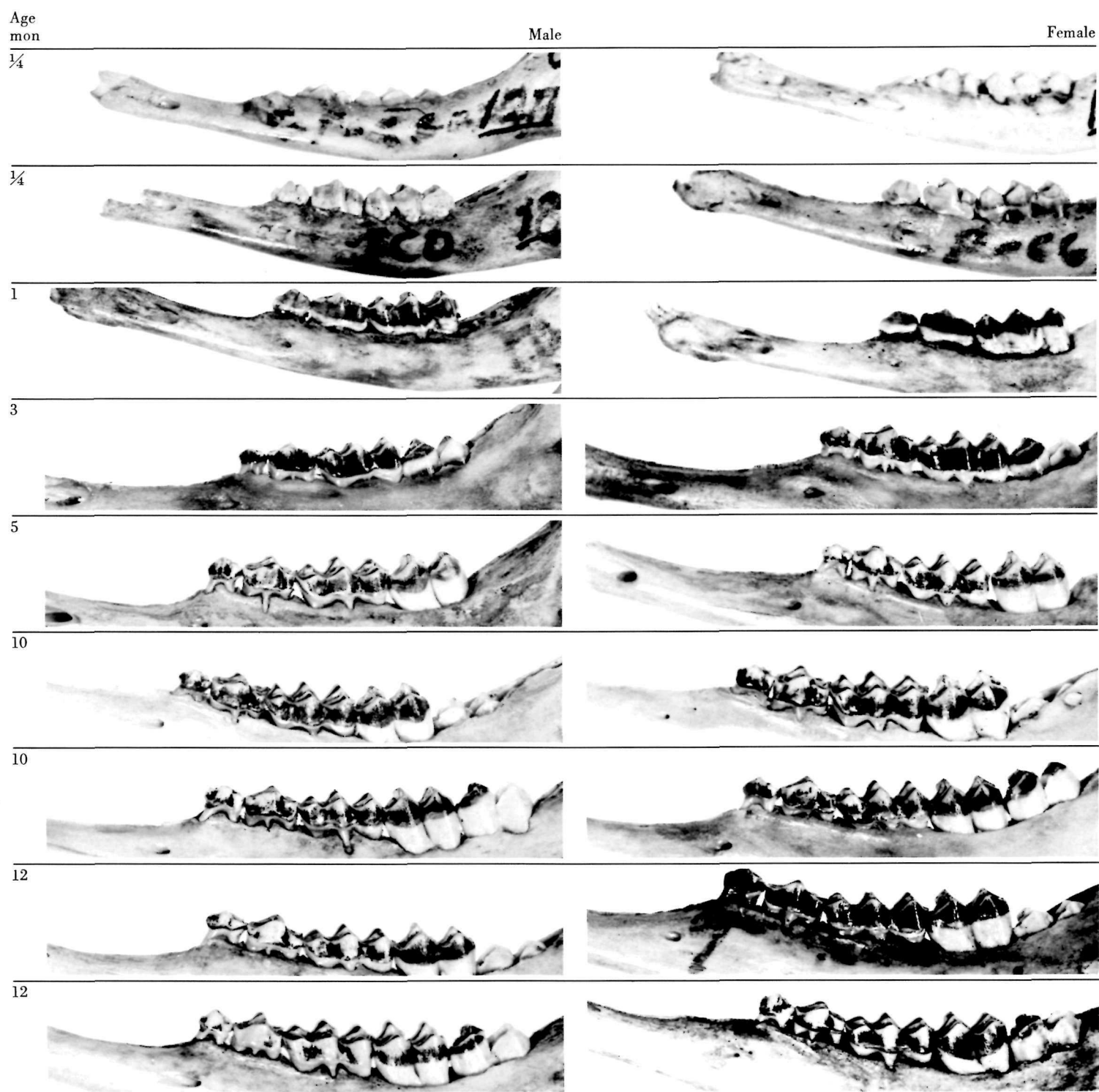
Diastema length, mm	p4 + ml, mm	Males, yr.			Females, yr.			Predicted sex
		3 +	3-4	5 +	3 +	3-4	5 +	
≥ 105		62	41	91	6*	0	8	Male
95-104	≥ 20.0	32	54	3	20	30	18	Undetermined
95-104	< 20.0	3*	0	6	41	4	49	Female
< 95		3*	5	0	33	66	25	Female
Sample size		191	111	80	298	56	242	

*Incorrect sex predicted.

diastema length for 4-year-old females is predictable, the range for 4-year-old males shows considerable overlap with older females and the accuracy is only 41 per cent (29 of 70). Sixty-seven per cent accuracy can be obtained when using mandibular length for sexing 4-year-old males. Table 13 shows the percentage predictions using high, medium and low diastema lengths, and the tooth wear index, to determine the sex of specimens 39 months and older. The percentages of specimens for which sex cannot be determined are higher when diastema, rather than mandibular, length is used. Bergerud (1964) stated that the diastema length was not sufficiently accurate to be useful in separating the sexes, but I found it only slightly less accurate than mandibular length.

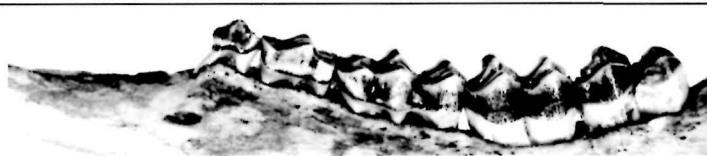
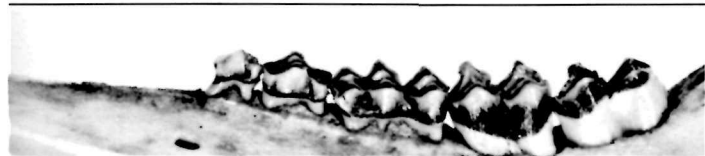
I found no mandibular or tooth measurement which would distinguish the sexes of specimens younger than 27 months. However, if the reproductive organs are missing but the carcass is available, the length of the hind foot could be used as it is mature by 22 months and is distinctly larger in males (Dauphiné, in prep.).

Plate A. Buccal view of a chronological series
of the left molariform tooth row in male and
female caribou

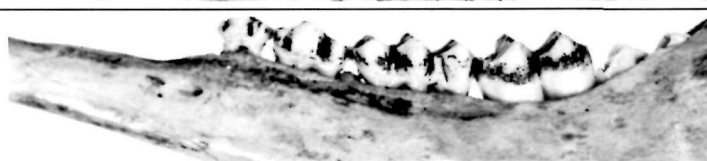


Male

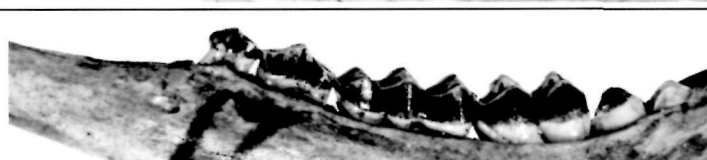
Female

Age
mon

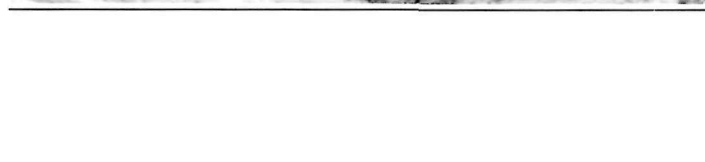
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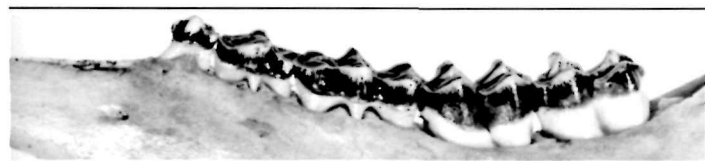
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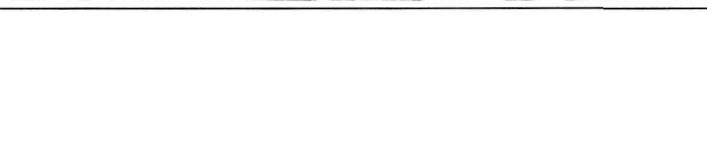
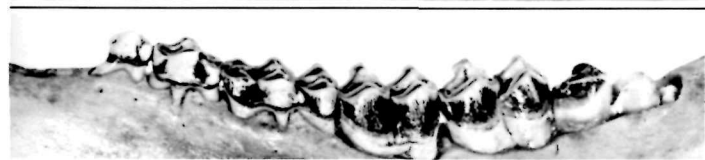
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13



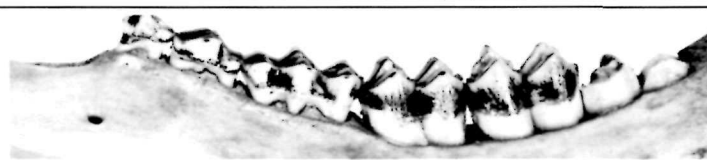
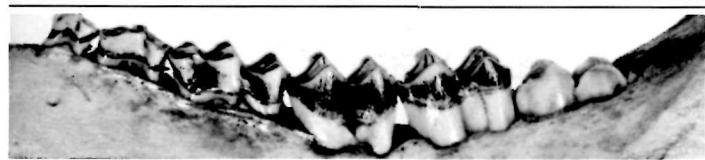
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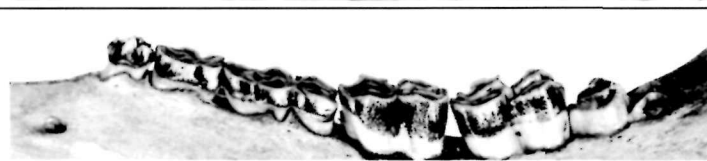
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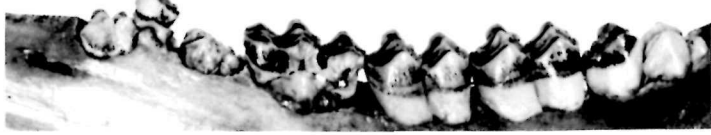

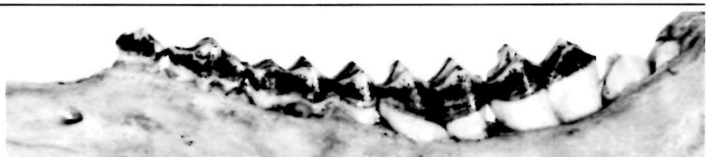










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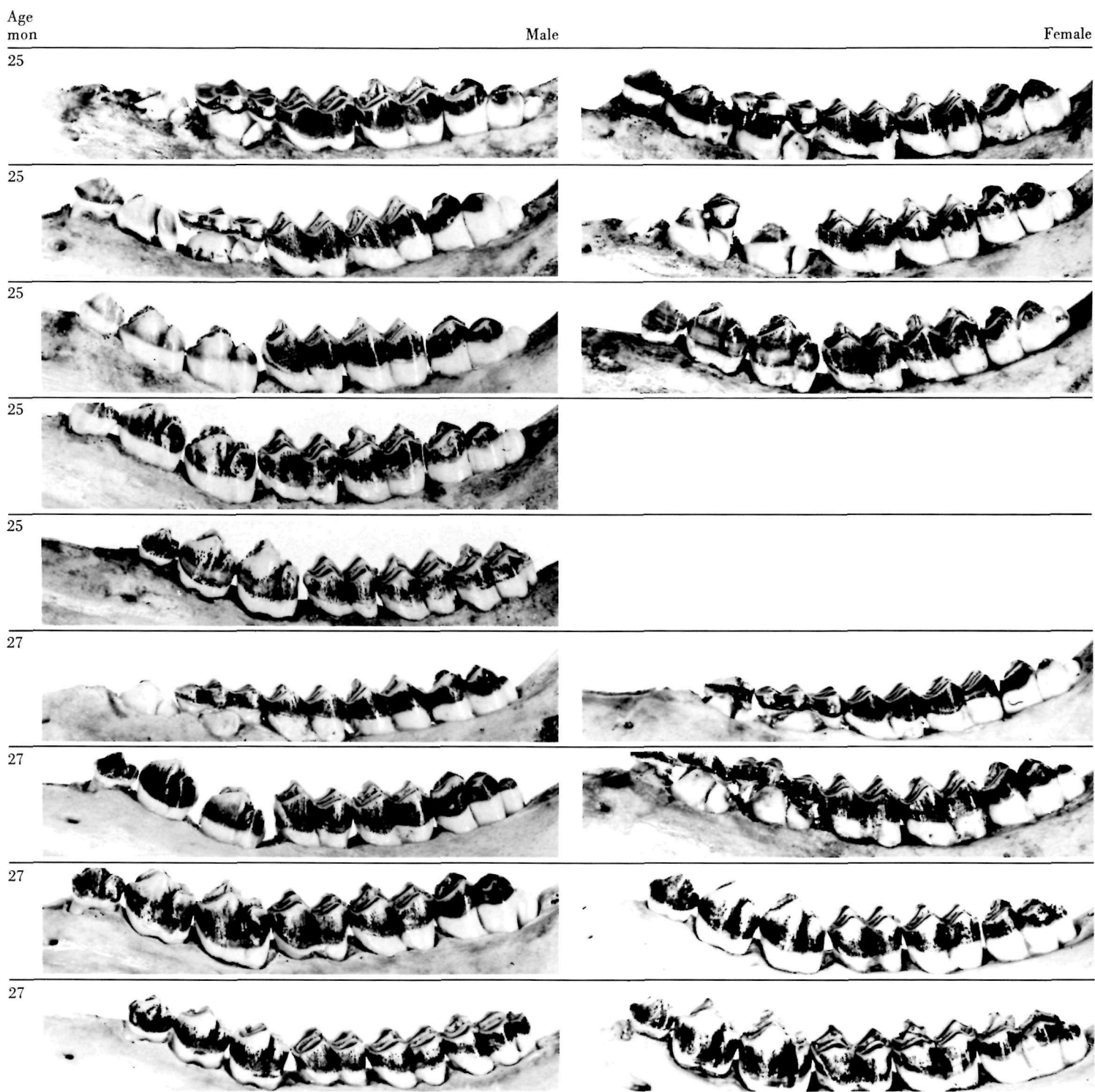


17



17

Age mon	Male	Female
17		
22		
22		
22		
22		
22		
22		
22		
22		



Male

Female

Age
mon



29



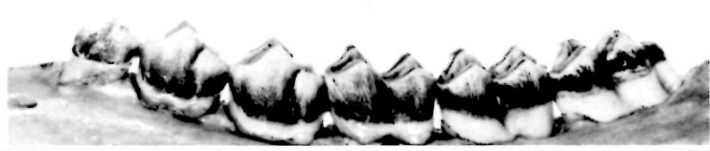
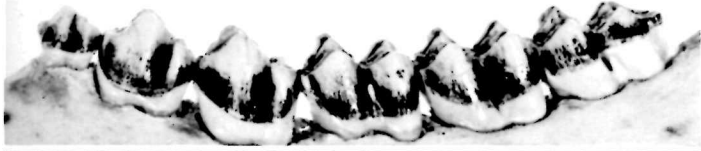
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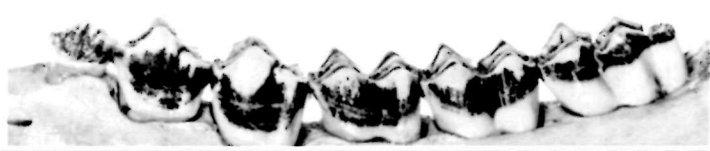
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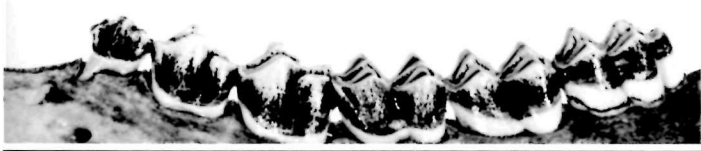
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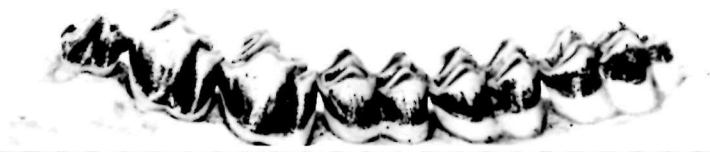
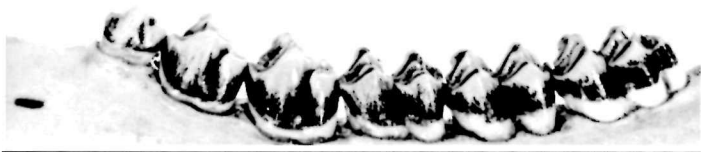
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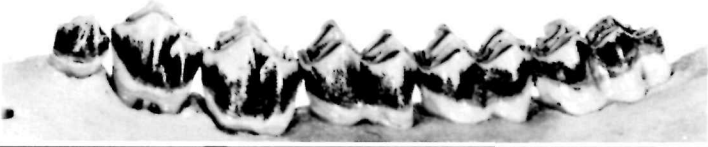





