Biology of the Kaminuriak Population of barren-ground caribou Part 4

by T. C. [...]

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Biology of the Kaminuriak Population of barren-ground caribou

Part 4: Growth, reproduction and energy reserves

by T. C. Dauphiné, Jr.

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Top. A herd of female caribou with their
young on the calving ground in June.

Bottom left. A thin, stained section of a
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most of the photograph – a corpus luteum
of pregnancy – were counted in order to
determine the number of calves a female
had produced.

Bottom centre. A female caribou with calf.

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Photos by T. C. Dauphiné, Jr.

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The author
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Perspective
From 1966 to 1968 the CWS, in co-operation with the governments of Manitoba, Saskatchewan, and the Northwest Territories, undertook a comprehensive field study of the biology of the Kaminuriak population of barren-ground caribou (*Rangifer tarandus groenlandicus*). The study originated from an urgent need to obtain detailed biological and ecological information necessary for sound future management of barren-ground caribou. The Kaminuriak population was selected because it was a relatively discrete population which occupied an area more accessible than most other migratory barren-ground caribou on the Canadian mainland.

The study was divided into four parts with a biologist assigned to each. The objectives were as follows: to determine the size of the population, to record seasonal movements, and to relate population size to range capacity, annual mortality, and natality (G. R. Parker 1972); to determine the sex and age composition from large, representative samples of the population (F. L. Miller 1974); to determine the relationship of forage use by caribou on the taiga winter range to forage abundance, distribution, and availability (D. R. Miller 1974, 1976); and to obtain detailed information on reproductive rate, growth and seasonal energy (fat) reserves (this Report).

Personnel were also co-opted from the game agencies of Manitoba, Saskatchewan, Alberta and the Northwest Territories.

In 1970 the results and recommendations of the research were reported to the Administrative and Technical Committees for Caribou Preservation. The adopted recommendations were made available to the game agencies of Manitoba, Saskatchewan, Alberta and the Northwest Territories.
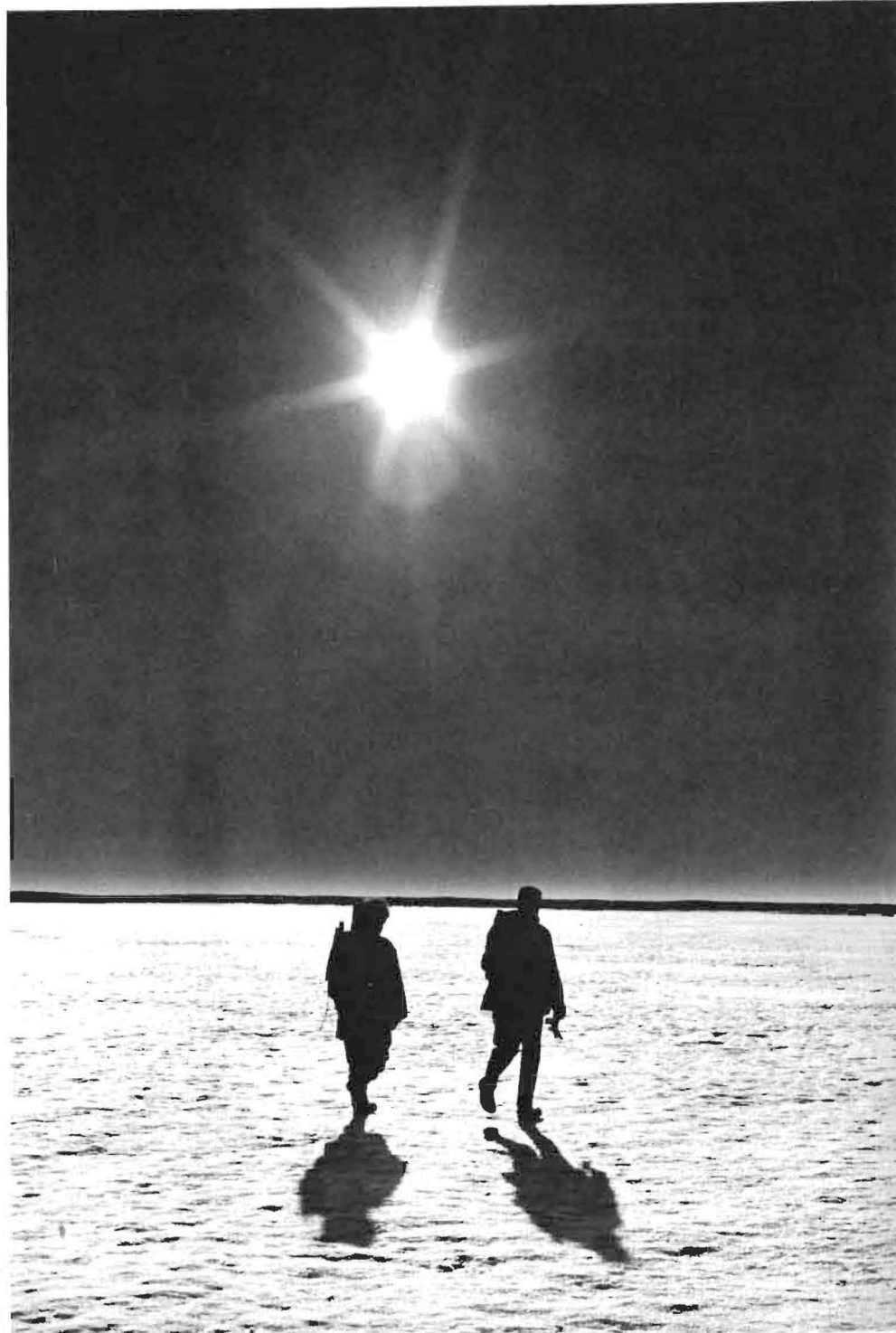
Abstract

This report describes the body growth, seasonal energy (fat) reserves, and productivity of the Kaminuriak caribou, a population of approximately 63 000 individuals of the barren-ground race (*Rangifer tarandus groenlandicus*) which inhabits northern Manitoba and Saskatchewan and an adjacent portion of the Northwest Territories. During the 28-month period between April 1966 and July 1968, 545 females and 398 males were shot and examined by biologists. Each carcass was weighed and measured, the quantity of stored fat was measured at four sites, and female reproductive organs were examined to determine current and past productivity.

Increases in body size and weight were restricted to a summer growth period lasting from June to October or November. Weight of calves increased approximately 800% during the first summer; at 5 months the average body weight of females and males was 42 and 47 kg respectively. Body weight increased up to $4\frac{1}{2}$ years in females and $6\frac{1}{2}$ years in males, although after $3\frac{1}{2}$ and $4\frac{1}{2}$ years respectively the amount added each year was not statistically significant. Mature caribou were heaviest in autumn when females (3 years and older) averaged 90 kg and males (4 years and older) averaged 147 kg. The heaviest individual female and male weighed 113 and 172 kg respectively. Adult females lost 11% of their mean autumn weight by late winter, and did not begin regaining weight until midsummer. Adult males lost about 30% of their maximum weight during the rut in October and began to regain weight in June. Other body measurements, such as heart girth, shoulder height, and total length, also fluctuated with season during and after the completion of growth. Skeletal maturation varied from the metatarsus, which attained adult size at $2\frac{1}{2}$ years in females and at $3\frac{1}{2}$ years in males, to the mandible, which grew until approximately $5\frac{1}{2}$ years in females and 6 years in males.

The size of fat deposits fluctuated markedly with season during and after the completion of body growth. Both sexes had maximum reserves in September. Males 4 years old and older mobilized fat only during the rut in October, when subcutaneous and visceral deposits were rapidly depleted. They recovered some lost fat in winter and the rest in the following summer. Younger males began mobilizing fat at the rut and continued mobilizing it for most of the winter; recovery did not begin until April. Pregnant females maintained high fat reserves in autumn, but experienced a slow and extensive decline during the winter, reaching their annual nadir in June and July during parturition and lactation. During the seasonal fluctuation of storage fat in the average adult caribou, the back fat deposit was 100% mobilized, the kidney and abdominal deposits were depleted by about 50 and 70% respectively, and the fat content of femur marrow was reduced by about 20%. A higher proportion of females than males mobilized marrow fat and in many females the amount of fat remaining fell to less than 50% (by weight) of the marrow tissue. The full recovery by both sexes of all fat deposits in summer appeared to be of critical importance to reproduction, growth, and winter survival.