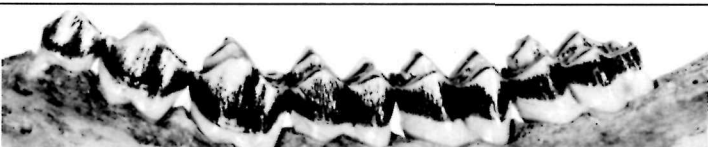






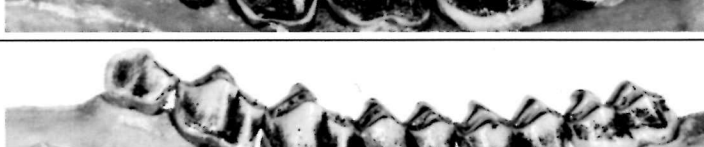
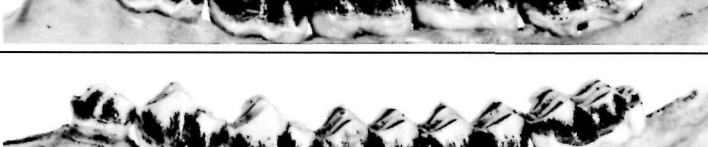
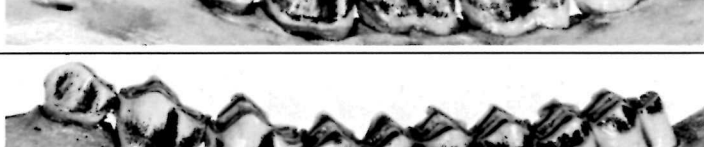
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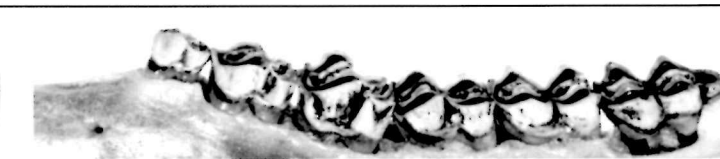



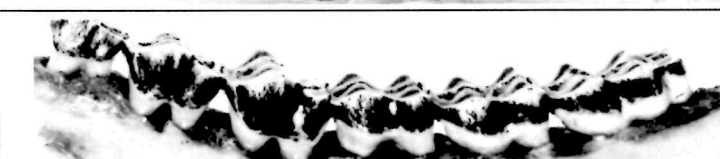

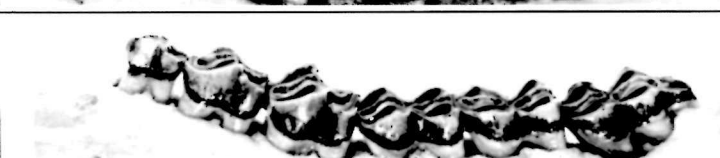
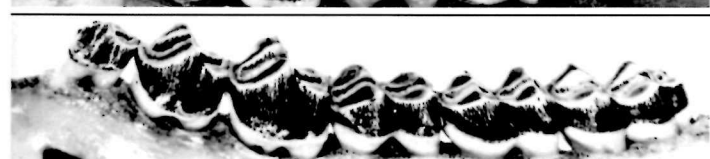

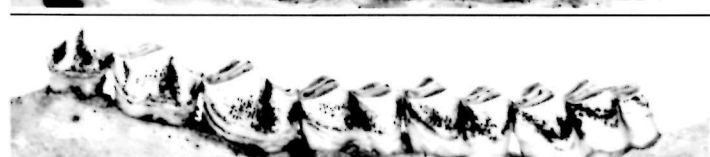
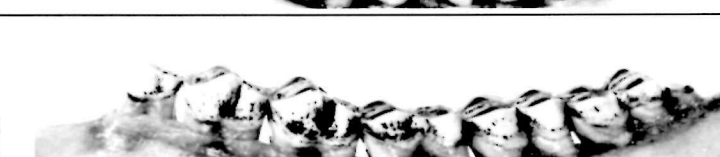



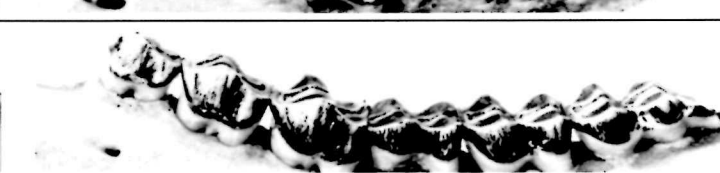



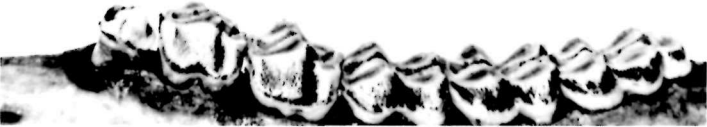

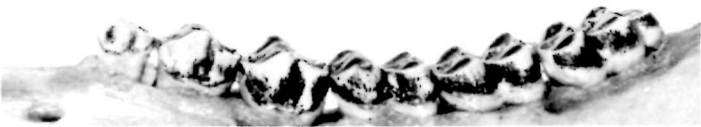

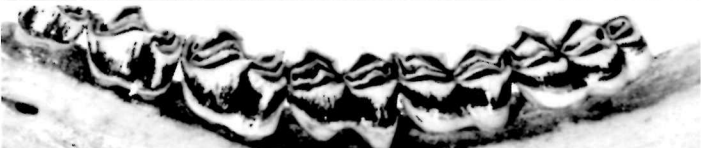







39



41

Age mon	Male	Female
41		
46		
46		
48		
49		
51		
53		
58		
60		

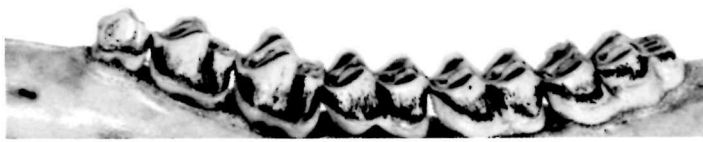
Male	Female	Age mon
		61
		63
		65
		70
		72
		73
		75
		77
		82

Age mon	Male	Female
84		
85		
87		
89		
94		
96		
97		
99		
101		

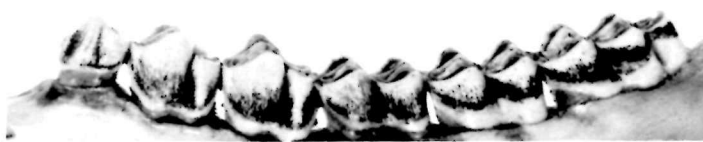
Male

Female

Age
mon



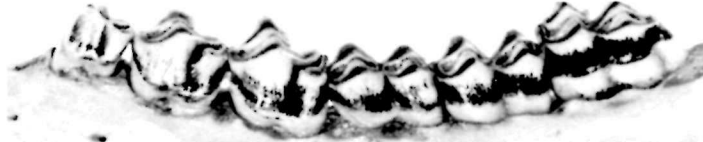
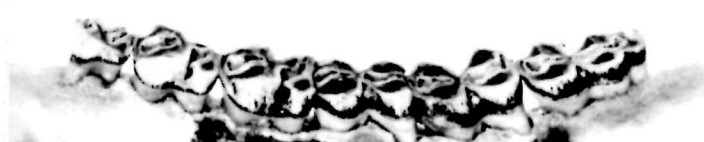
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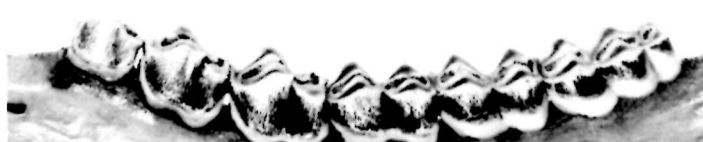
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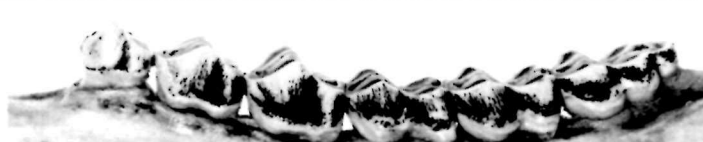
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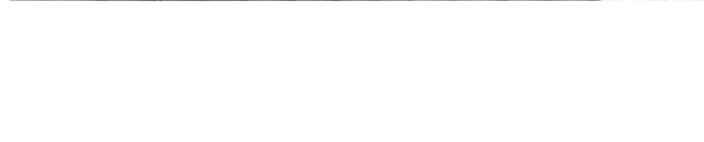
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113



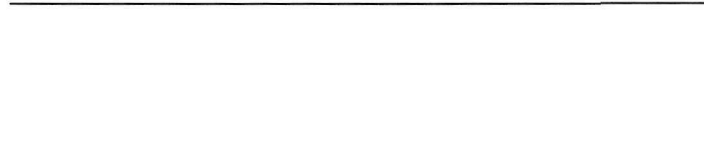
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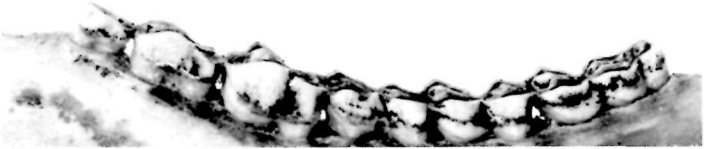
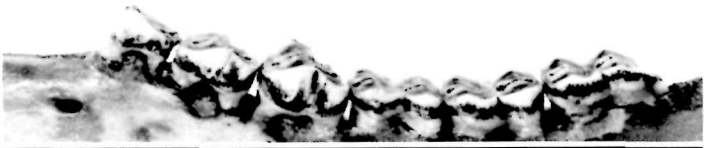
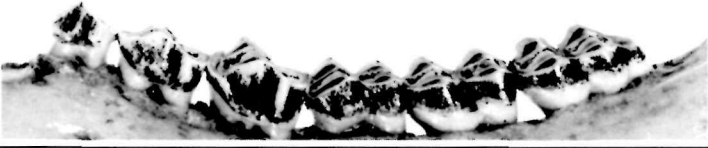

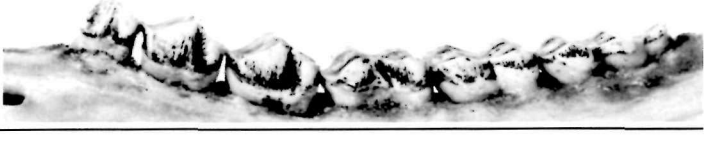

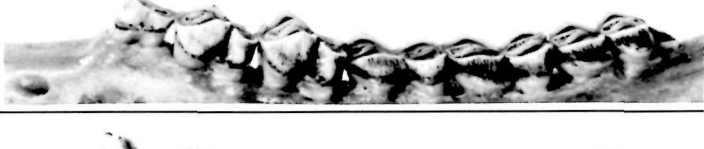


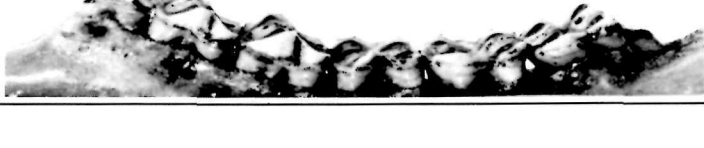
120



121



123

Age mon	Male	Female
125		
130		
132		
133		
137		
142		
154		
156		
166		


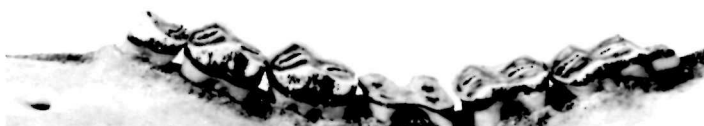

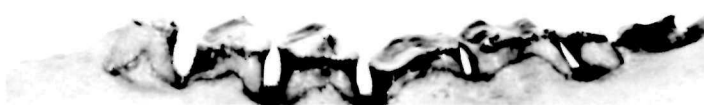

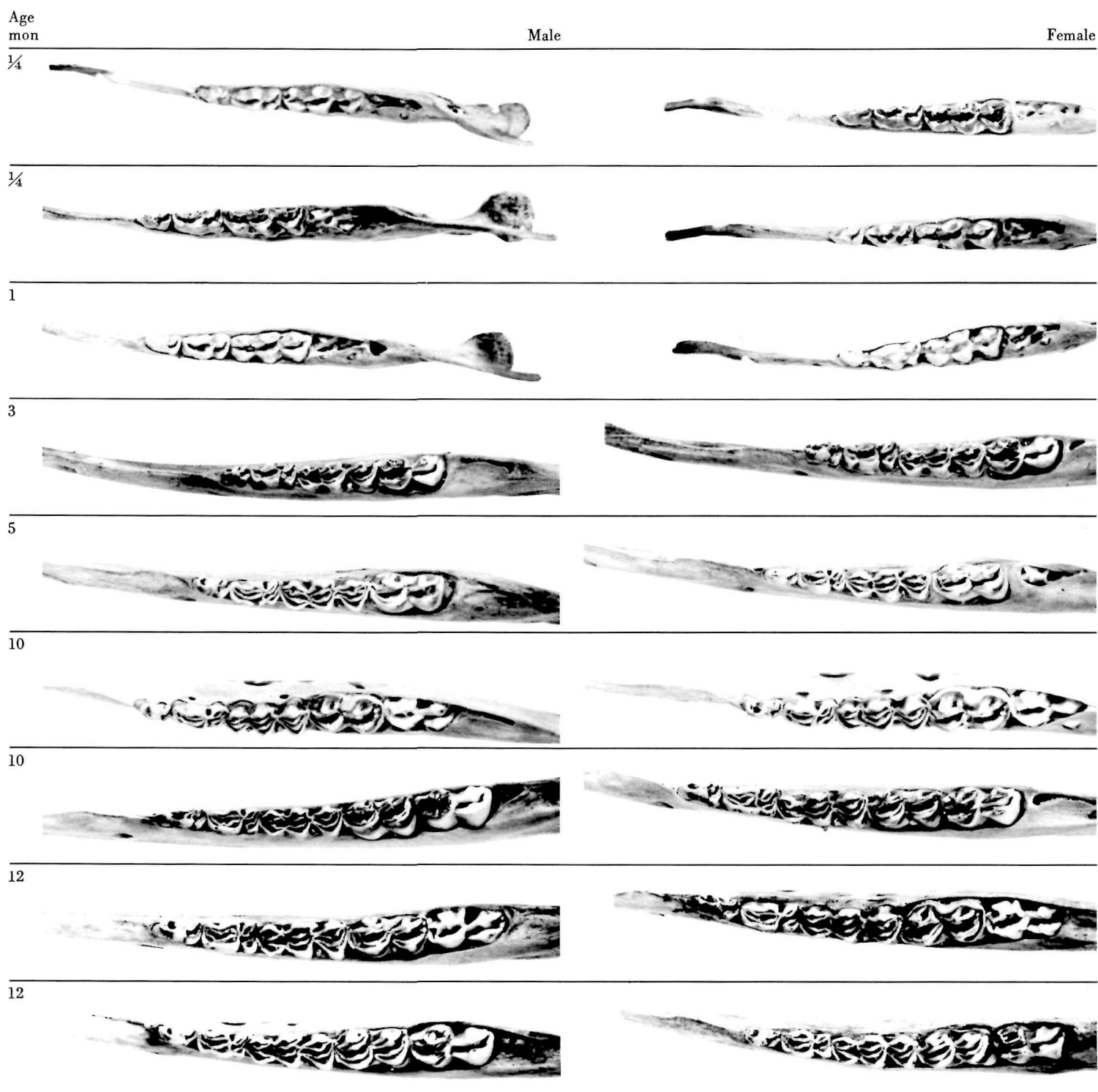









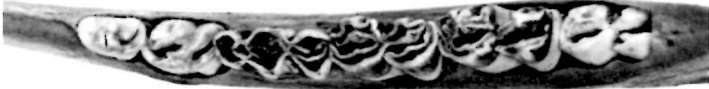



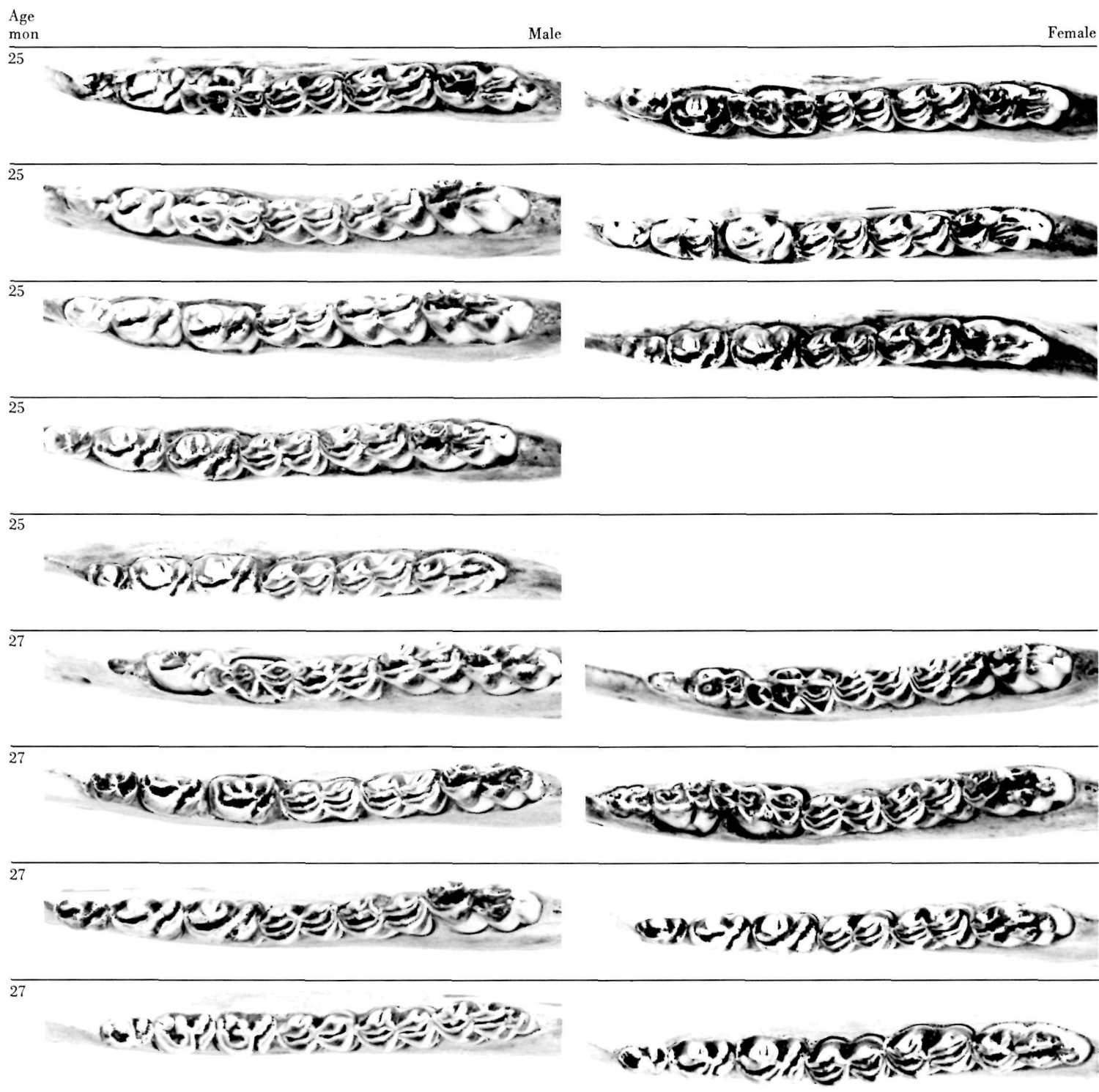










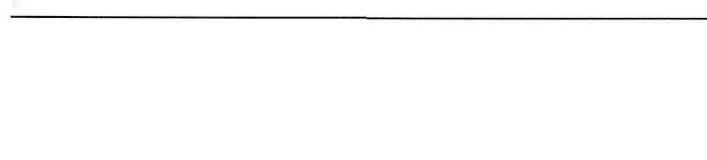

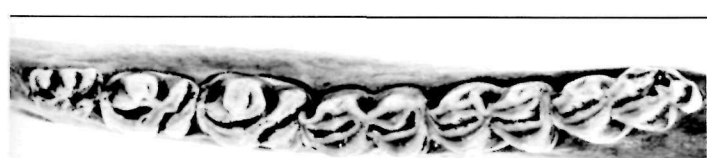





Male	Female	Age mon
		178
		181
		192
		195
		205













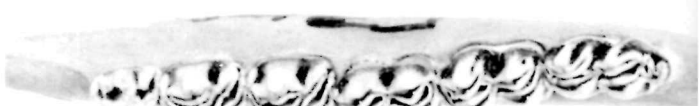




Plate B. Occlusal view of a chronological series of the left molariform tooth row in male and female caribou



Age mon	Male	Female
17		
22		
22		
22		
22		
22		
22		
22		
22		



Male	Female	Age mon
		29
		29
		34
		34
		36
		36
		37
		39
		41

Age mon	Male	Female
41		
46		
46		
48		
49		
51		
53		
58		
60		

Male

Female

Age
mon

61



63



65



70



72



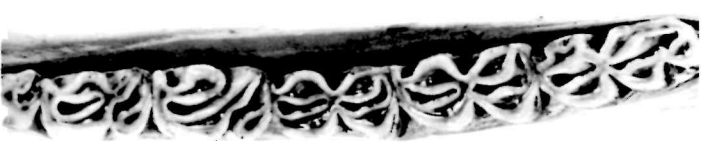
73



75



















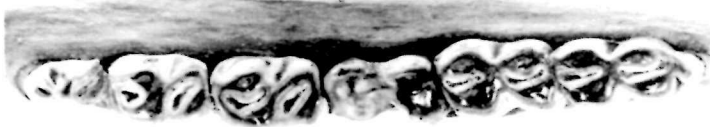






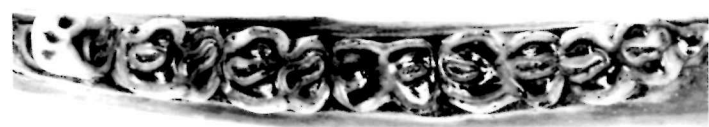
77








82



Age mon	Male	Female
84		
85		
87		
89		
94		
96		
97		
99		
101		

Age mon	Male	Female
125		
130		
132		
133		
137		
142		
154		
156		
166		

Male	Female	Age mon
		178
		181
		192
		195
		205

Socialization and population analysis

1. Social grouping

Caribou occur in groups of various kinds but I consider the *band* the primary distinguishable social group. Bands were categorized by representation of sex and age within them (Table 14). I base this classification on sex and age composition of collected samples. I have supplemented these data with observations on sex and age of animals remaining in the groups from which samples were collected, and impressions of the structures of groups seen both on the ground and from the air.

A *cow band* is composed of mature females, and may or may not include newborn calves. It may occur only on the calving ground.

A *bull band* is composed entirely of mature males 41 months or more. It may occur at any season of the year.

A *subadult band* is usually composed of 3-year-olds, of both sexes or of one sex, but may contain a few 4-year-olds. On the calving ground the pregnant 3-year-olds join the cow bands, the barren 3-year-olds remain in subadult bands. Subadult bands occur at all times of the year, but are most obvious in spring and autumn.

A *juvenile band* is composed of yearlings and/or 2-year-olds of either or both sexes. Juvenile bands occur throughout the year but are most obvious on the calving ground and in postcalving groups, and are often mixed in cow-juvenile bands.

A *cow-juvenile band* is composed of mature females and animals, of either sex, less than 34 months of age. These cow-juvenile bands are found throughout the year, often combined with bull and subadult bands, especially during the spring, summer and autumn migration periods.

A *cow-juvenile-bull band* is composed predominantly of cows and juveniles, but includes individual bulls or bull bands. It is usually encountered in the spring as the caribou migrate northward and during the autumn from pre-rut to post-rut. Caribou that winter on the open tundra often form this type of band.

Table 14
Caribou band types by collection periods, April 1966–July 1968

Band type	Number of bands					Total
	Apr.	June	July	Sept.	Nov.	
Cow	0	7	0	0	0	7
Bull	2	0	0	5	2	9
Juvenile	1	1	0	0	0	2
Subadult	8	2	0	1	2	13
Cow-juv.	10	12	0	5	3	30
Cow-juv.-bull	7	5	3	2	9	26
Bull-cow-juv.	4	0	4	4	4	16

A *bull-cow-juvenile band* is composed predominantly of mature males which have joined with mature cows and juvenile animals of either sex. Like the cow-juvenile-bull band, this type is usually encountered during the spring migration and autumn rutting periods.

Aerial surveys of small land units may give misleading ratios of mature males to mature females. Probably the only practical way of overcoming the problem of non-random distribution of caribou by sex and age is through repeated aerial surveys of large land units at the appropriate season of the year.

The high degree of segregation in the caribou bands and direct observations of caribou groups, particularly in the spring, lead me to believe that caribou are strongly socially cohesive animals.

Evidence of long-term social bonds in barren-ground caribou on mainland northern Canada has been reported by Parker (1972):

"In 13 instances, groups of caribou whose members were tagged at the Thelon site on or near the same date were shot together over 12 months after tagging. These cases suggest the existence of persistent social bonds between barren-ground caribou, particularly between adult males. Group sizes varied from two to four caribou. Four of the 13 groups consisted of two adult males shot more than 3½ years after tagging."

Statistical analyses of the data from radioed caribou (Miller *et al.*, 1974) de-

monstrated the following: (1) certain animals were usually seen on the same day, (2) certain animals were usually in the same groups, and (3) animals returned to the same groups after being separated for hours or days. The non-random association of the radioed caribou is believed to be a result of social cohesion. When one considers the sociability of caribou groups, one wonders how group unity would be perpetuated from one year to the next. I believe that this unity is maintained by the formation of postcalving aggregations.

I suggest that the primary function of postcalving aggregations is socialization, which provides favourable situations for the regrouping of previous winter bands. I have to make two main suppositions as the basis for this hypothesis.

First, the basic social unit of barren-ground caribou is the wintertime band. Although there are seven basic types of caribou bands, only four are usual in winter: bull, cow-juvenile, juvenile, subadult. The juvenile and subadult bands are usually mixed or in close association with the cow-juvenile bands. The membership of juvenile and subadult bands may be the result of the loss of maternal cows, and their locations with respect to adults may be governed by the antagonistic behaviour of the remaining mature cows or dominant subadults.

Second, the core of the wintertime cow-juvenile band is formed by a matriarchal bloodline, supplemented from time

to time by neighbouring caribou as and when the group accepts them.

The wintertime bull band is sustained by recruitment of subadult groups of 3- and 4-year-old males. Band members are usually similar in body and antler size; though antlers may vary, they are not usually as large as the antlers of prime bulls.

The bonds between members of the cow-juvenile bands begin to weaken as the caribou groups heed the stimuli that start them northward in the spring. More and more bands come together as the caribou move to the tree line. Once on the tundra, the parturient cows' vacillating antagonism is intensified, and many of the juveniles and subadults begin to drop behind. This response is often reinforced by the presence of deep, wet snow along the migration route which is a greater hindrance to young animals. The parturient cows arrive on the calving ground, often disperse just before parturition, and may remain alone, or nearly so, for a short post-partum period.

When their calves are born the cows begin to move about the calving ground, joining other cows, calves, and those juveniles and subadults that have arrived. As groups grow in number they become more attractive to the smaller ones until, finally, large groups merge with larger groups to form the postcalving aggregations of several thousand caribou. A postcalving aggregation has a distinct structure. Each has a core of maternal cows and their calves, seemingly equally spaced throughout. From the air or a vantage point on the ground the core looks elliptical or oval. Along its periphery are many groups of juvenile animals, usually in constant motion. They dart out and back without apparent purpose and venture out to investigate any unidentified object, such as a human observer, upwind of them.

Some caribou rejoin fellow members of previous winter bands during formation of and movement in postcalving aggrega-

tions. The basic social unit thus begins to take shape.

For those years in which large numbers of juvenile and subadult animals have left the cow movement, a mechanism must be postulated for reuniting the young with the mature animals, so that the tradition of the group can be retained through maintenance of the matriarchal bloodline within it. I believe this is accomplished when the postcalving group moves into the area occupied by the young animals and mature bulls which have moved northward after the cows. The cows and calves merge with the bulls, remaining juveniles, and subadults, and move off on their so-called midsummer migration. The animals continuously shuffle and reshuffle. By the onset of rut the basic social units have formed but remain for the most part in larger groupings until arrival on the wintering ground. The bull bands separate from the cow-juvenile bands and move off to their particular wintering areas, usually farther south in the case of the Kaminuriak Population.

During the fourth autumn of life most of the males enter the mature male segment of the population. It is during those autumn pre-rut staging periods that the males establish their bonds with other males of the same or similar age.

The basic male social unit, the bull band, is thus formed to maintain from year to year a distribution of breeding bulls with common learned behavioural habits, which assures, under normal conditions, a supply of breeders in the traditional rutting areas.

I now propose that the herding behaviour of barren-ground caribou may have evolutionary significance as a means of minimizing predation by wolves (*Canis lupus*). My supposition is based on the assumption that the territorial drives of wolves impose an upper limit on their densities. Even if an area, either a fixed land mass or the area occupied by a moving aggregation of caribou, contains more prey than is needed to support the wolves there, the resident wolves will not tolerate

intruders of their own kind. In addition, wolves having access to abundant prey do not routinely kill in great excess of their needs. This does not appear to be true for the June-July period when wolves often kill newborn calves and leave them uneaten (Miller and Broughton, 1974). Such killing is, however, probably restricted to young non-breeding wolves which are motivated by the need for practice and play. Adult wolves are usually governed more by restrictive consummatory drives and the need to conserve energy.

I believe that the caribou's gregarious behavioural response to predators is facilitated by their drive for socialization, hence my hypothesis, "the primary function of postcalving aggregations is socialization, which provides favourable situations for the regrouping of previous winter bands." This hypothesis suggests the necessary annual link for perpetuating the impetus that leads to a beneficial behavioural trait.

2. Population analysis

Of the 999 caribou in the collection, 943 were from the Kaminuriak Population and 56 were from the Beverly Population. Males totalled 436 and females 563 for a ratio of 77:100. The juvenile and subadult segments, 41 months of age or less, comprised 51.5 per cent of the collection. These segments included 258 males and 257 females for a ratio of 100:100. Adults, 46 months of age or more, were made up of 178 males and 306 females for a ratio of 58:100.