Over half of a theoretical cohort first ovulated at $1\frac{1}{2}$ years of age, the earliest age at which ovulation occurred. After reaching $3\frac{1}{2}$ years of age, almost all (96%) females ovulated annually. An average of 2.9 ova was produced per ovulating female during the rut, and 11% of those females produced between five and seven ova each. The rise in the incidence of conception with increasing age approximately paralleled that of ovulation, but followed one year later; 2% conceived at $1\frac{1}{2}$, 48% at $2\frac{1}{2}$, and 90% at $3\frac{1}{2}$ years and older. The size and fatness of a female affected the age of first conception but not of first ovulation. Failure to conceive after ovulation was the major cause of reproductive failure in mature cows; *in utero* mortality was negligible. Ovarian scars from past pregnancies indicated that the average cow bore a calf 4 out of every 5 years after her first pregnancy, and that conception occurred the year following a missed pregnancy. In a sample of 40 cows 4 years old or older none was completely barren and only one had lagged more than two pregnancies behind the average for her age group. In autumn, adult cows that did not become pregnant had lower fat reserves than those that did. During the ensuing idle year they attained larger fat reserves than breeding cows and resumed breeding the following autumn. These results suggest a cycle of gradual exhaustion of body condition during successive pregnancies, followed by a year's infertility and recuperation, and then renewed breeding. In addition, cows that lost their calves at or shortly after birth may have recuperated (because lactation was ended prematurely) only to the extent that they remained fertile but were incapable of producing calves with sufficient viability for survival.

Kaminuriak caribou were typical of most northern ungulates, having periodic growth, sharply fluctuating energy reserves, gradual attainment of puberty, and high adult productivity. However, in relation to other mainland caribou populations, growth was slow, mature size modest, and puberty late. During this study snow depths were above normal and females used most of their energy reserves during late gestation and lactation. The poor physical condition of some cows may have contributed to the deaths of their calves at or shortly after birth. Large differences in cohort survival, possibly stemming from the amount of food available to pregnant females on the winter range, will likely cause a continuous fluctuation in the size of the Kaminuriak population.

Résumé

Le présent rapport traite de la croissance, des réserves saisonnières d'énergie (lipides) et de la productivité des caribous de Kaminuriak, population d'environ 63 000 têtes de la race des toundras (*Rangifer tarandus groenlandicus*) qui occupent le nord du Manitoba et de la Saskatchewan

de même qu'une portion voisine des Territoires du Nord-Ouest. Entre avril 1966 et juillet 1968, les biologistes ont tué, puis examiné 545 femelles et 398 mâles. On a mesuré et pesé chaque dépouille, déterminé les réserves de lipides en quatre endroits et observé les organes de reproduction des femelles afin d'en évaluer la fécondité tant lors du décès qu'antérieurement.

La taille et le poids des animaux n'augmentaient qu'au cours de la période de croissance estivale, de juin à octobre ou novembre. Le poids des faons augmentait de quelque 800% au cours de leur premier été; à cinq mois, les femelles et les mâles atteignaient un poids moyen de 42 et de 47 kg respectivement. Le poids des femelles augmentait durant les premières quatre années et demie et celui des mâles, durant les premières six années et demie, encore que les variations annuelles de poids eussent été dénuées de signification statistique après trois années et demie de la vie d'une femelle et quatre et demie de celle d'un mâle. À l'automne, les adultes atteignaient leur poids maximum: 90 kg en moyenne pour les femelles (de 3 ans et plus) et 147 kg pour les mâles (de 4 ans et plus); la plus lourde des femelles pesait 113 kg et le mâle le plus lourd, 172 kg. À la fin de l'hiver, les femelles adultes avaient perdu 11% de leur poids automnal moyen et ne recommençaient à prendre du poids qu'au milieu de l'été suivant. Les mâles adultes perdaient en octobre, lors du rut, environ 30% de leur poids maximum pour ne reprendre du poids qu'en juin. D'autres paramètres, comme le tour de poitrine, la hauteur à l'épaule et la longueur de l'animal fluctuaient avec les saisons tant pendant la croissance qu'après celle-ci. Le développement du squelette variait: le métatarse atteignait sa taille définitive chez les femelles et en trois ans et demie chez les mâles tandis que la mandibule croissait pendant environ cinq ans et demie chez la femelle et six ans chez le mâle.

Tant pendant qu'après la croissance, la quantité des dépôts graisseux présentait des variations saisonnières marquées. Chez les deux sexes, ces réserves atteignaient un maximum en septembre. Les mâles de quatre et plus n'utilisaient ces lipides qu'au rut lors duquel ils consommaient rapidement ces dépôts sous-cutanés et viscéraux. Ils en récupéraient une partie pendant l'hiver et le reste l'été suivant. Chez les mâles plus jeunes, cette mobilisation des dépôts graisseux débutait à la période de rut et se poursuivait tout au long de l'hiver, la reconstitution de ces dépôts ne recommençant qu'en avril. Les femelles en gestation gardaient de grosses réserves de gras durant l'automne, qu'elles épuisaient lentement au cours de l'hiver, les menant à leur nadir en juin et juillet, moment du vêlage et de l'allaitement. Au cours des variations saisonnières des réserves de lipides chez le caribou adulte moyen, on a observé que les dépôts graisseux de la partie postérieure de l'animal étaient utilisés à 100%, ceux des reins et de la région abdominale, à environ 50% et 70% respectivement et ceux de la moelle du fémur, à environ 20%. Un plus grand nombre de femelles que de mâles ont dégradé les lipides de la moelle et, chez beaucoup des femelles, les réserves résiduelles descendaient à moins de 50% (en poids) du tissu. La reconstitution intégrale de ces dépôts graisseux l'été chez les deux sexes semblait avoir une importance critique dans la reproduction, la croissance et la survie l'hiver.

Plus de la moitié d'une cohorte a eu une première ovulation à un an et demi, soit l'âge le plus bas où ce phénomène s'est produit. Après trois ans et demi, la majorité (96%) des femelles entrent en ovulation annuellement. Les femelles en rut produisaient en moyenne 2.9 ovules et 11% d'entre elles ont libéré entre cinq et sept ovules. L'accroissement de la conception en fonction de l'âge correspondait à peu près à celui de l'ovulation, mais à un an d'intervalle; 2% des femelles ont été fécondées à un an et demi, 48% à deux ans et demi et 90% à trois ans et demi et plus. La taille et les réserves de graisse d'une femelle avaient une influence sur l'âge de la première conception mais non sur celui de la première ovulation. Le défaut à concevoir après l'ovulation constituait la principale cause de l'absence de reproduction chez les femelles adultes; la mortalité intrautérine était négligeable. Les cicatrices ovariennes des gestations antérieures indiquaient que la femelle moyenne portait un faon quatre années sur cinq après sa première gestation et que la conception se produisait l'année qui suivait une année sans grossesse. Dans un échantillon de 40 femelles de 4 ans ou plus, aucune n'était complètement stérile et une seule avait besoin de vivre plus de deux grossesses pour se conformer à la moyenne de son groupe d'âge. À l'automne, celles des femelles adultes qui n'avaient pas été fécondées possédaient des réserves de lipides moins abondantes que n'en avaient les autres. Dans l'année inoccupée qui suivait pour elles, ces femelles accumulaient de plus vastes réserves de graisses que leurs congénères qui s'étaient reproduites dans l'intervalle, de sorte qu'à l'automne suivant, elles se reproduisaient de nouveau. Ceci semble indiquer un cycle d'épuisement graduel de l'organisme au cours des périodes successives de gestation, suivi d'une année de stérilité et de reconstitution, puis d'un retour à la fécondité. De plus, les femelles qui avaient perdu leur faon à la naissance ou peu après ont pu, en raison de la fin prématurée de l'allaitement, reconstituer leurs forces au point de demeurer fécondes, mais en étant alors incapables d'accoucher de faons aptes à survivre.