Samples were collected during the major life history phases of the caribou's annual cycle. The sex, age, weight, collection date and location are recorded for the 999 animals in Miller (1970:App. 1). The sex and age composition of the sample by individual collection periods, by season, and by cohorts are given in Appendices 3a, 3b, and 3c respectively of Miller (1970).

During the three April collection periods we encountered caribou on their late winter staging areas and along the

routes of their northward migrations. Spring collections totalled 308 caribou:

- a. In 1966, 102 caribou were collected in Manitoba, northeast of Brochet on the Cochrane River area and 14 near our corraling camp at Kasmere Lake.
- b. In 1967 caribou were more widely dispersed, with the main wintering group on the Striding River area, District of Mackenzie, NWT. Seventy-five animals were taken on the Striding River; 16 east of the north end of Big Sand Lake and 12 west of Lac Brochet, Manitoba.
- c. In 1968, 72 caribou were taken in the Lac Brochet area and 31 east of Carlson Lake, Manitoba.

During springtime caribou were observed travelling in discrete bands or as large mixed groups composed of several bands. Juvenile and subadult bands became more evident as the migration accelerated. Bull and cow-juvenile bands often occupied the same lakes, but usually maintained their closed groups, even when bands came only within several metres of each other. Spring is an unsettling time for caribou and their numbers in a particular area may change overnight.

During the three June collection periods 273 caribou were obtained on the calving grounds. In 1966, 1967 and 1968 collections of 85, 45 and 90 caribou were made about 12 km east of Gibson Lake, NWT, within a 25-km radius of the base camp. In addition, 40 and 13 caribou were taken respectively 50 and 120 km from the base camp in 1967.

In 1966 about 20 per cent of the calving ground was north of the collection area. In 1967 the calving ground extended only slightly north of the collection area and in 1968 its northern boundary was at the north end of the collection area.

Snow and slush appeared least in depth and extent during the spring migration in 1966, slightly more in 1967 and most in 1968. As a result the numbers of juveniles and subadults that reached the collection area were greatest in 1966 and least in 1968. The calving period in June

1966 was also the only calving period during the study when 36-month-old males were taken from the calving ground. In 1967 we saw and collected fewer juveniles and subadults on the calving ground; and in 1968 we took only three yearlings and three 2-year-olds there.

A July collection of 101 animals was made in 1968. Forty-five Kaminuriak caribou were collected from the area east of the Kazan River and south of Baker Lake, NWT. Fifty-six Beverly caribou were taken along the Thelon River, just west of Aberdeen Lake, NWT. The primary objective of the July sampling was to obtain data at what we had deduced was the nadir of nutritional condition.

Calving segments travel on the tundra in large postcalving aggregations during July. When these aggregations merge with adult bull groups the degree of segregation within and between groups varies considerably. Large groups often remain somewhat segregated internally due to the cohesion of many of their subgroups. Stampede-like movements of caribou are associated with periods of high insect activity and the groups are constantly shuffling, splitting, and regrouping in an apparent attempt to escape harassment.

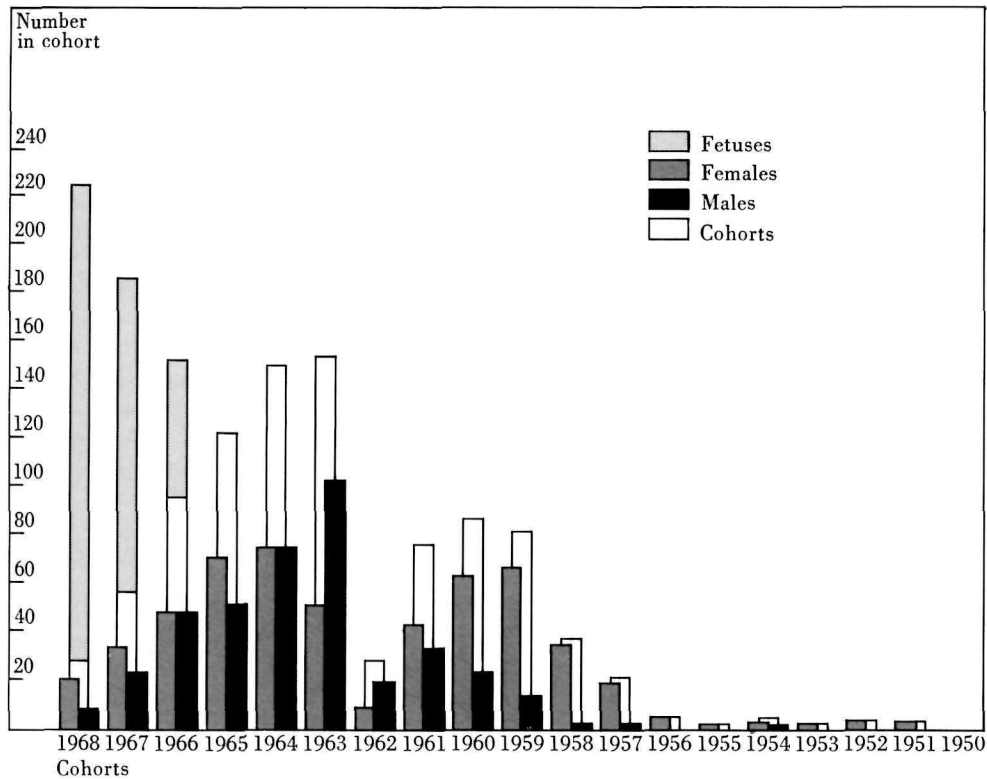
During the two September collection periods 111 specimens were obtained:

- a. In 1966, 26 caribou were collected between Tatinnai and Otter lakes, NWT.
- b. In 1967, 77 caribou were taken between Maguse and Camp lakes and 8 north of Padlei Lake, NWT.

Most of the caribou on the collection area in autumn 1966 were adults in bull bands and large pre-rutting bull groups. Few groupings of cows, juveniles, and subadults were seen in the immediate area. Large groups of female and immature caribou to the east of South Henik Lake were moving westward toward the bull concentrations, when the onset of freeze-up forced us to terminate our field activities on September 25. In September 1967, the caribou were collected from large mixed groupings and segregated pre-rutting

Figure 21
Sex and age composition of caribou by cohort,
April 1966–July 1968

Figure 21



bands. The bulls and cows were mixed to various degrees throughout the collection area, and we often encountered large groups of adult cows and immature animals flanked by adult bulls.

During the two November collection periods 206 caribou were obtained in Manitoba:

- In 1966, 91 caribou were taken from the Cochrane River area, 5 from Maria Lake, and 5 from Eyrie Lake.
- In 1967, 54 caribou were taken from the Cochrane River area, 39 east of Lac Brochet, and 12 from Eyrie Lake.

In November the caribou moved into their wintering grounds in large mixed groups and bands. Many adult males had moved or were moving to their wintering areas. Mature breeding bulls had cast or were casting their antlers. Antlered sub-adult and young adult males were still

sexually aroused and sparring contests were observed.

The age composition throughout the 13 collection periods revealed poor representation of animals born in 1962. Differential natality and/or mortality of cohorts could be important determinants of total population strength. The 1962 cohort vividly illustrates these effects on a cohort (Fig. 21).

The 1962 cohort was represented by animals that were 4, 5 and 6 years old when collected. Only 30 caribou (11 females, 19 males) were collected from the 1962 cohort. Reproductive success within the 1962 cohort had been exceedingly low and apparently favoured survival of males. As approximately 86 per cent of the adult females in the population are producing young each year, we must assume that either the survival of calf crop in 1962

Table 15

Numbers of female Kaminuriak caribou collected by age, year, and collection periods, April 1966 – April 1968

April 1968

Age, yr.	Collection, excluding June											Collection, June only				
	1966				1967				1968			1966–1968				
	1	3	4	Σ	5	7	8	Σ	9	11	Σ	2	6	13	10	Σ
0		0	5	5		6	8	14		4	4	8	7	0	16	31
1	6	1	1	8	7	2	9	18	7	3	10	6	3	2	2	13
2	6	0	11	17	9	8	11	28	6	2	8	10	8	4	3	25
3	5	1	8	14	9	2	8	19	5	2	7	12	4	2	9	27
4	0*	0*	4*	4*	8	1	3	12	8	4	12	0*	2	2	10	14
5	2	2	5	9	0*	0*	0*	0*	2	2	4	4	2*	0*	5	11
6	9	3	4	16	7	4	3	14	1*	0*	1*	6	1	0	2*	9
7	9	0	7	16	5	6	4	15	6	0	6	12	11	7	9	39†
8	2	1	7	10	3	2	5	10	2	2	4	3	7	1	2	13
9	0		2	2	3	4	3	10	5	1	6	6	4		14	24†
10	1		1	2	0	2	1	3	2	1	3		3		5	8
11	0			0	2	0	1	3		2	2		1		3	4
12	1			1	1	0		1								
13	0			0	1	0		1					1			1
14	2			2	1	0		1								
15					1	0		1		1	1					
16						1		1					1			1

*Weak cohort.

†Omitted because of atypical distribution.

Table 16

Numbers of male Kaminuriak caribou collected by age, year, and collection period, April 1966 – April 1968 (collections 2, 6, 10 had only cow-calf and juvenile groups)

Age, yr.	Collection												Calving groups			
	1966				1967				1968				2			
	1	3	4	Σ	5	13	7	8	Σ	9	11	Σ	2	6	10	Σ
0		1	6	7			4	6	10				5	6	8	19
1	3	1	6	10	7	4	2	7	20	4	2	6	6	5	1	12
2	12	2	9	23	7	1	7	5	20	8	1	9	4	2	1	7
3	15	6	20	41	14	1	3	12	30	11	2	13	3			3
4	3*	2*	4*	9*	7	2	19	17	45	16	1	17				
5	11	1	1	13	2*	1*	0*	1*	4*	6	7	13				
6	9	2		11	4	2	3	1	10	5*	1*	6*				
7	4	3		7	5	0	6		11	7	3	10				
8	0			0		1	1		2	0	1	1				
9	1			1			2		2	2	2	4				
10	0			0							0	0				
11	0			0							1	1				
12	1			1												

*Weak cohort.

was very low, or the mortality of juveniles and subadults of that cohort was exceedingly high. That cohort should have totalled about 12 per cent of the overall collection, if the calf production in 1962 was similar to that in 1961 and 1963, and the mortality within the three cohorts was constant. Yet only 3.0 per cent of the expected proportion of the sample was attributable to the 1962 cohort, suggesting that caribou born in 1962 died at a rate at least four times as high as caribou born in 1961 and 1963.

Observations made by Ruttan (1962) in August 1962 at Little Duck Lake, Manitoba, suggest that the calf crop was either low or suffered great mortality between June and August. Ground segregation of 1,400 caribou yielded values of only 16 (1.2 per cent) calves, and aerial counts of 1,252 caribou only 49 (3.9 per cent) calves. J. D. Robertson (pers. comm.) said that he had never seen caribou in such poor physical condition as during the spring migration of 1962. Records from Brochet, Manitoba, show that the accumulated snow depth for March 1962 far exceeded all other records for that month from 1955 to 1968 (Parker, 1972: Table 5). All of the above factors help to account for the consistently poor representation of the 1962 cohort from April 1966 to July 1968.

A weak cohort (1962) is apparent in the tabulations of both males and females (Tables 15 and 16). The number of animals expected in the 1962 cohort was calculated separately for the sexes by multiplying the total number of animals collected in that year by the number of animals in the cohort during the 2 years not involved, then dividing the product by the total number of animals in the 2 years not involved (see cohort adjustments Tables 17, 18).

The 1962 cohort may be considered atypical, as there was no other weak cohort in the ten year-classes represented in the collection. Therefore, an adjustment has been applied to raise the affected frequencies to normal levels (Tables 19, 20). The

Table 17

Cohort adjustment for female Kaminuriak caribou,
based on 266 females, 22 + months, used in life table

Age, yr.	1966	1967	1968	Adjustments
4	4*	12	12	$1966 = 64 \times (12 + 12) / (92 + 38) = 12$
5	9	0*	4	$1967 = 92 \times (9 + 4) / (64 + 38) = 12$
6	16	14	1*	$1968 = 38 \times (16 + 14) / (64 + 92) = 7$
2, 3, 7+	64	92	38	

*Weak cohort.

Table 18

Cohort adjustment for male Kaminuriak caribou,
based on 168 males, 46 + months, used in life table

Age, yr.	1966	1967	1968	Adjustments
4	9*	45	17	$1966 = 9 \times (45 + 17) / (15 + 16) = 18$
5	13	4*	13	$1967 = 15 \times (13 + 13) / (9 + 16) = 16$
6	11	10	6*	$1968 = 16 \times (11 + 10) / (9 + 15) = 14$
7+	9	15	16	

*Weak cohort.

Table 19

Adjusted numbers of female Kaminuriak caribou in
collection, April 1966 – April 1968

Age, yr.	After adjustment for cohort				Starting number, %			
	1966	1967	1968	1966–68	1966	1967	1968	1966–68
0	35*	41*	21*	97*	100.0	100.0	100.0	100.0
2	17	28	8	53	49.0	68.0	37.4	54.5
3	14	19	7	40	40.3	46.1	32.7	41.1
4	12	12	12	36	34.6	29.1	56.1	37.0
5	9	12	4	25	25.9	29.1	18.7	25.7
6	16	14	7	37	46.1	34.0	32.7	38.0
7	16	15	6	37	46.1	36.4	28.0	38.0
8	10	10	4	24	28.8	24.3	18.7	24.7
9	2	10	6	18	5.8	24.3	28.0	18.5
10	2	3	3	8	5.8	7.3	14.0	8.2
11	0	3	2	5	0.0	7.3	9.3	5.1
12	1	1	0	2	2.9	2.4	0.0	2.1
13	0	1	0	1	0.0	2.4	0.0	1.0
14	2	1	0	3	5.8	2.4	0.0	3.1
15	0	1	1	2	0.0	2.4	4.7	2.1
16	0	1	0	1	0.0	2.4	0.0	1.0

*No. at 0 mon. = (pregnancy rate) (no. 34 + mon.) /
2 i.e., $1/2 [0.477 (3\text{-yr. } \varphi) + 0.896 (4\text{-yr. } \varphi)]$.
Actual starting values: 1966 = 34.7, 1967 = 41.2,
1968 = 21.4, and 1966–68 = 97.3.

Table 20

Adjusted numbers of male Kaminuriak caribou in collection, April 1966–April 1968

Age, yr.	After adjustment for cohort				Starting number, %			
	1966	1967	1968	1966–68	1966	1967	1968	1966–68
4	18	45	17	80	37.0*	37.0*	37.0*	37.0*
5	13	16	13	42	26.7	13.2	28.3	14.4
6	11	10	14	35	22.6	8.2	30.5	16.2
7	7	11	10	28	14.4	9.0	21.8	13.0
8	0	2	1	3	0.0	1.6	2.2	1.4
9	1	2	4	7	2.1	1.6	8.7	3.2
10	0		0	0	0.0		0.0	0.0
11	0		1	1	0.0		2.2	0.5
12	1			1	2.1			0.5

*Estimated by assuming male and female mortality is equal for the first 4 yr. of life, and the factor of $80/36 = 2.22$ is the over-sampling factor for the adult male groups: 37.0% taken from smoothed female life table calculations.

Table 21

Chi-square tests of homogeneity of ages of female caribou collected in June versus those females collected in other seasons

Age, yr.	Apr.*	June†	Sept.*	Nov.*	Σ
7	20	39	6	11	76
8	7	13	3	12	35
9	8	24	4	5	41
10+	12	14	3	3	32
Total	47	90	16	31	184

* $\chi^2 = 7.01$, 3 df, $P > 0.05$.