Le caribou de Kaminuriak possédait toutes les caractéristiques de la plupart des ongulés du nord, c'est-à-dire une croissance périodique, des réserves énergétiques très fluctuantes, une puberté atteinte graduellement et une productivité élevée chez l'adulte. Toutefois, en comparaison d'autres populations de caribous du continent, la croissance en était lente, la taille d'adulte petite et la puberté tardive. Au cours de l'étude, l'enneigement était plus élevé que la normale et les femelles avaient consommé la plus grande partie de leur réserve énergétique à la fin de la gestation et au cours de l'allaitement. L'état physique lamentable de certaines femelles peut avoir contribué à la mort de leur faon à la naissance ou peu après. D'importantes différences du taux de survie par cohorte, fonction peut-être de la quantité de nourriture à la disposition des femelles en gestation sur les territoires d'hiver, amèneront vraisemblablement des fluctuations à l'effectif des caribous de Kaminuriak.

Резюме

В настоящем отчете дается описание роста тела, сезонных запасов энергии (жира) и воспроизводительности карибу Каминурьяк, насчитывающего примерно 63 000 голов племени (Rangifer tarandus groenlandicus), проживающего на бесплодных землях северной Манитобы и Саскачевана, а также прилежащей части Северо-Западных территорий. В течение 28 месяцев от апреля 1966 г. до июля 1968 г. было повалено и исследовано биологами 545 коров и 398 быков. Корпус каждого животного был взвешен и измерен, причем количество жира измерялось в четырех местах, и маточные органы воспроизведения подвергались обследованию с целью выяснения настоящего и прошлого воспроизведения.

Увеличение размеров тела и увеличение веса ограничивались летним периодом роста, который продолжался с июня до октября или ноября. Вес телят увеличивался примерно на 800% в течение первого лета: в возрасте 5 месяцев средний вес корпуса коров и бычков составлял 42 и 47 кг соответственно. Увеличение веса корпуса продолжалось вплоть до возраста 4,5 лет у коров и 6,5 лет у быков, хотя после 3,5 и 4,5 лет соответственно годовая надбавка веса не являлась статистически значимой. Взрослые карибу достигали наибольшего веса осенью, когда коровы старше 3 лет весили в среднем 90 кг, а быки возрастом старше 4 лет - 147 кг в среднем. Наиболее крупные корова и бык весили 113 и 172 кг соответственно. Взрослые коровы теряли 11% своего среднего осеннего веса к концу зимы и не набирали вес вплоть до середины лета. Взрослые быки теряли около 30% своего максимального веса во время октябрьского полового возбуждения и начинали набирать вес в июне. Прочие размеры тела, например обхват в зоне сердца, высота к лопатке и общая длина также изменялись посезонно, как во время, так и после завершения роста. Скелетное возмужание менялось от метатарсуса, достигающего полный рост в 2,5 года у коров и в 3,5 года у быков, до мандибля, который рос примерно до возраста в 5,5 лет у коров, и 6 лет у быков.

Размер жировых отложений изменялся заметно с сезоном до и после завершения роста тела. Максимальный резерв наблюдался у обоих полов в сентябре. Быки возрастом в 4 года и старше начинали расходовать жировые отложения лишь в течение периода полового возбуждения в октябре, когда подкожные и внутренние жировые отложения сильно истощались. Быки восполняли некоторое количество потерянного жира зимой и в течение остатка следующего лета. Молодые бычки начинали расходовать жир в течение периода полового возбуждения и продолжали его расходовать в течение большей части зимы; восстановление не начиналось раньше апреля. Стельные коровы поддерживали высокий запас жира осенью, но этот запас медленно, но неустанно уменьшался в течение зимы, достигая годичного минимума в июне и июле во время мета и лактации. В течение сезонных изменений запасов жира среднего взрослого карибу его запасы жира на хребте расходовались полностью, отложения почечного и брюшного жира уменьшались примерно на 50% и 70% соответственно, в то время как содержание жира в костном мозге уменьшалось примерно на 20%. Расход жира костного мозга наблюдался более усугубленным у коров, чем у быков, и у многих остаточное содержание жира уменьшилось до значения меньше чем 50% (по весу) от костной ткани. Полное восстановление всех жировых отложений у обоих полов в течение лета, кажется, имеет принципиальное значе-

Figure 1
Range of the Kaminuriak population of barren-
ground caribou with locations where specimens
were collected in 1966, 1967, and 1968. Dates of
each collection and the number of males and
females in each age class are shown in Tables 1
and 2

Introduction

ние для воспроизведения, роста и спо-
собности выживания зимой.

Более половины состава теорети-
ческого стада впервые подвергалось
овуляции в возрасте 1,5 года, что явля-
лось также наиболее ранним возрастом
появления овуляции вообще. После до-
стижения возраста 3,5 лет почти все
коровы (96%) овулировали ежегодно.
В среднем, на овулирующую корову
было произведено 2,9 яйца во время
полового возбуждения, причем 11%
этих коров производили от пяти до се-
ми яиц каждая. Увеличение случаев
оплодотворения с увеличением возра-
ста в общем соответствует увеличению
овуляции, но следует годом позже; 2%
были оплодотворены в возрасте 1,5 го-
да, 48% - в 2,5 года и 90% - в воз-
расте 3,5 лет и больше. Размер и
количество жира коровы оказали влия-
ние на возраст при первом оплодотво-
рении, но не первой овуляции. Отсут-
ствие оплодотворения после овуляции
явилось самой крупной причиной сни-
жения воспроизведения у взрослых ко-
ров; потеря плода не является значи-
мым фактором. Яичниковые шрамы от
прошлых беременностей свидетельст-
вовали о том, что в среднем корова те-
лилась 4 раза в течение каждых 5 лет
после первой беременности и что опло-
дотворение происходило через год по-
сле несовершившейся беременности. В
числе 40 исследуемых коров возрастом
в 4 года и старше не оказалось ни од-
ной полностью яловой, и лишь одна
отстала на две беременности от сред-
него значения в своей возрастной груп-
пе. Осенью взрослые коровы, которые
не забеременели, обладали меньшим
жировым запасом по сравнению с те-
ми, которые забеременели. В течение
следующего бесплодного лета они при-
обрели больший запас жира, чем кор-
мящие коровы, и были оплодотворены
следующей осенью. Эти результаты
приводят к заключению, что существу-

ет цикл постепенного исчерпывания
телесного состояния в течение повтор-
ных беременностей, сменяющийся го-
дом бесплодности и восстановления с
последующим возобновлением бере-
менности. Далее, коровы, потерявшие
своих телят при или вскоре после ро-
дов, смогли восстановить (вследствие
досрочного прекращения периода лак-
тации) силы лишь до предела, позво-
ляющего им оставаться плодовитыми,
но не позволяющего им произвести те-
лят с достаточной способностью к вы-
живанию.

Карибу Каминурьяк являлись ти-
пичными представителями северных
копытных четвероногих, обладающих
периодическим ростом, сильно колеб-
лющимися запасами энергии, посте-
пенным половым созреванием и высо-
ким воспроизведением в зрелом возра-
сте. Но по сравнению с прочим конти-
нентальным населением карибу их ско-
рость роста является более медленной,
размер после возмужания — менее
крупным и половое созревание — бо-
лее поздним. Глубина снега во время
проведения настоящего исследования
была выше нормальной, и коровы ис-
пользовали большую часть запасов сво-
ей энергии во время поздней беремен-
ности и лактационного периода. Пло-
хое физическое состояние некоторых
коров могло способствовать гибели их
телят при или вскоре после их рожде-
ния. Большие колебания в процессе
выживания стад, вызванные, возможно,
количеством доступного стельным ко-
ровам корма на зимних пастбищах,
вызовут, очевидно, и впредь изменения
в количестве голов стад карибу Ками-
нурьяк.