† $\chi^2 = 13.04$, 6 df, $P < 0.05$.

Table 22

Over-representation of male Kaminuriak caribou, April 1966–April 1968

Age, yr.	Over-representation*				Starting number, %			
	1966	1967	1968	1966–68	1966	1967	1968	1966–68
0	35†	41†	21†	97†	100.0	100.0	100.0	100.0
2	23	19‡	9	51	66.3	46.1	42.1	52.4
3	41	29‡	13	83	118.2	70.4	60.7	85.3
4	9§	43‡	17	69	51.9	104.4	79.4	80.2

*Males in 3- and 4-yr. -old classes are over-represented. This is assumed to be due to (a) segregation of mature males from cow-calf groups; (b) relative over-sampling of mature males in an attempt to balance sample—this may be misleading if females have longer life expectancy.

†No. at 0 mon. = (pregnancy rate) (no. 34 + mon.) / 2 i.e., $1/2 [0.477 (3\text{-yr. } \varphi) + 0.896 (4\text{-yr. } \varphi)]$. Actual starting values; 1966 = 34.7, 1967 = 41.2, 1968 = 21.4 and 1966–68 = 97.3.

‡Sample 13, and all June samples deleted.

§Weak cohort (1962).

number of animals expected in a given year was calculated separately for the sexes from the proportion of that age in the samples shot in the two years, when the age was normally represented, by dividing the total number of animals collected in that year.

Occurrence of females by age was too low to show significant differences for individual collection years. Therefore, all females were combined by season, but as large variations were observed in the age structure by season, chi-squared tests were used to test for differences between seasons (Table 21). Restrictions of the data required that cohorts be ignored and that tests be applied only to females 7 years of age or older. Because June did not fit the assumption that the frequencies of females would be expected to decline, it was omitted, and the homogeneity of April, September, and November was tested (Table 21).

June samples of both females and males were omitted from life table calculations and cohort adjustment, and the other seasons were combined to give year totals before cohort adjustment. Because of the high degree of segregation young males were apparently over-represented in the sample. The calculations in Table 22 show that males between 29 months and 58 months are considerably over-represented in the collections. It is known that adult males were often separated from the cow-calf or cow-juvenile groups, so it would be difficult to accurately balance the sampling from the two parts of the population.

The age at which males are accepted into the adult male group is expected to be about 41 months, probably the usual age of first breeding. On the assumption of a two- or three-fold bias in the sampling of males, the over-representation of 3- and 4-year-olds probably shows that these animals are no longer being shot with the cow-calf groups in most cases, but are grouped in subadult male bands.

It could be assumed that 4-year-old males were adults, and 3-year-old males were of uncertain social status. The decision

Figure 22
Observed and adjusted female and male representation for Kaminuriak caribou by age

is reinforced by the tabulation of June samples 2, 6 and 10 (Table 16) when no adult males were shot, but some 3-year-olds were still with the cow-juvenile groups. The values for males 0 to 3 years old could be taken from the female life table on the assumption of identical age composition over that period in both sexes (258 males: 257 females in collection). There is, however, some evidence from the composition of groups and the September to November weight loss (Dauphiné, in prep.), that breeding is not prevalent until the males are older than 48 months. Therefore, I used the same mortality for both sexes over the first 4 years of life for the life tables and survival curves.

The over-sampling adjustment was made by assuming the adjusted percentage survival for 4-year-old females could be applied to the 4-year-old males. Presumably up to that age there would be little difference in mortality between the sexes. The numbers of males 0, 1, and 3 years old were calculated by use of the over-sampling adjustment value of 2.22. The observed 2-year-old males fell on the fitted value (Fig. 22). The resulting fitted curves for males and for females are given in Figure 22.

Animals under 21 months were markedly under-represented (Tables 15 and 16) possibly because of some subconscious selection of larger specimens during shooting. I therefore omitted ages 0 to 1 years from all calculations.

Eberhardt (1969) discusses population analysis and the use of life tables in detail. He points out the many problems and assumptions that are necessary as a basis for evaluating samples through the use of life tables.

The juvenile and adult sex ratios obtained in our collection are in agreement with sex ratios from Alaskan populations of caribou (Skoog 1968:491), and the aerial counts of the Kaminuriak Population tend to add further support to the sample (Parker 1972:54-70). However, despite the agreement of the observed sex ratios,

Figure 22

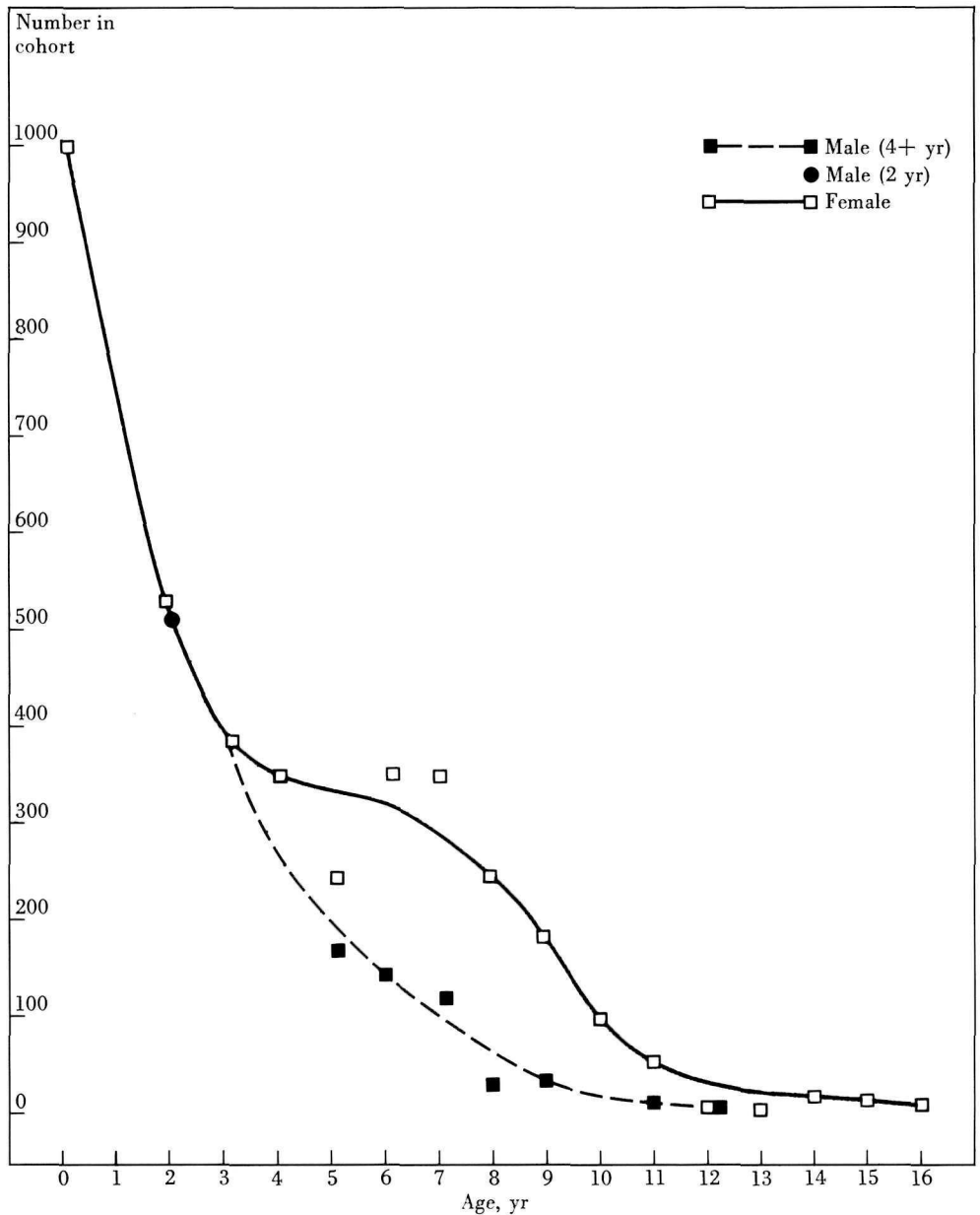


Table 23
Life table for female Kaminuriak caribou, 1966–68

Age, yr.	Observed	Adjusted	1000 m_x^*	1000 l_x	1000 d_x	1000 q_x	e_x
0		97.3†	000	1000	277	277	4.20
1		70.3‡	000	723	178	246	4.61
2	53	53.0	090	545	134	246	4.96
3	40	40.0	238	411	41	100	5.41
4	36	36.0	410	370	16	43	4.95
5	25	34.4	477	354	13	37	4.15
6	37	33.2	483	341	25	73	3.29
7	37	30.7	436	316	69	218	2.51
8	24	24.0	469	247	83	336	2.07
9	18	16.0	466	164	82	500	1.87
10	8	8.0	419§	82	31	378	2.24
11	5	5.0		51	14	274	2.30
12	2	3.6		37	12	324	1.99
13	1	2.4		25	9	360	1.70
14	3	1.6		16	6	375	1.38
15	2	1.0		10	6	600	0.90
16	1	0.4		4			0.50

* m_x = 50% based on age-specific pregnancy rates (Dauphiné, in prep.).

†Starting population estimated from pregnancy rate for 3-yr.-old (47.7%) and mature (86.9%) females.

‡Estimated by assuming that mortality in 2nd and 3rd years is equal: avg. mortality, all age groups = $996/4692 = 0.21$; avg. mortality, first 10 yr. = $918/4471 = 0.21$; avg. mortality, 3+-yr. olds = $407/2424 = 0.17$.

§Avg. for 10+-yr.-old females.

Table 24
Life table for male Kaminuriak caribou, 1966–68

Age, yr.	Observed	Adjusted	1000 l_x^*	1000 d_x	1000 q_x	e_x
0			1000*	277	277	3.14
1			723*	178	246	3.15
2			545*	134	246	3.02
3			411*	41	100	2.84
4	80	80.0	370	157	424	2.09
5	42	46.0	213	56	263	2.27
6	35	34.0	157	46	293	1.90
7	28	24.0	111	55	495	1.48
8	3	12.0	56	28	500	1.45
9	7	6.0	28	14	500	1.39
10	0	3.0	14	7	500	1.29
11	1	1.5	7	3	429	1.07
12	1	0.8	4			0.50

*Estimated by assuming male and female mortality is equal for the first 4 yr. of life, and the factor of $80/36 = 2.22$ is the over-sampling factor for the adult male groups: avg. mortality, all age groups = $996/3635 = 0.27$; avg. mortality, first 10 yr. = $986/3614 = 0.27$; avg. mortality, 4-yr.-olds = $366/956 = 0.38$.

these ratios are considered questionable because of the high degree of segregation within and among sampled groups. Therefore separate life tables for female and male caribou have been produced to evaluate other statistics of the population.

The age distribution of the 943 caribou in the sample was considered representative of the Kaminuriak Population. The individuals were grouped by ages: 0–5 months, 0 year; 10–17 months, 1 year; 22–29 months, 2 years; 34–41 months, 3 years; and so on to 190–197 months, 16 years. This method of grouping assumes that most deaths will be between November and April (not during calving, for females, or during breeding, for males).

Calculation of the starting population is based on a stationary population size; that is, the same number of births were assumed for each year. A related study has given pregnancy rates of 47.7 per cent for 3-year-old females and 89.6 per cent for 4+-year-old females (Dauphiné, in prep.). Thus, using the adjusted values from Table 19 the number of births expected is: $(47.7/100)40 + (89.6/100)196 = 194.6$. Assuming a sex ratio of 1:1 at birth, this figure gives a predicted 97.3 females as the starting population for life table calculations (Tables 23, 24).

The yearly frequency and the total frequency of animals were expressed as percentages of the starting population, to estimate the surviving percentage at each age level. These yearly values are reasonably consistent with one another, making it justifiable to combine them to calculate the life table.

The frequencies were plotted to allow fitting of a smooth curve to the data and an adjusted number of each age level was read off. The numbers were then tabulated in column 3 of life tables (Tables 23 and 24).

The remainder of the calculation used the standard method representing the frequency as the surviving number from a starting population of 1,000 (tabulated as l_x), finding number of deaths (d_x) by subtracting adjacent counts, and calculating

Figure 23
Conditions for a stable population of breeding
age female caribou

the yearly death rate q_x as d_x/l_x . The definitions and formulae for the components of a life table are as follows:

l_x = fraction of population surviving to age x ;

d_x = fraction of population which dies between x and $x + 1$, ($d_x = l_x - l_{x+1}$);

q_x = mortality during the next year, ($q_x = d_x / l_x$);

e_x = expectation of life, in years (i.e. sum l_x from the bottom up to and including x); and
 m_x = percentage of females of age x that have produced female calves. Mean annual mortality can be estimated for any interval using $\bar{q}_x = d_x / e_x$, summation over the years involved.

To study the relationship between age-specific survival rates and pregnancy rates we can use the structural modelling approach as described in Henny *et al.* (1970). With the simple equation of a stable population (Henny *et al.*, 1970:equation 1), we can show that changes in adult female survival or pregnancy rates must be accompanied by a change in survival of the young to maintain stable population size. Conversely, this relationship can be used in management studies to predict changes in the population.

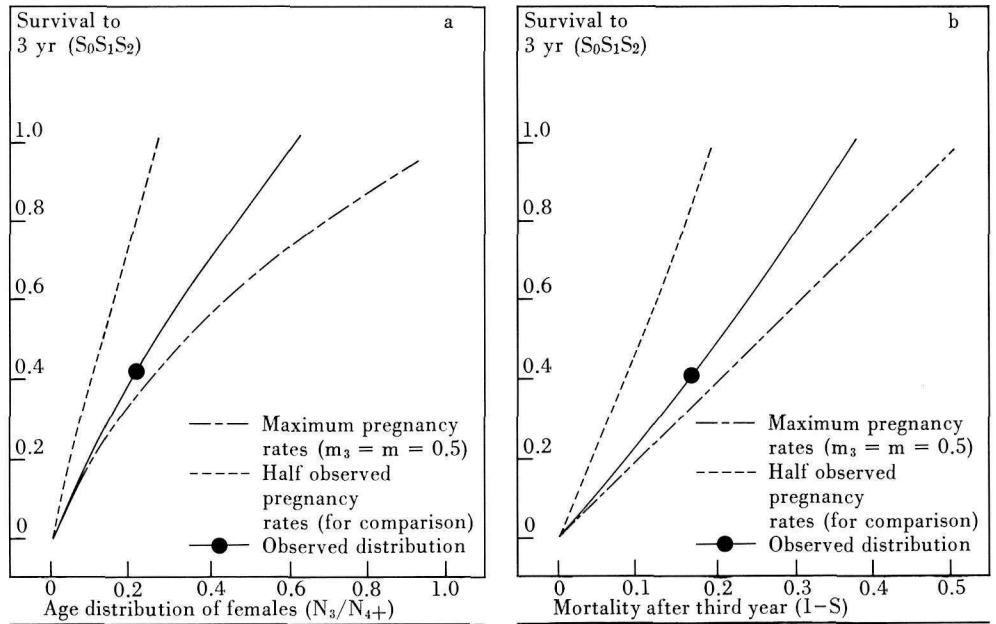
$$m_1s_0 + m_2s_0s_1 + m_3s_0s_1s_2 + m_4s_0s_1s_2s_3 + \dots = 1$$

(Henny *et al.*, 1970:equation 1) where
 m_x = pregnancy rate at age x (for female calves, i.e., half the pregnancy rate) and
 s_x = survival rate from age x to age $x + 1$. The formula can be expressed as equation 13 of Henny *et al.* (1970), assuming constant number of females of breeding age in successive years. In this case, since $m_1 = m_2 = 0$ and $m_4 = m_5 = \dots = m$ we find the condition is:

$$N_3 + N_{4+} = (m_3N_3 + mN_{4+}) s_0s_1s_2 + s(N_3 + N_{4+})$$

that is, the number of breeding age females during the current year equals the survivors next year plus primiparous females, where
 N_3 = no. of 3-yr-old females
 N_{4+} = no. of 4+-yr-old females

Figure 23



s = average survival of adult females
 $s_0s_1s_2$ = survival of females from birth to 3 yr.