Although the Kaminuriak population
had been included in aerial surveys made
since formal investigations of barren-
ground caribou began in the late 1940's, the
physical growth, condition, and produc-
tivity of the population were unknown
when the present study began. CWS biol-
ogists and others had investigated these
subjects in the neighbouring Beverly pop-
ulation, located 150 to 300 km west of the
Kaminuriak population. McEwan (1963)
described the annual cycle of testicular
activity, age-specific pregnancy rates, and
aspects of ovarian morphology and phys-
iology. The chronology of calving and, to a
lesser extent, breeding was described by a
series of observers (summarized by Kelsall
1968). Kelsall (1968) measured term and
near-term fetuses. A measure of environ-
mental resistance was obtained by com-
paring measurements of wild caribou in
various sex and age groups with measure-
ments of captive caribou of the same pop-
ulation raised on a high nutritional plane
(McEwan and Wood 1966, McEwan 1968).
An annual rhythm in the acquisition and
mobilization of fat was observed in Beverly
caribou (McEwan and Wood 1966, Mc-
Ewan 1968, Kelsall 1968), although indi-
vidual fat deposits were not measured.
Hanbury (1904:9), in July 1899, made the
only recorded observation of malnourished
caribou found in the region now occupied
by the Kaminuriak population: ". . . at this
time their flesh was hardly fit to eat, being
discoloured all through. The marrow, usu-
ally a luxury, was now of the consistency
of blood and water, owing to the 'fly time',
the wretched beasts being kept on the run
day and night."

I sought information on growth,
fertility, and energy balance for this part
of the research on the Kaminuriak pop-
ulation. My specific objectives were:
1. To describe the growth and development
of body size and the effect of seasonal
changes in nutritional environment and
reproductive activity on body size;
2. To determine changes in fat reserves
associated with season, sex and age;

Figure 1

•••••• Tree line
▨ Kaminuriak
Population
1966–68

Miles 0   50   100

Kilometres 0   50   100
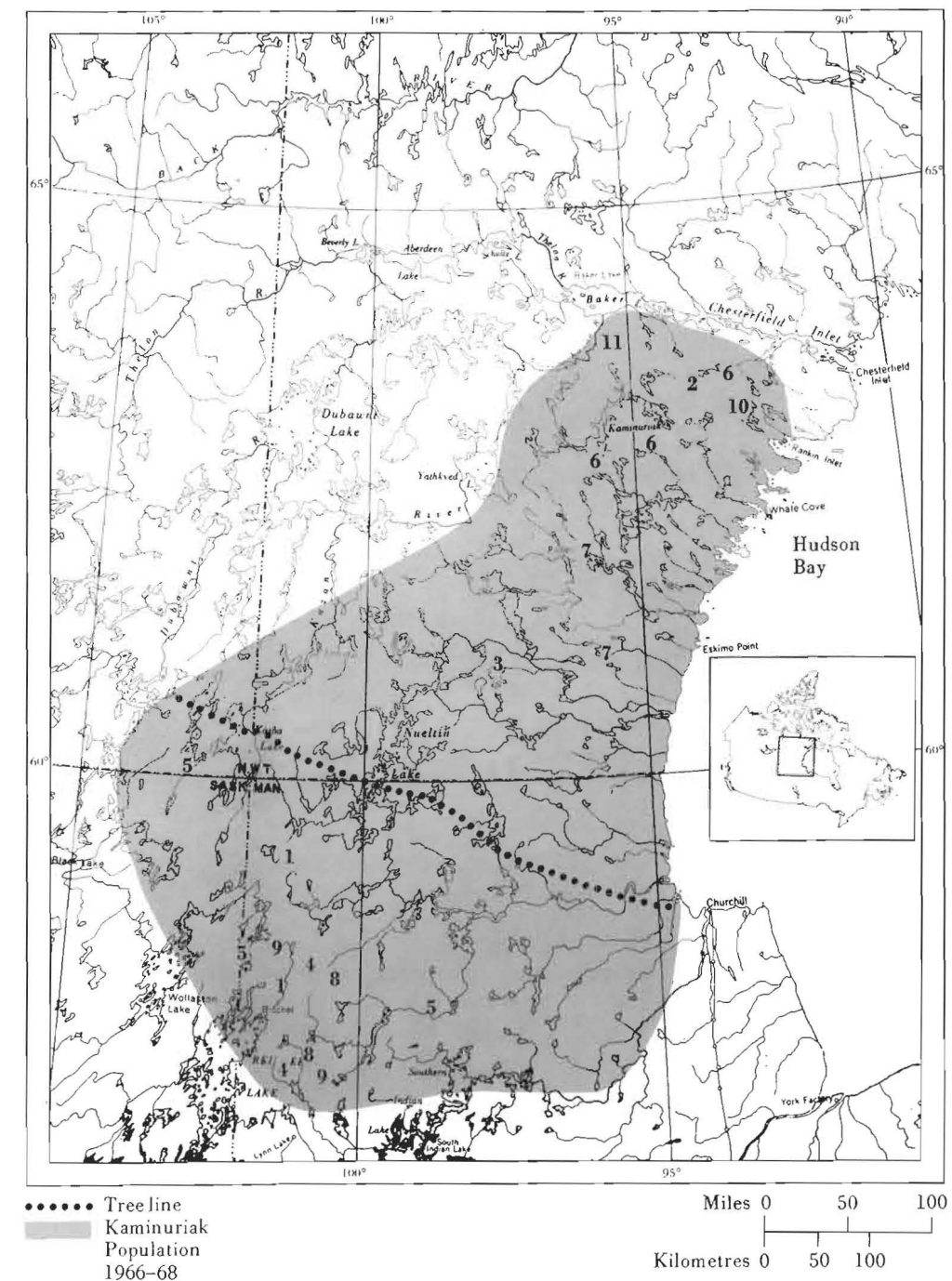
3. To determine age-specific rates of ovulation, conception, and births; and
4. To determine the relationship between breeding performance and the size of energy reserves in females.

Caribou were shot and autopsied to collect the above information. The butchered carcasses were then delivered to native settlements.

According to a review by Parker (1972), surveys of the Kaminuriak population have estimated its size at 120 000 in 1950, 149 000 in 1955, and 40 000 in 1958 (the last not based on a systematic survey). Parker (1972:23) estimated that the population numbered 63 000 before calving in 1968 and concluded that, "Because the present range and distribution of the Kaminuriak Population resemble those described by the early historical records, it is reasonable that the size of the present population is also similiar." Before 1966, the approximate geographic distribution of the Kaminuriak population had been outlined by tagging (Miller and Robertson 1967) and by aerial surveys (Banfield 1954, Loughrey 1955, Malfair 1963). The distribution of the population from 1966 to 1968 was described by Parker (1972). The boundaries of its range, which comprises approximately 282 000 km² in northern Manitoba, northeastern Saskatchewan, and the District of Keewatin, Northwest Territories, are shown in Figure 1. The population is migratory and occupies only part of the range at any one time. From November to May most of the population inhabits the lichen woodlands and lakes of the taiga in Manitoba and Saskatchewan, although a variable but usually small portion may winter on tundra near the Hudson Bay coast. In May the females migrate north to the calving ground near Kaminuriak Lake at the northern extremity of the population's range. Calving takes place in June; during the study period most births occurred between June 10 and 15 (Parker 1972). Males and most non-breeding females migrate north later and at a slower pace than breeding females, and join them

in early July. The mixed herds make several rapid but shorter movements until early fall (Parker 1972, Miller et al. 1974). The rut begins about October 19 and may last until late November (Dauphiné and Mc-Clure 1974), when most of the population has completed the migration south to the winter range.

Detailed descriptions of the physiography and vegetation of the region occupied by the Kaminuriak population are available in publications by Wright (1955), Rowe (1959), Ritchie (1962), and Miller (1976), and only a brief summary will be presented here. Most of the study area is underlain by Pre-Cambrian Shield, commonly exposed at the surface in central Keewatin and covered by a thick mantle of till elsewhere. Most of the region is a flat or gently rolling plain, although there are extensive boulder fields and rough, low hills in northwestern Manitoba and central Keewatin. Permafrost is continuous in the soils of the tundra region described below and discontinuous in the taiga. Innumerable streams and lakes comprise approximately one-quarter of the land surface. Moraines, eskers, drumlins, and other forms of glacial topography are prominent features of the landscape.

Four major vegetation zones exist in the study area; closed coniferous forest, open coniferous forest, forest-tundra, and tundra.

Black spruce (*Picea mariana*) is the major component of the closed coniferous zone, where it occurs in open muskegs on wet sites and forms closed stands on dryer uplands. The latter sites are susceptible to fire, after which birch (*Betula papyrifera*), poplar (*Populus* spp.), white spruce (*P. glauca*), and fir (*Abies balsamea*) form temporary seral associations with black spruce. Jack pine (*Pinus banksiana*) grows on outcrop ridges and sandy plains.

The open coniferous forest is similar to the above except that the dominant *P. mariana* grows in open stands and there is a conspicuous ground cover of lichens (chiefly *Cladonia* spp.), ericaceous shrubs, low willows (*Salix* spp.) and dwarf birch (*B. glandulosa*). Extensive stands of jack pine occur on sites susceptible to recurrent fire.

In the forest-tundra vegetation zone only slopes and bottomlands are forested. Where it occurs on wet peat, the forest forms a black spruce – moss – muskeg

community. It forms a closed stand of white spruce on well-drained alluvium. Beach ridges, eskers, rock outcrops and the summits of hills are occupied by tundra plants, which form heath communities on dry sites, and sedge (*Carex* spp.) bogs in wet areas.

The tree-line lies diagonally across the centre of the study area in a SE–NW orientation, beginning at the Hudson Bay coastline near the Tha-anne River, and intersecting Padlei, North Henik Lake, Watterson Lake, Hicks Lake, and the southern tip of Dubawnt Lake (Rowe 1959). North of the tree-line lies tundra composed of several vegetational communities. A dwarf-shrub heath community occupies extensive areas in central Keewatin. Characteristic of lowlands, it is dominated by birch, Labrador tea (*Ledum groenlandicum*), purple Lapland rhododendron (*Rhododendron lapponicum*), bearberry (*Arctostaphylos* spp.), white heather (*Phyllodoce caerulea*), bilberry (*Vaccinium vitis-idaea*), and alpine cranberry (*Viburnum oxycoccus*) with ubiquitous clumps of sedges and grasses (*Gramineae*). On dryer and better drained sites, the dwarf-shrub heath community merges into the lichen and moss heath community. There, reindeer lichens (*Cladonia* spp.) and mosses form a dense carpet, and ground birch, rhododendron, and willow are the only prominent woody species. Alluvial flats are covered by extensive grassland communities which, with time, are invaded by the heath communities. A fourth community, the willow and alder (*Alnus* spp.) thicket, is confined to the margins of watercourses.

The climate of the tundra is characterized by strong winds, especially in fall and winter. The highest winds have been recorded along the flat, treeless Hudson Bay coast. Tundra summers are cool, with mean July and August temperatures of 10°C or less. During these months, afternoon temperatures average less than 16°C and night temperatures average below 7°C. Winter temperatures are extremely low, occasionally dropping below −50°C. The

mean temperature is below 0°C for each month from October to May, and is −32°C in January, the coldest month. The annual temperature range is among the widest on the continent. The growing season is restricted, with an average frost-free period of only 67 days.

Total annual precipitation is about 41 cm (40% snow) in the forested area, and about 25 cm (60% snow) in the northern barrens. About three-quarters of the precipitation falls between May and October. Average annual snowfall ranges from 127 to 152 cm (from north to south) along the coast and approximately 30 cm less in the interior. Blizzards are common, and on the open tundra the strong winds cause drifting on at least 100 days of the winter period. Snow covers the ground for about 8 months, and scattered patches may last much longer (Kendrew and Currie 1955:97–119).

Study area

Figure 2
Areas of the carcass where measurements of body size and fat reserves were taken

1. Collection of specimens

Canadian Wildlife Service field parties collected caribou over a 28-month period between April 1966 and July 1968. The timing of collections was designed to sample the full range of the caribou's annual reproductive and nutritional cycle: we chose April for the effects of winter temperatures and restricted availability of forage; June for the effects of spring migration, difficult foraging conditions, and calving; September as a period when forage was readily available and highly nutritious and when stress from weather, insects, migration, or reproduction was low; and November for the effects of rutting stress. A supplementary collection was made in July 1968 in order to determine the effect of lactation and insect harassment and to obtain adult males which had been inadequately sampled in June.

Our collection schedule also provided samples of females at important stages of the annual reproductive cycle. In September, about one month before the rut, we obtained females in proestrus. Pregnant females were collected in November–December, April, and June, and lactating females in June and July. The rate and pattern of body growth was approximated by measuring young calves and older animals at the beginning and end of the summer growth period.

Field parties shot the caribou specimens and moved them to a central point for processing. The specimens were randomly selected in different locations to obtain a representative sample. External measurements were recorded, and each specimen was dissected for information on its diet, reproduction, organ size, pathology, parasites, and fat reserves. The carcasses were butchered by native assistants and delivered to the nearest native settlements for distribution. F. L. Miller (1974) subsequently determined the age to the nearest year of each specimen by histological examination of the annulations in the dental cementum of its mandibular teeth. He assumed all births were in June.

2. Measurement of growth

2.1. Whole body weight

Each carcass was weighed whole to the nearest pound by suspending it from a spring scale with a capacity of 400 lbs. Weights were later converted to kilograms.

2.2. External body measurements

A series of body measurements (see Fig. 2) was taken with a flexible tape as the specimen lay on its left side with legs and neck extended. Unless otherwise specified, body measurements were made to the nearest 5 mm. Total length was measured along the dorso-medial line from the tip of the nose to the end of the last tail vertebra. Heart (chest) girth was measured around the carcass immediately posterior to the fore limb and the posterior edge of the scapula. Shoulder height was measured along the radial surface of the right foreleg and flank from the base of the radial dew hoof (proximal sesamoid) to the dorsal tip of the spinous process of the second or third thoracic vertebra.

2.3. Internal body measurements

Metatarsus length was measured to the nearest 1 mm along the plantar surface of the exposed bone between the distal tip of the Tuber calcis and the distal end of the large metatarsus. The mandibles were measured to the nearest 0.1 mm from the posterior rim of each ramus to the most anterior portion of the alveolar bone below the first incisor, and the two measurements averaged.

3. Measurements of fat deposits

3.1. Subcutaneous fat

After each caribou had been skinned, the thickness of the layer of subcutaneous or "back" fat on its rump was measured by Riney's (1955) method. With a vernier caliper we measured the greatest thickness of the fat, to the nearest 1 mm, along a cut made anteriorly from the base of the tail at an angle of 45° from the spine (Fig. 3). During skinning, care was taken to insure that no fat was removed with the hide.
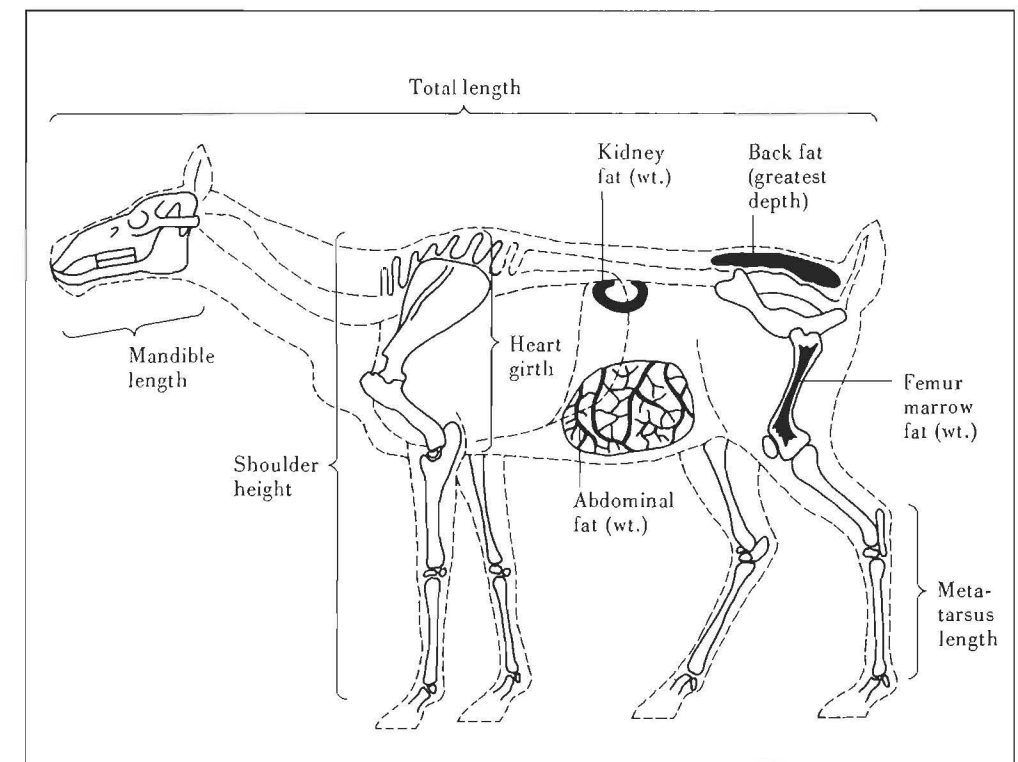
3.2. Perirenal fat