There are four factors involved: pregnancy rates, adult age distribution, average adult survival, and survival to breeding age. If we know any two of these, the other two are determined by the equation for a stable population. The relationships are:

$$s_0s_1s_2 = 1 / \{m_3 + (mN_{4+} / N_3)\} \text{ and } s_0s_1s_2 = 1 / \{m_3 + [ms / (1 - s)]\}$$

The solid curves in Figure 23 show these relationships with pregnancy rates from our sample ($m_3 = 0.477/2$, $m = 0.896/2$) (Dauphiné, in prep.). The dashed lines show maximum pregnancy rates, that is, every breeding age female producing a calf ($m_3 = m = 0.5$). The dotted lines show half the observed pregnancy rates.

A truly representative sex ratio can be obtained only if the two sexes are unsegregated during seasonal movements, and their habits do not vary at other times of the year to an extent which makes samples unreliable (Mayr, 1939). This is indeed not

the case for barren-ground caribou. Skoog (1968:461) considered it difficult to obtain valid sex ratios for caribou and Kelsall (1968:157) stated that sexual segregation appeared highly variable and dynamic.

Because of great variation in the proportion of bulls in mixed groups during the rut, no group can be assumed representative of the population. Estimates of the sex ratio of the population must be based on large samples. An example of the influence of segregation by group-type on the adult sex ratio in limited samples is shown by comparing cow-juvenile-bull bands to the rest of the shot collection (Table 25). Within the age range 41–195 months (Table 26), 125 of the total 484 caribou shot were in cow-juvenile-bull bands where males comprised only 26 per cent, significantly lower than the 42 per cent in the rest of the sample ($\chi^2 = 10.3$, 1df, $P < 0.01$). In the age range 0–39 months 92 of the total 414 caribou were in cow-juvenile-bull bands where males comprised 47 per cent compared with 47 per cent in the rest of the sample (no significant difference).

Table 25

The strength of age and sex classes in 898 caribou from the Kaminuriak Population and 217 caribou collected in 26 cow-juvenile-bull bands, April 1966–June 1968

Age, mon.	Female %		Male %		Total %	
	Overall	Cow-juv.-bull bands	Overall	Cow-juv.-bull bands	Overall	Cow-juv.-bull bands
Juvenile						
0–13	9.2	8.3	7.3	6.0	16.6	14.3
15–25	6.6	6.9	5.7	6.9	12.2	13.8
Subadult						
27–39	8.8	7.4	8.5	6.9	17.3	14.3
Juvenile and subadult						
0–39	24.6	22.6	21.5	19.8	46.1	42.4
Adults						
41–195	33.4	42.9	20.5	14.7	53.9	57.6
Total						
0–195	58.0	65.4	42.0	34.6	100.0	100.0

An estimate of the age composition of the Kaminuriak Population based on the total of 26 cow-juvenile-bull bands collected from April 1966 to April 1968 is presented in Table 26. Cow and bull bands reflect segregation by sex and age, and juvenile and subadult bands reflect segregation by age. Cow-juvenile bands usually lack subadults, and always lack mature bulls. Therefore, only samples from cow-juvenile-bull and bull-cow-juvenile bands can reflect overall adult male: adult female ratios. The bull-cow-juvenile bands alone are not a good measure because both ground and aerial observations (Parker, 1972) show the population contains more cows than bulls.

For ease of comparison, I have followed the classification of sex ratios used by Skoog (1968:490). The primary sex ratio which must be determined at conception was not obtained. The secondary sex ratio which occurs at birth was derived from the April and June fetal counts. It was not possible to determine the exact ages of newborn calves, and the calves that were obviously only several hours old were too few to use for obtaining a secondary sex ratio. The calf sex ratio was determined by the counts for 3- to 5-month-old animals. The tertiary sex ratio was based on 12-month-

old animals and the yearling sex ratio was taken from 15- to 17-month-old animals. The quaternary sex ratio was calculated from 22-month-old rather than 24-month-old animals because of the additional segregation which occurs on the calving ground in June. The adult sex ratio included all animals between 36 and 118 months of age. The quinary sex ratio included caribou 120 months and more.

Table 27 gives a comparison of the sex ratios for the Nelchina caribou (Skoog, 1968) and the Kaminuriak caribou. The ratios, except calves and senile animals, are in close agreement. The low value for Kaminuriak male calves most likely results from sampling error. The difference in the quinary sex ratio is probably real and will be discussed later.

As I did, Kelsall (1968:60), Bergerud (1969:50) and Skoog (1968:490) found the secondary sex ratio slightly in favour of males. Sex ratios in favour of males (except calf ratio) continued in Kaminuriak caribou until the quaternary stage. There were more males than females in the samples from 3 to 6 years of age, but from that point females greatly outnumbered males.

The 39 per cent males in the 3+-year segment of the Kaminuriak Population falls between the values of 35 and 42 per cent

Table 26

Age composition of the Kaminuriak Population based on samples from 26 cow-juvenile-bull bands collected from April 1966 – April 1968

Age class mon.	Number			%
	Female	Male	Total	
0–13	18	13	31	14.3
15–25	15	15	30	13.8
27–39	16	15	31	14.3
41–49	17	9	26	12.0
51–61	7	15	22	10.2
63–73	8	5	13	6.0
75–85	19	2	21	9.7
87–97	10	1	11	5.1
99–109	16		16	7.4
111–121	9		9	4.2
123–133	4		4	1.8
135–145				
147–157				
159–169	1		1	0.4
171–181	1		1	0.4
183–193				
195–205	1		1	0.4
0–205	142	75	217	100.0
%	65.4	34.6	100.0	

Table 27

Sex ratios for the Kaminuriak caribou, and the Nelchina caribou in Alaska

Sex ratio	Males per 100 females	
	Kaminuriak	Nelchina
Primary	0	0
Secondary	122	104
Calf	89	117
Tertiary	122	122
Yearling	122	122
Quaternary	127	100
Adult	64	45
Quinary	6	30

males for two Alaskan populations (Skoog, 1968). The Arctic Alaskan herd (42 per cent males, 3+ years) was exposed only to natural mortality factors and aboriginal hunting, whereas the Nelchina herd (35 per cent males, 3+ years) was exposed to selective harvesting by sport and meat hunters (Skoog, 1968:491). St. Matthew Island reindeer (41 per cent males, 3+ years) had no predators and lived on overgrazed range (Klein, 1968).

The percentage of adult males in seven different wintering groups of caribou in Canada ranged from 21 to 39 (Kelsall, 1968: Table 15). Two of those values, 21 and 27 per cent, both taken in 1948, were for breeding segments of the Kaminuriak Population. Those estimates suggest there were 12–18 per cent fewer males in the breeding segment in 1948 than in 1968. The difference could be explained by greater hunting pressure in the 1940's. Banfield (1954) estimated that the Manitoba–Keewatin (Kaminuriak) Population totalled about 145,000 in 1948, and the annual kill was 42,000. Parker (1972) estimated the Kaminuriak Population at approximately 63,000 in 1968 and its annual harvest at about 4,000. If those estimates are correct, in 1948 the annual kill was about 10 times as large as in 1968, although the population was only 2.3 times larger. Thus, according to these estimates, hunters were taking about 29 per cent and 6 per cent of the total population respectively in 1948 and 1968. The changes in harvest size alone could clearly account for the smaller percentage of males in the breeding segment of the population in 1948 than in 1968, assuming selectivity for males by hunters.

The harvest of male caribou from the Kaminuriak Population by Eskimos and Indians is probably responsible to a degree for the quinary sex ratio of 6 per cent. There is also the possibility of selective predation by wolves on older males whose wintering grounds are further south and whose speed and vigour are reduced. The adult sex ratio indicates that adult males are dying at a greater rate than females, and the primary mortality factor is probably hunting by Eskimos and Indians. Parker (1972: Fig. 33) showed that hunters from three of the four native settlements killed mostly males. Skoog (1968:464) noted that caribou meat hunters follow the fat cycle. This means that Eskimo hunters would be selecting large males, if available, in summer and early autumn. Groups of Kaminuriak adult males winter closer to the Brochet Indian settlement than do the

cow-calf groups. Therefore, in most years late winter kills include larger numbers of adult males than of cows and calves.

Once it is established that there are enough breeding males and rising breeders in the population to service the breeding females the most important consideration becomes one of age distribution. The large base of juvenile and subadult animals in our collection indicates that the population has a high potential for rapid expansion in total numbers, if conditions are favourable. The relative numbers of calves, yearlings, and 2-year-olds provide a basis for evaluating the relative success of recent reproduction (Skoog, 1968:492). Our collection shows a progressive increase in these age classes within each year, 1966–1968. These data could indicate larger calf crops and/or higher calf and juvenile survival in 1963, 1964, and 1965 than in 1966 and 1967 (Fig. 21). This supposition is supported in part by the fact that the 1963, 1964, and 1965 cohorts are the ones best represented throughout the collection (Fig. 21). In the adult segment of the collection, high representation by animals 3–6 years old (3–5 years, Skoog 1968:492) suggests a healthy, expanding or at least stable population. High representation in the adult segment continued until the 9th year (Fig. 24).

Extremes of longevity found for the genus *Rangifer*, in years, are as follows: 12, Hadwen and Palmer (1922); 13, Bromée-Skuncke (1952); 14, Georgeson (1904); 15, Flower (1931), Palmer (1938); 15+, Skoog (1968); 17, Bergerud (1971); 18–20, McEwan (1963); and 20, Flerov (1952). It appears that caribou in the Kaminuriak Population live as long as would be expected for the species.

Only 37 caribou (2 males and 35 females), or 3.7 per cent, in the collection lived to their 10th year and only 21 caribou (2 males and 19 females), or 2.1 per cent, lived through their 10th year. The oldest male was 142 months old, and the oldest females were 205 months old from the Beverly Population and 195 months from the Kaminuriak Population. The senescent

females produce young, but would contribute little to the population because of their rarity. For management purposes caribou beyond 10 years of age can be considered extraneous.

Based on the adult male:female ratio of 58:100 and on equal mortality of males and females throughout adulthood, 11 males that had lived through their 10th year of life should have been collected. The results suggest that males died at a greater rate than females once the prime of life was reached, as we obtained only 18 per cent of the expected male sample. Under the existing rates of predation by man and wolves and other accidental mortality, few caribou in the Kaminuriak Population survive long enough to express their physiological longevity.

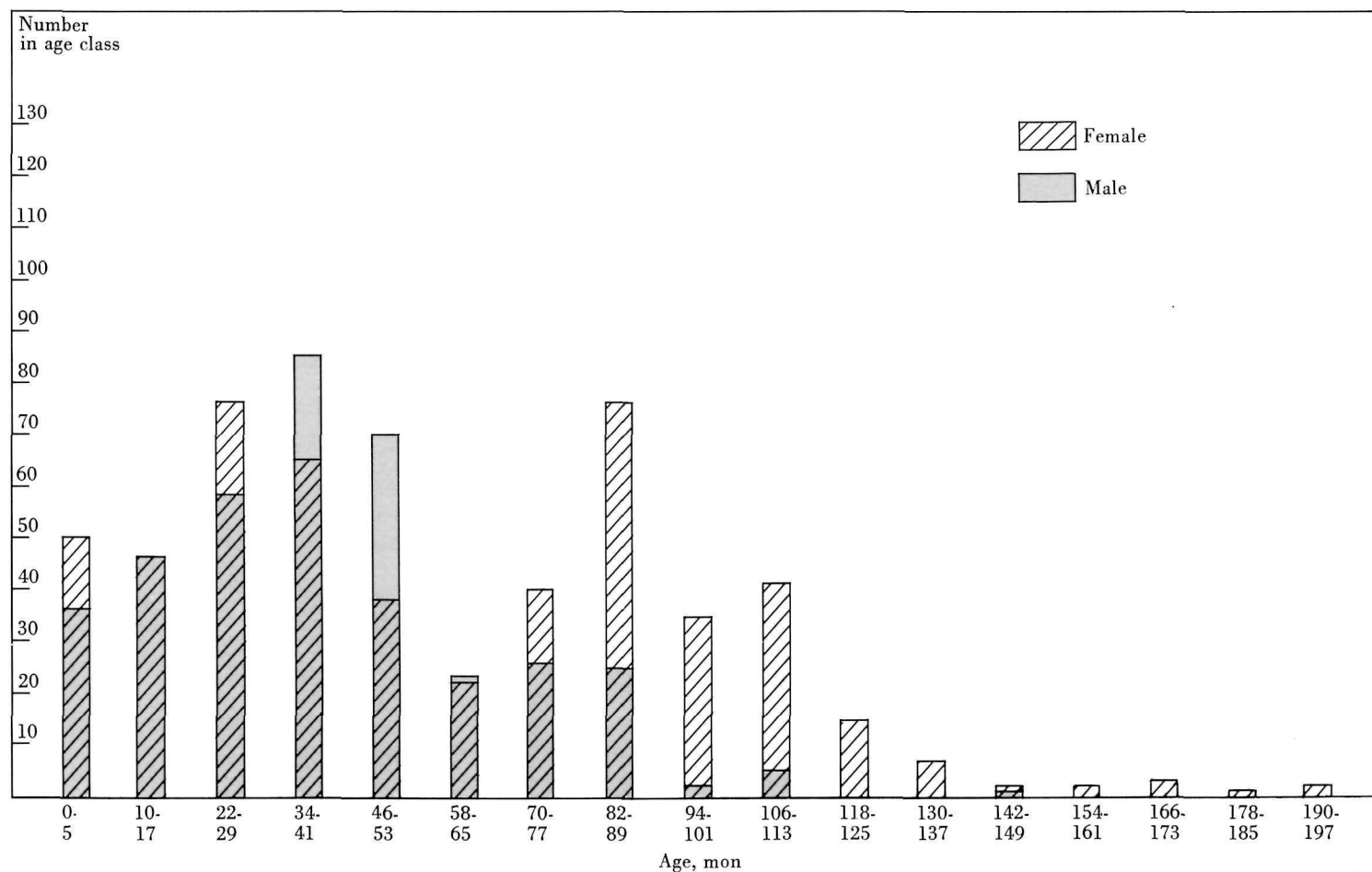
The 1959, 1960, and 1961 cohorts were all well represented in each year's collection and the occurrence of individuals from each cohort moved chronologically from a peak in the 1959 cohort in 1966 to a peak in the 1961 cohort in 1968. This condition would be expected if the calf crops and survival rates were similar for those three cohorts, and its detection suggests that our sampling of the age distribution of the adult segment was representative of the population.

Differential mortality among cohorts could have considerable impact on the total size of the population, and possibly even more influence on the subsequent number of breeding females, if early mortality is always higher among female caribou. This intra-cohort mortality would be even more important if an excessive death rate occurred within two or three successive cohorts, especially while the population was being heavily harvested.

The curve for females shows low mortality from 3 to 7 years (Fig. 22), possibly reflecting the past history of the herd. The curve for males shows a greater slope after 5 years (Fig. 22). Possibly the slope of the male curve has been reduced by the assumption that the 4-year-olds have the same mortality as the females.

Figure 24

Frequency of occurrence by sex and age classes for pregrowth-growth periods (excluding July 1968 sample), April 1966-June 1968

Figure 24

Selective predation by wolves may also be a contributing factor to the greater mortality of old bulls. Thus, it cannot be determined whether the distinct difference between the life tables for females (Table 23) and males (Table 24) is in part due to a natural difference in life span, or whether selective hunting is the sole or primary cause.

By the use of the life tables (Tables 23, 24) a value can be obtained for the calf crop as a percentage of the total sample: calf crop = $(2000/8335)100 = 24$ per cent at birth.