The kidneys and perirenal fat were removed. Apart from the fact that we removed and weighed both kidneys and averaged the two values, the removal followed the method described by Riney (1955). A cut was made through the fat at the ends of each kidney, perpendicular to the spine (Fig. 4). The kidneys with adhering fat were separated from the dorsal wall of the abdominal cavity and parted from each other at the dorsal line. Each kidney (with *capsula adiposa*) was weighed to the nearest 0.1 g with and without fat. The weight of the fat was obtained by subtraction.

Due to a large seasonal fluctuation in the weight of kidneys from the caribou collected (Dauphiné 1975), I did not use the "kidney fat index" — (kidney fat weight/kidney weight) x 100 — proposed by Riney (1955).

3.3. Omental and mesenteric fat

The abdominal cavity was opened along the ventral line. All the fat attached to the folds of the mesentery and the omentum was stripped off, pressed into a ball and weighed to the nearest gram (Fig. 5).

3.4. Fat content of femoral marrow (by wt.)

All marrow was removed from the medulla of the right femur and preserved in 10% formalin. Later, the marrow was drained of formalin and homogenized. With an alcohol–ether solvent all lipids were extracted from a 2-g sample of homogenized marrow. The solvent was evaporated and the remaining fat was weighed and expressed as a percentage of the 2-g marrow sample.

3.5. Adjusted body weight

In order to avoid variations in weight caused by pregnancy, for some analyses of

Figure 3
Measuring the depth of subcutaneous back fat on a barren-ground caribou

Figure 4
Ventral view of kidneys and perirenal fat in barren-ground caribou. A cut was made through the fat at each end of the kidneys, and the kidneys with adhering fat were removed for weighing

Figure 5
Stripping abdominal fat off the mesentery and omentum before weighing

condition the body weight of each female was adjusted by subtracting the weight of the uterus and its contents.

4. Examination of female reproductive organs

4.1. Uteri, embryos, and fetuses

The uterus was removed from each female, and after the ovaries were separated at the junction of the ovarian hilus and ligament, it was fixed in 10% formalin, and stored in a mixture of nine parts 70% ethanol and one part glycerine until examined in the laboratory. The uterine body and horns were slit open and searched macroscopically. According to its contents, size, and degree of muscularization, each uterus was graded as nulliparous (never pregnant), parous (pregnant in past), post-partum (enlarged from recent pregnancy), or gravid (containing fetus). Gravid uteri obtained late in the gestation period were weighed fresh and discarded after the fetus was removed.

The crown-rump lengths of embryos collected in November and December were measured as described by Cheatum and Morton (1946) to the nearest 0.1 mm. The length and morphological development of the embryos were subsequently used to estimate their ages and dates of conception (Dauphiné and McClure 1974). Fetuses obtained in April and June were sexed, drained, and weighed still wet on a spring scale to the nearest 0.5 lb (later converted to kg). Each fetus's total length was measured from the tip of the nose to the distal vertebra of the tail along the dorsal line. The length of its right hind foot was measured from the distal end of the Tuber calcis to the distal edge of the hoof.

4.2. Ovaries

Ovaries were fixed in 10% formalin in the field. In the laboratory they were placed in a mixture of nine parts 70% ethanol and one part glycerine before examination and permanent storage. Ovaries collected in April, June, July, and September were sliced saggitally at approximately

Figure 3

Figure 4

1-mm intervals with a scalpel. Samples of macroscopically visible corpora lutea and other structures requiring closer examination were separated, sectioned, stained with hematoxylin, phloxine, and orange G (HPO), and identified histologically as described below. Ovaries obtained in November and December were embedded in paraffin, serially sectioned at 10μ and stained with Masson's Trichrome (App. 1). similar to the technique employed by Gibson (1957) and Thomas (1970). Masson's Trichrome and HPO both differentiated cytoplasm, nuclei and connective tissue, with the former giving better results. The identification of different types of corpora lutea was based on knowledge of the cow's reproductive status (pregnant, lactating, etc.) and on morphological and histological descriptions from caribou (McEwan 1963: 40–51), and deer (*Odocoileus* spp.) (Gibson 1957:21–41, Thomas 1970:75–112). My criteria are given below. Measurements are from my unpublished data.

Corpus luteum of pregnancy
Functional: prominent, occupying most of ovary (average maximum diameter 11.5 mm, SE (standard error) = 0.2, range = 8.7–14.1 mm, n = 45); lutein cells "large" (average diameter of 40μ reported by McEwan 1963) with homogeneous cytoplasm and large transparent nuclei; intercellular space negligible. Regressing: at 5 months post-partum, average maximum diameter 2.7 mm (0.1, 0.7–4.5 mm, 49); lutein cells disintegrating, lipid vacuoles in cytoplasm, nuclei opaque and pyknotic, capillaries with collapsed lumen and invading connective tissue prominent in luteal tissue. At 17 or more months post-partum, average maximum diameter 1.9 mm (0.05, 0.7–4.2 mm, 149); luteal tissue evacuated; occasional vacuolated cells with pigment granules; dense circular clusters of collapsed capillaries; complete infiltration by connective tissue trabeculae.

Figure 5

Corpus luteum of estrus (non-pregnancy)
Functional: size medium — no measurements available; luteal tissue as in functional corpus luteum of pregnancy but cells "small" (average diameter of $10–15\mu$ reported by McEwan 1963); capillaries confined to periphery of corpus, intercellular space considerable. Regressing: size medium to very small, average maximum diameter 1.3 mm (0.1, 0.4–6.7 mm, 137); degeneration of luteal tissue as in corpus luteum of pregnancy (above); capillaries rare and confined to periphery of corpus; connective tissue transparent, sparse.

The average diameter across the largest exposed section of each corpus luteum was measured to the nearest 0.1 mm in all ovaries. Graafian follicles were measured and tallied in three diameter classes: $\geqslant 2$ < 5, $\geqslant 5 < 8$, and $\geqslant 8$ mm.

4.3 Udder

The udder was examined *in situ* and classified as dry, lactating colostrum, or lactating milk.

5. Statistical methods

A three-factor analysis of variance determined the variation in body size and fat deposits contributed by the age of specimens and the month and year in which they were collected. Snedecor's (1956:268) method of treating unequal sample sizes was used. Differences between collection years were not consistently significant ($P < 0.05$) so measurements obtained in different years were pooled. Differences between years are discussed in the Results. Measurements of each variable for the 357 females $2\frac{1}{3}$ years old and older were combined in one sample, and those of the 122 males $4\frac{1}{3}$ years old and older in another by co-variate adjustments for the effect of age (Snedecor 1956:394) in order to provide larger seasonal samples for the testing of seasonal differences. This age combination was possible because these age groups shared the same seasonal pattern in all variables. In younger males and females the trends of seasonally changeable vari-

Results and discussion

ables differed by age. Tests of seasonal differences were therefore conducted separately by age class. In all tests 0.05 was the probability level at which the null hypothesis was rejected. Accordingly, level of probability is given only where it was 0.01 or less.