If we assume that half the calf mortality occurs in the first six weeks of life

then:

calf crop = $(1723/8058)100 = 21$ per cent at 6 weeks.

With assumptions of mortality used in the life table, we find that the age distribution without calves (that is, just before calving) is expected to be as follows in percentages: yearlings, 22.8; 2-year-olds, 17.2; 3-year-old females, 6.5; 4+-year-old females, 31.8; 3-year-old males, 6.5; and 4+-year-old males, 15.1.

The calculated life expectancy at birth was 4.20 years for females and 3.14 years for males; and at breeding age (females 3 years, males 4 years) 5.41 years for

Figure 25
Combined Kaminuriak male and female values
compared with Banfield's (1955) observed and
adjusted data

females and 2.09 years for males. Average mortalities for all age groups of females and for the first 10 years for males were similar: 21 per cent for females and 27 per cent for males. Average mortality for females in the breeding segment (3+ years) was 17 per cent and for males (4+ years) 38 per cent.

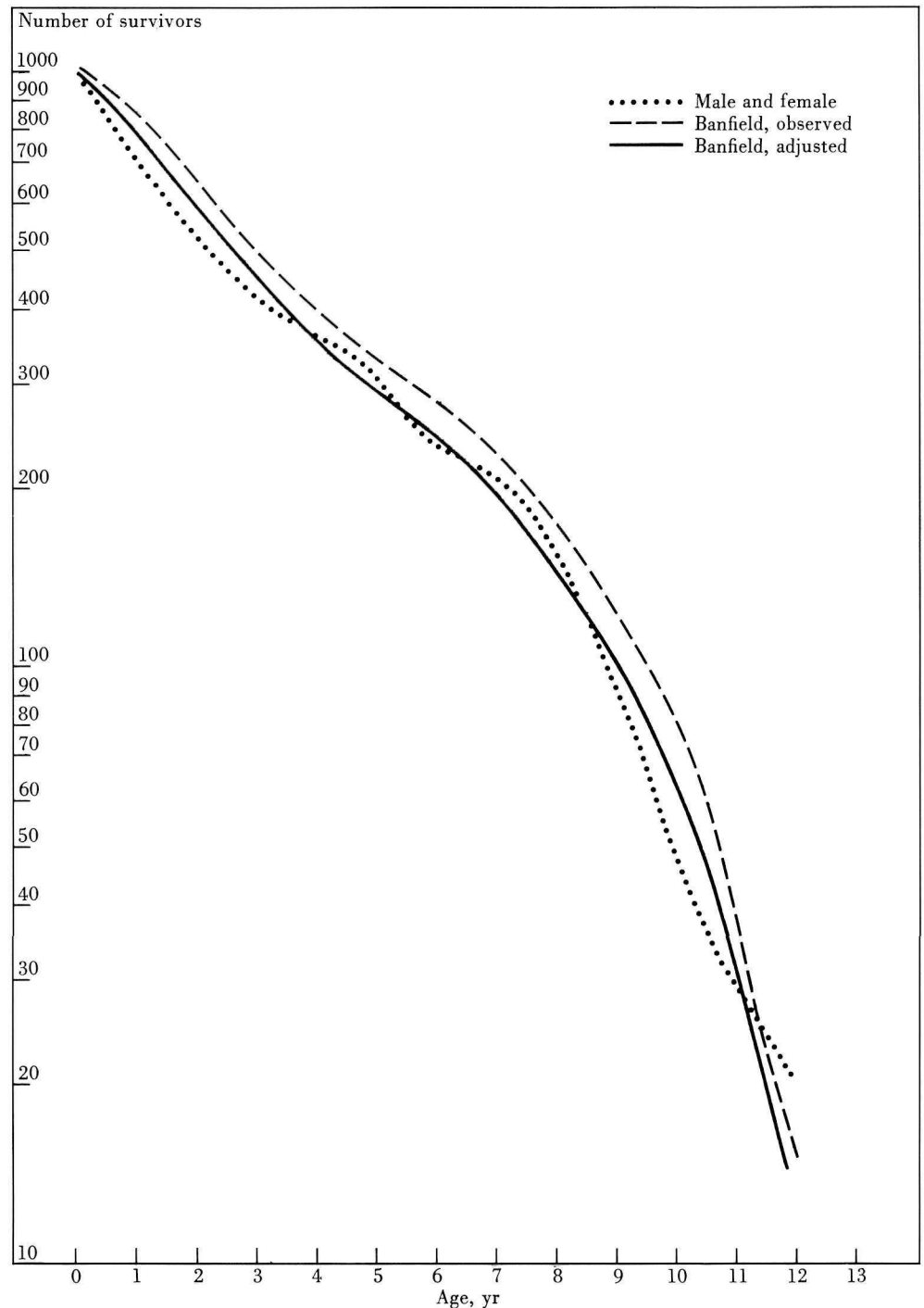
Banfield (1955) produced a time-specific life table based on 292 mandibles collected in 1948 and 1949 on the summer and winter ranges of caribou in northern Canada. While Banfield's life table is for both sexes, it provides interesting comparisons with my female and male life tables. Caughley (1966) noted that Banfield (1955) had confounded the collection of l_x and d_x data, and did not accept the life table for comparing mortality patterns between species. However, as the majority of specimens obtained by Banfield (1955) were hunter-killed, Caughley's objection is not serious.

When the numbers of survivors in the Kaminuriak female and male life tables are averaged and compared with the adjusted values from Banfield's life table, the results are similar (Fig. 25). I adjusted Banfield's data by an increase of 11 per cent in the number of calves based on the ratio of calving females to total animals in the age range of 3 years or older in this study.

In his abstract, Banfield (1955:143) reported that "the average mortality rate for the first 10 years of life was 71%." Later, he stated (1955:146): "A fitted curve for the first section of the curve up to the 10th year has an indicated average mortality rate of 71%. This is similar to the rate calculated for a number of species by Kurten (1953)." Although the curve is correct, the 71 per cent value is an error hitherto undetected or unreported (Banfield, pers. comm.); the correct figure is 21 per cent.

Total mortality was 92 per cent for the first 10 years in Banfield's (1955) life table and 92 per cent for females and 99 per cent for males in my table. The figure for males is probably slightly excessive and the true rate is likely more than 95 per cent.

Figure 25



The graphs for age-specific survival rates and pregnancy rates (Fig. 23) could be used in management. For example, with the observed pregnancy rates and $s_0s_1s_2 = 0.20$ (that is, if we had evidence that only 20 per cent of the females survived to breeding age) we know that a stable population requires $1 - s = 0.09$ (91 per cent survival for adults) and the number of 3-year olds should be 9 per cent of the number of older females. If instead we know that $N_3/N_{4+} = 40/196 = 0.204$, as in our sample with the observed pregnancy rates, we find that it is necessary to have $s_0s_1s_2 = 0.41$ (41 per cent of female calves survive to breeding age) and average adult mortality would be $1 - s = 0.17$ for a stable population. Note that these relationships do not allow for fluctuations such as years of higher productivity of calves or higher mortality.

Parker (1972) estimated by aerial surveys that only 22 per cent of the 1968 Kaminuriak calf crop survived to 1 year of age. When we apply the mortality to 3 years of age, (24.6% annually) as determined in the construction of the life tables, we find that only 12 per cent of the females from the 1968 cohort would live to breeding age (3 years). Based on the curve for mortality after the third year (Fig. 23), persistence of a stable population at the 1968 level would require mortality of only 6 per cent of the adult females annually.

Histological examination of the annuli in the dental cementum is a satisfactory technique for age determination of caribou. Ages assigned in this way are not exact due to problems of interpretation, but it is the most precise method of determining the age of caribou with full permanent dentition.

The reliability of the technique can be validated only by examining the teeth of specimens that were tagged as calves. More data must be obtained on the possibility of individual variations in the apposition of dental cementum and the controlling internal and external factors of cemental growth.

Age-estimation methods using readily obtainable dental variables were developed. While not necessarily as accurate as the histological approach, they are simpler, quicker and more economical and do not require elaborate equipment.

A graphical tooth-wear key based on the summation of the average heights of the p4 and m1 gave estimates within 1 year of the true ages as estimated by cemental annulations for males, within 2 years for females.

Consideration of additional variables, mandibular length and dentine width increased the predictive power for the age of the younger animals but decreased the accuracy for older animals.

The quantitative tooth-wear method will be valuable in assigning approximate ages to large numbers of specimens, so that a curve can be fitted to the age frequencies to estimate age composition. However, variations in the rates of tooth wear would require that categories were delimited for each population. The level of accuracy is satisfactory for providing basic information for management of caribou on a sustained yield basis.

Mandibular and diastema lengths showed significant increases with age, particularly in males. But the variable is of little use in differentiating older age groups, because the major growth takes place before the animal reaches 5 years.

Separation of sexes by mandibular length was 95 per cent successful for animals at least 5 years old but much less so for younger animals. The mandibular and diastema lengths were highly correlated and the relationship of the two variables was the same for both sexes. The diastema length can therefore be used to identify sex if the mandible is damaged. The use of mandibular length and the average heights of p4 and m1 for estimating the sex and age of caribou killed by hunters is simple and economical.

Ages can be determined by eruption and replacement of the mandibular teeth for all caribou through 21 months and for many animals up to 28 months. All permanent mandibular teeth had erupted by 20 months. The state of the closure of root apices can be used to separate 2-year-olds from 3-years-olds. The apices of the roots of the p4 and m3, the last to mature, are open at 24 months but closed at 36 months.

Visual examination of the attrition patterns of mandibular teeth as a basis for assigning age-classes has some merit as a preliminary management tool. Three primary causes of variations in the wear patterns must be kept in mind: (1) malocclusion from misalignment of the maxillary and mandibular tooth rows, (2) variations in the curvatures of the rami of individual caribou, and (3) variations in primary and secondary axes of the mandibular blades.

The value of age determination by visual examination of the teeth is limited by variation in both tooth wear and the ability of observers to evaluate wear patterns. A good approach to the use of jaw boards would be to classify the caribou by age-classes: juvenile, 1–2 years, 3 years, 4–5 years, 6–9 years, and 10+ years. Although not applicable for establishing information on cohorts, these classes would be sufficient to demonstrate trends in age structure for management purposes.

The primary distinguishable social group is the band, categorized by sex and age composition as follows: cow, bull, sub-adult, juvenile, cow-juvenile, cow-juvenile-bull and bull-cow-juvenile.

A truly representative sex ratio of an animal population can be obtained only if the two sexes are unsegregated during seasonal movements and their habits do not vary at other times of the year to an extent which makes samples unreliable. This is not the case for barren-ground caribou. Aerial surveys of small land units may give misleading ratios of mature males to mature females. The problem of non-random distribution of caribou by sex and age could be practically overcome by the use of photography and of repeated aerial surveys of large land units at the appropriate season of the year.

If there are enough male breeders and rising breeders in the population to service the breeding females, age distribution becomes the most important consideration. At the time of study breeding males appeared to be well represented in the Kaminuriak Population. The large base of juvenile and subadult animals in this collection indicates that the population has a high potential for rapid expansion in total numbers. In the adult segment of the collection high representation of prime animals, 4–6 years old, suggests a healthy, expanding or at least stable population. High representation in the adult segment continued until the 9th year of life. It appears that caribou in the Kaminuriak Population live as long as would be expected for the species. Differential mortality between cohorts could have considerable impact on the total size of the population, and possibly even more influence on the subsequent number of breeding females.

The high degree of segregation within and among the caribou groups and direct observations of caribou particularly in the spring, lead me to believe that caribou are socially cohesive. I suggest that (1) the primary function of postcalving aggregation is socialization; (2) the core of the wintertime cow-juvenile band is formed by a matrilineal bloodline; and (3) the basic male social unit, the bull band, maintains from year to year a distribution of breeding bulls from common stock with learned behav-

ioural habits that will assure, under natural conditions, a self-sustaining supply of breeders on the traditional rutting areas.

I believe that the postcalving clumping of caribou would limit the loss to wolf predation, if wolves regulate themselves spatially on the tundra. Spatial regulation of wolves in forested areas has been suggested by Pimlott *et al.* (1969) and Parker (1972). Bergerud (1971) has postulated that the formation of postcalving aggregations is an adaptation by caribou to wolf predation in open country. Spatial regulation of wolves would also redirect predation to the crippled and debilitated caribou on the peripheries and back trails of the aggregations, making the weakened individuals buffers to the healthy caribou.

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Appendices

Appendix I

A review of literature related to age determinations of cervids prior to 1971 by eruption, replacement, wear, and histological examination of mandibular teeth

The first attempts to determine the age of North American cervids by examining teeth were made by Cahalane (1932) for white-tailed deer (*Odocoileus virginianus*), and by Cowan (1936) and McLean (1936) for black-tailed deer (*O. hemionus columbianus*). Severinghaus (1949) described the first workable age classification, for white-tailed deer, based on eruption and wear. His technique was applied by other biologists to mule deer (*O. h. hemionus*) and black-tailed deer. Moreland (1952) described an adaptation of the method for black-tailed deer. Jones (1953) discussed its use in determining the age of Inyo mule deer (*O. h. inyoensis*). Robinette *et al.* (1957) described tooth wear classes for Rocky Mountain mule deer in Utah and Colorado, based on a molar-ratio technique. Taber and Dasmann (1958) produced a table of eruption and replacement of the teeth of black-tailed deer in California. Brown (1961) determined the ages of black-tailed deer by tooth wear and replacement in the State of Washington.

Banfield (1949), Murie (1951), Swanson (1951), Quimby and Gaab (1952, 1957), Hancock and Low (1956), Greer and Yeager (1967), and Keiss (1969) have used dentition to determine the ages of elk (*Cervus canadensis*). Quimby and Gaab (1957) have assigned age classes to elk based on tooth replacement and wear. Greer and Yeager (1967) found that the morphology of upper canine teeth differed in male and female elk. Canine eruption development and wear were similar in both sexes but could be used to determine age. Eleven biologists in Colorado used canine eruption and wear to estimate the ages of elk, and Keiss (1969) compared these estimates with those based on dental cementum.

Simkin (1967) compared the results of estimating the age of moose (*Alces alces*) in Ontario by a tooth-wear technique described for this species by Passmore, Peterson and Cringan (1955) with results based on an examination of sections of incisor cementum and on the weights of eye lenses.

Gruener (1931) criticized the first report, by Mishin (1930), of an eruption-wear method for determining the age of reindeer (*Rangifer tarandus tarandus*). Sokolov (1937) gave a more detailed account of the teeth in wild and domesticated reindeer. Eruption-wear-replacement patterns were then described for Scandinavian reindeer by Bromée-Skuncke (1952) and Bouchud (1953), for Canadian caribou by Banfield (1951, 1954, 1961), and for Alaskan caribou by Chatelain (1954), Watson and Keough (1954) and Skoog (1956, 1968).

It soon became evident that the wear method for determining the age of cervids was severely limited.

The rate of tooth wear varies locally and considerable error on the observer's part is possible. Observers using the wear method in Michigan consistently underestimated the ages of 5-month-old, 1½-year-old and 2½-year-old deer, thus producing inflated survival rates (Ryel, Fay and Van Etten, 1961). Fourteen observers each examined 50 jaws from black-tailed deer whose ages were known, and estimated correctly only 43 per cent of the time (Brown, 1961). Eleven biologists used the eruption-wear method on 200 elk, and their estimates agreed with ages determined by readings of the dental cementum in just 50 per cent of the cases (Keiss, 1969).

The rate of tooth wear in cervids varies with differences in such factors as climate, soil type, quality and quantity of plant species eaten and abrasives they contain, and gene pool of the population. Because of the shortcomings of the eruption-wear technique, workers turned their attention to developing a more precise method. This led to the recognition of annulations in the dentine and the annual deposition of dental cementum in the teeth of many animal species.

Eidmann (1932) believed that the number of annulations in the secondary dentine, plus 3 years to account for the time before the formation of the first layer, could be used to determine age in red deer (*Cervus elaphus*) and he examined the secondary dentine in incisors of this species as early as 1932. Rieck (n.d. In Lowe, 1967) applied Eidmann's (1932) method to fallow deer (*Dama dama*) in Germany. But it was not until the work of Scheffer (1950) and Laws (1952) that the annuli method gained prominence.

Literature on histological examination of cervid teeth is varied but meagre. Modifying McEwan's (1963) second technique for caribou, Gilbert (1966) determined the ages of white-tailed deer from Nova Scotia, New Brunswick, Ontario and British Columbia. He decalcified il in 30 per cent formic acid, cut 10-micron longitudinal sections and stained them with Delafield's haematoxylin. He tested the accuracy of the technique, by comparison with a sample of teeth from 10 white-tailed deer from Michigan whose ages were known. Ransom (1966) used m1 to estimate the ages of 16 white-tailed deer of known age from Michigan and Minnesota. His was a non-histological technique, similar to Mitchell's (1963) for red deer. He bisected m1 transversely, ground the anterior portion smooth and wet it with 70 per cent alcohol. Viewed under a dissecting microscope, the layers in the cementum did not vary more than plus or minus one layer for any of the deer whose ages were known. Campbell (1967) used three techniques (Novakowski, 1965a; Gilbert, 1966; Ransom, 1966) on m1 from 75 Illinois white-tailed deer whose ages were known. He found that Novakowski's (1965a) and Ransom's (1966) techniques produced no cemental layers distinct enough for pre-

cise identification; but using Gilbert's (1966) technique, he was able to estimate all ages correctly. Olson (1967) histologically examined il from Indiana, Missouri and Wisconsin white-tailed deer. He decalcified with 5 per cent nitric acid, cut 10-micron sagittal sections, and stained with haematoxylin and eosin. The results were governed more by storage method than by histological technique. Of 114 specimens stored dry and 59 preserved in solution, 52 and 82 per cent respectively showed countable annulations in the dental cementum. Gilbert and Stolt (1970) working with 682 white-tailed deer from Maine found that individual biologists placed, by tooth-wear method, an average of 4 of every 10 deer into an age class different from that determined by Gilbert's (1966) method of annuli counts.

Low and Cowan (1963) correctly estimated the ages of 20 black-tailed deer. They decalcified il with 5 per cent formic acid, cut 10-micron sagittal sections and stained them with Erlich's haematoxylin. Erickson (1967) and Erickson and Seliger (1969) estimated correct ages of 16 mule deer. They decalcified il, cut the teeth into 95-micron transverse sections and stained with Harris haematoxylin. After comparing the various techniques—cemental annuli, molar tooth ratios (Robinette *et al.*, 1957), visual evaluation of the molariform tooth row, and weights of eye lenses—Erickson *et al.* (1970) concluded that counting annulations was the best technique for estimating the age of mule deer.

Mitchell (1963, 1967) determined the ages of more than 500 red deer from the highlands and islands of Scotland by examining the m1. He viewed transverse sections of dental cementum by reflected light under a binocular dissecting microscope (Mitchell, 1963). He has also described the growth of dental cementum, some factors influencing cemental growth, and the use of annulations to estimate age (Mitchell, 1967). Working with red deer from the Isle of Rhum, Lowe (1967), examined the secondary dentine deposited within the crown of the il and the number of layers in the pad of cementum beneath the crown of the m1. Surprisingly, he found eruption, replacement and wear a more reliable technique than counting annuli in the secondary dentine and dental cementum.

Klevezaal' and Kleinenberg (1967) found clear annulations in the dentine of teeth from spotted deer (*Cervus nippon*) and a roe deer (*Capreolus capreolus*). They worked with haematoxylin-stained transverse sections of the incisors and molariform teeth.

Using Mitchell's (1963) technique on m1 of wapiti collected in western Canada, Flook (1970) examined sections with a stereo microscope, under direct light at 16× magnification. In 1967 Keiss (1969) used Erickson's (1967) rapid dental-cementum technique to correctly determine the ages of 13 elk whose ages were known. Keiss also arrived

at estimates for 200 elk killed by hunters in Colorado.

In examining the histology and anatomy of the elk canine, Seliger, Erickson and Denny (1969) noted that the apical half of the cementum contained annuli.

Sergeant and Pimlott (1959) developed the method of determining the age of moose from the annuli of the il and demonstrated, from longitudinal, polished sections, that these were apposed seasonally. Olson (1967) unsuccessfully attempted to estimate the age of moose from Isle Royale, using the method he applied to the il of white-tailed deer; he believed that the unfavourable results derived from prolonged drying of the teeth before they were processed. The ages of 140 moose from Isle Royale were determined by counting annulations in the cementum of molariform teeth (Wolfe, 1969), using a procedure described by Mitchell (1963). The polished sections were thinly coated with light oil or colourless nail polish, for greater legibility, and were read under reflected light with a 20× binocular microscope (Wolfe, 1969).

Thus far, only two studies (McEwan, 1963; Reimers and Nordby, 1968) have reported on age determination in *Rangifer* by examination of dental cementum. McEwan (1963) used two techniques on barren-ground caribou in Canada. In his second method, McEwan decalcified about 100 il in a solution of 30 per cent formic acid for 24 hours, cut them into 7-micron sections and stained the sections with Delafield's haematoxylin. Both methods produced histological sections in which the annuli in the dentine and cementum were legible.

More recently, Reimers and Nordby (1968) have used the annulations in dental cementum of the il to determine the ages of 37 adult Norwegian reindeer whose ages were known, and of 1,100 reindeer from two populations. They used a rapid freeze-sectioning technique to detect the annuli. The teeth were decalcified in 5 per cent (0.8 N) nitric acid for 24 hours, cut into median, longitudinal, frozen sections at 30 microns, and stained with Mayer's haemalum (without chloralhydrate) for 10 to 15 minutes. Eight to ten sections were mounted in heated gelatin-glycerol and read under the microscope at 125×. Reimers and Nordby (1968) consider counting cemental annuli in teeth a reliable method for age determination in reindeer.

Appendix 2

A summary of mammals examined by various authors prior to 1971 for possible use of teeth in determining age

Order & family	Species	Author
Marsupialia		
Phalangeridae	Brush-tailed possum	Pekelharing, 1970
	<i>Trichosurus vulpecula</i>	
	Brush wallaby	Pekelharing, 1970
	<i>Macropus rufogrisea</i>	
Insectivora		
Soricidae	Common shrew	Klevezal', 1966; Kleinenberg & Klevezal', 1966
	<i>Sorex araneus</i>	
Vespertilionidae	Big brown bat	Christian, 1956
	<i>Eptesicus fuscus</i>	
	Large mouse-eared bat	Klevezal', 1966
	<i>Myotis myotis</i>	
	Red noctule	Klevezal', 1966
	<i>Nyctalus noctula</i>	
Rodentia		
Castoridae	Beaver	Klevezal' & Kleinenberg, 1964, 1967; Van Nostrand & Stephenson, 1964; Novakowski, 1965b
	<i>Castor fiber</i> , <i>C. canadensis</i>	
Sciuridae	European suslik	Meier, 1957
	<i>Citellus pygmaeus</i> , <i>C. citellus</i> *	
	Thin-toed suslik	Klevezal', 1966
	Long-clawed ground squirrel*	
	<i>Spermophilopsis leptodactylus</i>	
	Gray marmot	Kleinenberg & Klevezal', 1966
	<i>Marmota baibacina</i>	
	California ground squirrel	Adams & Watkins, 1967
	<i>Spermophilus beecheyi</i>	
Muridae	Field mouse,	Klevezal' & Lavrova, 1966
	Striped field mouse*	
	<i>Apodemus agrarius</i>	
	Norway rat	Klevezal' & Lavrova, 1966
	<i>Rattus norvegicus</i>	
	Tamarisk gerbil	Klevezal', 1966
	<i>Meriones tamaricinus</i>	
	Common hamster	Klevezal', 1966
	<i>Cricetus cricetus</i>	
	Muskrat	Klevezal', 1966
	<i>Ondatra zibethica</i>	
	Water rat, water vole*	Klevezal', 1966
	<i>Arvicola terrestris</i>	
	Common vole	Klevezal' & Lavrova, 1966
	<i>Microtus arvalis</i>	
	Pine vole	Klevezal' & Lavrova, 1966
	<i>Microtus majori</i> ,	
	<i>Pitymys majori</i> *	
Cetacea		
Physeteridae	Sperm whale	Nishiwaki & Yagi, 1954; Nishiwaki <i>et al.</i> 1958; Nishiwaki <i>et al.</i> 1961; Berzin, 1961, 1964; Ohsumi <i>et al.</i> 1963; Bow & Purday, 1966
	<i>Physeter catodon</i>	

Order & family	Species	Author
Delphinidae	Beluga <i>Delphinapterus leucas</i>	Sergeant, 1959
	Pilot whale <i>Globicephala melaena</i>	Khuzin, 1961, 1963; Sergeant, 1959
	Bottle-nosed dolphin <i>Tursiops truncatus</i>	Sergeant, 1959; Rebach & Cornell, 1968
	White-sided dolphin <i>Delphinus delphis</i>	Kleinenberg & Klevezal', 1962; Klevezal', 1966
	Blue-white dolphin, Spotted dolphin* <i>Prodelphinus caeruleoalbus</i> , <i>Stenella caeruleoalbus</i> *	Nishiwaki & Yagi, 1953
	Finback whale <i>Balaenoptera physalus</i>	Klevezal', 1966
	Sei whale <i>Balaenoptera borealis</i>	Klevezal', 1966
Carnovira		
Ursidae	Brown bear <i>Ursus arctos</i>	Hittell, 1860; Smirnov, 1960; Mundy & Fuller, 1964
	Black bear <i>Ursus americanus</i>	Rausch, 1961; Marks & Erickson, 1966; Sauer <i>et al.</i> 1966; Stoneberg & Jonkel, 1966; Craighead <i>et al.</i> 1970
	Polar bear <i>Thalarchos maritimus</i>	Reimers & Nordby, 1968
Canidae	Arctic fox <i>Alopex lagopus</i>	Klevezal', 1965, 1966
	Coyote <i>Canis latrans</i>	Linhart & Knowlton, 1967
Felidae	Lynx <i>Lynx lynx</i>	Reimers & Nordby, 1968
Mustelidae	Sable <i>Martes zibelina</i>	Klevezal', 1965, 1966
	Mink <i>Mustela vison</i>	Klevezal', 1965, 1966
	Sea otter <i>Enhydra lutris</i>	Klevezal' & Marakov, 1966
	Wolverine <i>Gulo gulo</i>	Reimers & Nordby, 1968
Procyonidae	Racoon <i>Procyon lotor</i>	Grau <i>et al.</i> 1970
Pinnipedia		
Odobenidae	Walrus <i>Odobenus rosmarus</i>	Chapksii, 1952; Mansfield, 1958a; Krylov, 1965
Otaridae	Southern sea lion <i>Otaria byronia</i>	Laws, 1962
	Otary <i>Eumetopias jubata</i>	Fiscus, 1961; Spalding, 1964
	South African fur seal <i>Arctocephalus pusillus</i>	Rand, 1956 (<i>In</i> Laws, 1962)
	Southern fur seal <i>Arctocephalus tropicalis</i>	Laws, 1962

Continued on page 86

Order & family	Species	Author
Otaridae	South American fur seal	Laws, 1962
continued	<i>Arctocephalus australis</i>	
	Northern fur seal	Chiasson, 1957; Scheffer & Kraus, 1964; Anas, 1970
	<i>Callorhinus ursinus</i>	
Phocidae	Harbor seal	Mansfield & Fisher, 1960; Tikhomirov & Klevezal', 1964
	<i>Phoca vitulina</i>	
	Harp seal	Fisher, 1954
	<i>Phoca groenlandica</i>	
	Ringed seal	McLaren, 1958; Tikhomirov & Klevezal', 1964
	<i>Pusa hispida</i> , <i>Phoca hispida</i> *	
	Caspian seal	Chapskii, 1965
	<i>Pusa caspica</i>	
	Baikal seal	Klevezal', 1961
	<i>Pusa sibirica</i>	
	Greenland seal	Chapskii, 1952; Rasmussen, 1957; Yakovenko, 1960, 1961
	<i>Pagophilus groenlandicus</i>	
	Ribbon seal	Tikhomirov & Klevezal', 1964
	<i>Histiophoca fasciata</i>	
	Sea hare, Bearded seal*	Tikhomirov & Klevezal', 1964
	<i>Erignathus barbatus</i>	
	Gray seal	Hewer, 1960, 1964
	<i>Halichoerus grypus</i>	
	Crabeater, Crab-eater seal*	Laws, 1953a, 1958
	<i>Lobodon carcinophagus</i>	
	Sea leopard, Leopard seal*	Laws, 1953a, 1957
	<i>Hydrurga leptonyx</i>	
	Weddell seal	Mansfield, 1958b; Stirling, 1969
	<i>Leptonychotes weddelli</i>	
	Ross seal	Laws, 1953a
	<i>Ommatophoca rossi</i>	
	Hooded seal	Laws, 1953a; Rasmussen, 1957; Yakovenko, 1959; Popov, 1960
	<i>Cystophora cristata</i>	
	Northern sea elephant, South Atlantic elephant seal*	Laws, 1953a, 1953b, 1960, 1962; Carrick & Ingham, 1962
	<i>Mirounga leonina</i>	
	Hawaiian monk seal	Kenyon & Fiscus, 1963
	<i>Monachus schauinslandii</i>	
Sirenia		
Dugongidae	Sea cow	Scheffer, 1970
	<i>Dugong dugong</i>	
Perissodactyla		
Equidae	Wild ass, Onager*	Klevezal', 1966
	<i>Equus hemionus</i>	
Artiodactyla		
Bovidae	Bison	Armstrong, 1965; Novakowski, 1965a
	<i>Bison bison</i>	
	Dall sheep	Hemming, 1967, 1969
	<i>Ovis dalli</i>	
	Barbados sheep, Domestic sheep*	Saxon & Higham, 1968
	<i>Ovis aries</i>	

Order & family	Species	Author
Antilocapridae	Pronghorn antelope <i>Antilocapra americana</i>	McCutchen, 1969
Cervidae	White-tailed deer <i>Odocoileus virginianus</i>	Gilbert, 1966; Ransom, 1966; Campbell, 1967; Olson, 1967; Gilbert & Stolt, 1970
	Black-tailed deer <i>Odocoileus hemionus columbianus</i>	Low & Cowan, 1963
	Mule deer <i>Odocoileus hemionus hemionus</i>	Erickson, 1967; Erickson & Seliger, 1969; Erickson <i>et al.</i> , 1970
	Red deer <i>Cervus elaphus</i>	Eidmann, 1932; Mitchell, 1963, 1967; Lowe, 1967; Reimers & Nordby, 1968
	Fallow deer <i>Dama dama</i>	Rieck, n.d. (<i>In</i> Lowe, 1967)
	Roe deer <i>Capreolus capreolus</i>	Klevezal', 1966; Reimers & Nordby, 1968
	Spotted deer, Sika deer* <i>Cervus nippon</i>	Klevezal', 1966; Prisyazhnyuk, 1968
	Elk <i>Cervus canadensis</i>	Keiss, 1969; Seliger <i>et al.</i> , 1969; Flook, 1970
	Moose <i>Alces alces</i>	Sergeant & Pimlott, 1959; Olson, 1967; Reimers & Nordby, 1968; Wolfe, 1969
	Caribou <i>Rangifer tarandus</i>	McEwan, 1963; Reimers & Nordby, 1968
Primates		
Hominidae	Man <i>Homo sapiens</i>	Reimers & Nordby, 1968

*Common and scientific names from Walker (1964).

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