Further statistical procedures are described in the sections where they are used.

1. Description of samples

The field parties obtained 398 male and 545 female caribou from the Kaminuriak population in 11 collections taken during the 28-month period between April 1966 and July 1968.

Female and male specimens were divided by age class and date of collection in Tables 1 and 2 respectively. Table 3 gives a summary of the total numbers of males and females obtained in the various seasons of 1966–68. The geographic location of each collection is shown in Figure 1, with reference numbers assigned chronologically in Tables 1 and 2. Approximately 100 specimens were taken in each collection except the last (July 1968) and in September 1966 when logistical problems prevented more than 28 animals being collected. Few adult males were obtained in June because they were far from the calving grounds to which priority was given. Because we shot caribou from many different herds and at many widely-separated locations, I assume that the specimens collected represent the average condition of growth, nutrition and productivity prevailing in the Kaminuriak population between 1966 and 1968.

2. Growth

Evaluation of growth and mature development of Kaminuriak caribou was based on six body measurements taken from 398 males ranging from birth to 11 years of age and from 545 females ranging from birth to 16 years of age. General physical development was represented by body weight, heart girth, shoulder height, and total length. Skeletal growth was represented by metatarsus and mandible lengths. To obtain a dynamic representation of growth, specimens of each sex were grouped by age to form an array of mean measurements. Growth curves formed by the progression of means over age were plotted for metatarsus length, mandible length, shoulder height, total body length, heart girth, and body weight (Figs. 6–11). Full statistics on the means of each variable (sample size,

s, 95% confidence limits, and range) are filed with a copy of this manuscript in report libraries[1] of the Canadian Wildlife Service and are available on loan.

Analysis of variance (Tables 4 and 5) indicated no significant difference between specimens on the basis of genetic stock or nutritional environment ("Other" sources of variation in Tables 4 and 5). However, one or more significant between-year differences did occur for all growth variables except metatarsus length (see Tables 4 and 5). Differences between years were inconsistent in that they did not occur between all seasons for any variable or in any one season for all variables. They were therefore attributed to sampling error and not to real differences between samples collected in different years. When pooled, specimens of the same age represented the "average" growth attained by three successive cohorts.

2.1. Rates and pattern of growth

The plotted means of each variable formed the upper portion of a sigmoid curve characteristic of growth and maturity (Figs. 6–11). Each variable's rate of growth was influenced by season so that growth was not distributed uniformly along the curve. Inspection showed that almost all growth occurred in summer and early autumn, i.e. between April–June and November–December sampling periods. In males 3 years old and older, the growing season terminated at the rut in mid-October. Periods of growth, stability, or decrease in various body measurements were quantified by dividing the year into two 6-month periods (June–November and December–May) and calculating the average change per month during each period (Table 6). Each variable exhibited growth between June and November–December samples and relative stability between November–December

[1]Addresses: 2721 Highway 31, Ottawa, Ont. K1A 0H3; 1110-10025 Jasper Avenue, Edmonton, Alta. T5H 3A9; and 351 St. Joseph Boulevard, Hull, Que. K1A 0H3.

Table 1
The numbers of female caribou collected from the Kaminuriak population in 1966, 1967, and 1968, grouped by date of collection and age class

Collection reference number (Fig. 1)	Dates of collection	<1	≥1 <2	≥2 <3	≥3 <4	≥4 <5	≥5 <6	≥6 <7	≥7 <8	≥8 <9	≥9 <10	≥10 <11	≥11 <12	≥12 <13	≥13 <14	≥14 <15	≥15 <16	≥16	Total
1	1966 April 7–22	6	6	5	0	2	9	9	2	0	1	0	1	0	2				43
2	June 5–July 5	8	6	10	12	4	6	12	3	6	0	0							67
3	Sept. 17–24	0	1	0	1	0	2	3	0	1	0	0							8
4	Nov. 21–Dec. 1	5	1	11	8	4	5	4	7	7	2	1							55
Total		19	14	26	21	10	22	28	12	14	3	1	1	1	2				173
5	1967 April 10–28	7	9	9	8	0	7	5	3	3	0	2	1	1	1	1			57
6	May 25–June 13	7	5	12	6	4	2	1	18	8	4	3	1		1			1	73
7	Sept. 15–21	6	2	8	2	1	0	4	6	2	4	2						1	38
8	Nov. 28–Dec. 12	8	9	11	8	3	0	3	4	5	3	1	1						56
Total		28	25	40	24	8	9	13	31	18	11	8	3	1	2	1		2	224
9	1968 April 12–May 2	7	6	5	8	2	1	6	2	5	2								44
10	June 12–16	16	2	3	9	10	5	2	9	2	14	5	3						80
11	July 14–17	4	3	2	2	4	2	0	0	2	1	1	2				1		24
Total		27	11	10	19	16	8	8	11	9	17	6	5				1		148
Total	1966–68	74	50	76	64	34	39	49	54	41	31	15	9	1	4	1	1	2	545

Table 2
The numbers of male caribou collected from the Kaminuriak population in 1966, 1967, and 1968, grouped by date of collection and age class

Collection reference number (Fig. 1)	Dates of collection	<1	≥1 <2	≥2 <3	≥3 <4	≥4 <5	≥5 <6	≥6 <7	≥7 <8	≥8 <9	≥9 <10	≥10 <11	≥11 <12	Total
1	1966 April 7–22	3	12	15	3	11	9	4	0	1	0	0	1	59
2	June 5–July 5	5	6	4	3	0	0	0	0	0				18
3	Sept. 17–24	1	1	2	6	2	1	2	3	0				18
4	Nov. 21–Dec. 1	6	6	9	20	4	1	0	0	0				46
Total		15	25	30	32	17	11	6	3	1			1	141
5	1967 April 10–28	7	7	14	7	2	4	5	0	0				46
6	May 25–June 13	6	9	3	1	2	1	2	0	1				25
7	Sept. 15–21	4	2	7	3	19	0	3	6	1	2			47
8	Nov. 28–Dec. 12	6	7	5	12	17	1	1	0	0				49
Total		23	25	29	23	40	6	11	6	2	2			167
9	1968 April 12–May 2	4	8	11	16	6	5	7	0	2				59
10	June 12–16	8	1	1	0	0	0	0	0	0				10
11	July 14–17	0	2	1	2	1	7	1	3	1	2		1	21
Total		12	11	13	18	7	12	8	3	3	2		1	90
Total	1966–68	50	61	72	73	64	29	25	12	6	4		2	398

Table 3
A seasonal summary of the numbers of male and female caribou in each age class collected from the Kaminuriak population in 1966, 1967, and 1968 (male/female)

Season of collection	<1	≥1 <2	≥2 <3	≥3 <4	≥4 <5	≥5 <6	≥6 <7	≥7 <8	≥8 <9	≥9 <10	≥10 <11	≥11 <12	≥12 <13	≥13 <14	≥14 <15	≥15 <16	≥16	Total
April	14/20	27/21	40/19	26/16	19/4	18/17	16/20	0/7	3/8	0/3	0/2	1/2	0/1	0/3	0/1			164/144
June	19/31	16/13	8/25	4/27	2/14	1/11	2/9	0/39	1/13	0/24	0/8	0/4		0/1			0/1	53/220
July	0/4	2/3	1/2	2/2	1/4	7/2	1/0	3/0	1/2	2/1	0/1	1/2				0/1		21/24
September	5/6	3/3	9/8	9/3	21/1	1/2	5/7	9/6	1/3	2/4	0/2					0/1		65/46
Nov.–Dec.	12/13	13/10	14/22	32/16	21/7	2/5	1/7	0/11	0/12	0/5	0/2	0/1						95/111
Total	50/74	61/50	72/76	73/64	64/34	29/39	25/49	12/54	6/41	4/31	0/15	2/9	0/1	0/4	0/1	0/1	0/2	398/545

Table 4
Analysis of variance in six measurements of body size from female caribou (27 months and older) of the Kaminuriak population

Source of variation	Metatarsus length (cm) F (d.f.)*		Mandible length (mm) F (d.f.)		Shoulder height (cm) F (d.f.)		Total length (cm) F (d.f.)		Heart girth (cm) F (d.f.)		Body weight (kg) F (d.f.)	
Collection	0.88	(7)	1.75	(10)	3.69	(10)‡	5.32	(10)‡	23.00	(10)‡	18.94	(10)‡
Season	1.00	(4)	1.37	(4)	1.57	(4)	2.94	(4)†	43.20	(4)‡	39.50	(4)‡
Sept. and Nov.–Dec. vs. others	0.02	(1)	0.03	(1)	1.73	(1)	4.10	(1)†	107.72	(1)‡	136.82	(1)‡
April vs. June and July	0.03	(1)	1.04	(1)	0.63	(1)	2.37	(1)	5.04	(1)†	0.11	(1)
June vs. July	0.53	(1)	0.46	(1)	2.14	(1)	0.49	(1)	0.96	(1)	1.23	(1)
Sept. vs. Nov.–Dec.	1.21	(1)	0.07	(1)	0.01	(1)	2.12	(1)	2.75	(1)	3.17	(1)
Year (within season)	0.72	(3)	2.00	(6)	5.10	(6)‡	6.91	(6)‡	9.65	(6)‡	5.19	(6)‡
Aprils	2.11	(1)	0.60	(2)	4.52	(2)†	0.91	(2)	18.55	(2)‡	7.36	(2)‡
Junes	0.06	(1)	1.08	(2)	7.20	(2)‡	11.22	(2)‡	9.25	(2)‡	1.04	(2)
Septembers			8.48	(1)‡	1.39	(1)	2.11	(1)	12.47	(1)‡		
November–Decembers	0.00	(1)	0.11	(1)	6.90	(1)‡	15.30	(1)‡	1.07	(1)	2.08	(1)
Age	2.42	(5)†	14.61	(5)‡	1.74	(5)	7.45	(5)‡	5.25	(5)‡	13.38	(5)‡
2 years vs. older	0.13	(1)	6.10	(1)†	0.43	(1)	0.86	(1)	0.29	(1)	13.41	(1)‡
3 years vs. older	0.28	(1)	31.02	(1)†	2.51	(1)	13.70	(1)‡	1.01	(1)	14.56	(1)‡
4–9 vs. 10+	0.03	(1)	3.89	(1)	0.05	(1)	0.39	(1)	5.31	(1)†	0.00	(1)
4–5 vs. 6–9	8.02	(1)‡	17.30	(1)†	3.67	(1)	8.87	(1)‡	5.94	(1)†	12.90	(1)‡
10–11 vs. 12+	0.98	(1)	0.37	(1)	0.46	(1)	4.36	(1)†	0.14	(1)	0.00	(1)
Age and season	0.93	(12)	1.00	(12)	1.35	(12)	1.39	(12)	1.17	(12)	0.47	(12)
Other	1.01	(40)	1.05	(58)	1.13	(59)	0.82	(60)	1.34	(60)	0.89	(60)
Within-group standard deviation	0.861		7.05		4.34		6.24		5.22		7.00	
Degrees of freedom for error	160		222		222		230		228		226	
No. of animals	225		308		309		318		316		314	
Overall mean	36.73		261.5		97.18		163.4		114.2		81.85	

* F, ratio of inter-seasonal variation to average within-sample variation;
d.f., degrees of freedom.
† P <0.05.
‡ P <0.01.

Table 5
Analysis of variance in six measurements of body size from male caribou (58 months and older) of the Kaminuriak population

Source of variation	Metatarsus length (cm) F (d.f.)*		Mandible length (mm) F (d.f.)		Shoulder height (cm) F (d.f.)		Total length (cm) F (d.f.)		Heart girth (cm) F (d.f.)		Body weight (kg) F (d.f.)	
Collection	1.14	(6)	1.23	(8)	7.89	(8)‡	4.66	(8)‡	10.61	(8)‡	52.90	(8)‡
Season	1.56	(4)	1.51	(4)	6.79	(4)‡	2.96	(4)†	9.49	(4)‡	101.70	(4)‡
September vs. others	5.22	(1)†	0.43	(1)	6.74	(1)†	11.45	(1)‡	98.40	(1)‡	163.97	(1)‡
April and Nov. vs. June and July	0.22	(1)	1.30	(1)	11.45	(1)‡	2.17	(1)	9.84	(1)‡	15.30	(1)‡
June vs. July	0.71	(1)	1.03	(1)	2.14	(1)	0.20	(1)	28.16	(1)‡	27.11	(1)‡
April vs. Nov.–Dec.	0.06	(1)	0.52	(1)	0.39	(1)	5.35	(1)†	0.06	(1)	0.03	(1)
Year (within season)	0.30	(2)	0.96	(4)	8.96	(4)‡	6.38	(4)‡	12.40	(4)‡	4.12	(4)‡
Aprils	0.09	(1)	0.20	(2)	12.40	(2)‡	11.81	(2)‡	22.08	(2)‡	6.85	(2)‡
Septembers			1.12	(1)	8.77	(1)‡	1.41	(1)	0.05	(1)	0.32	(1)
November–Decembers	0.51	(1)	2.33	(1)	1.86	(1)	0.22	(1)	2.95	(1)	2.51	(1)
Age	0.97	(2)	3.38	(2)†	3.14	(2)	5.59	(2)‡	0.89	(2)	6.70	(2)‡
5 years vs. older	0.50	(1)	4.34	(1)†	3.17	(1)	7.35	(1)‡	0.92	(1)	11.24	(1)‡
6 years vs. older	1.73	(1)	1.96	(1)	2.67	(1)	3.10	(1)	0.97	(1)	1.43	(1)
Age and season	2.13	(4)	2.30	(4)	0.22	(4)	0.52	(4)	0.63	(4)	0.39	(4)
Other	0.44	(9)	0.55	(16)	0.81	(16)	0.95	(16)	1.52	(16)	1.24	(16)
Within-group standard deviation	0.985		8.340		4.200		6.426		5.576		8.085	
Degrees of freedom for error	41		61		66		97		97		97	
No. of animals	63		92		97		97		97		97	
Overall mean	39.28		288.99		106.24		180.01		127.99		114.31	

* F, ratio of inter-seasonal variation to average within-sample variation;
d.f., degrees of freedom.
† P <0.05.
‡ P <0.01.

Table 6
Average monthly rates of growth by 6-month age interval for six body measurements of Kaminuriak caribou

Body measurement	Sex	Six-month age intervals									
		0–6	7–12	13–17	18–24	25–29	30–36	37–41	42–48	49–53	54–60
Metatarsus length (cm)	M	1.6	0.1	0.5	0.25						
	F	1.4	0.1	0.5							
Shoulder height (cm)	M	5.1	0.6	1.2	0.6		0.8				
	F	4.7	0.4	1.2	0.3	0.4					
Total body length (cm)	M	12.1	0.8	3.0	−0.5	2.5		0.3			
	F	9.2	1.0	2.5	0.2	1.0	−0.2	0.7	0.5		
Heart girth (cm)	M	9.3	−1.2	2.0	−1.8	3.3	−1.8	4.0			
	F	8.5	−0.8	3.5	−1.5	2.5	−1.7	2.0	0.8		
Average mandible length (mm)	M	13.0	2.5	4.2	1.7	1.8	0.3	1.3			
	F	13.2	2.8	3.5	0.5	1.7	0.5				
Body weight (kg)	M	6.8	0.1	3.7	−0.5	4.0	−1.5	3.7	−1.5	2.3	−1.3
	F	5.8	0.4	3.2	−0.8	2.8	0.8	2.3	−1.3	1.5	

Figure 6
Metatarsus length of male and female barren-
ground caribou of each age collected from the
Kaminuriak population in April, June, July,
September and November of 1966, 1967, and
1968
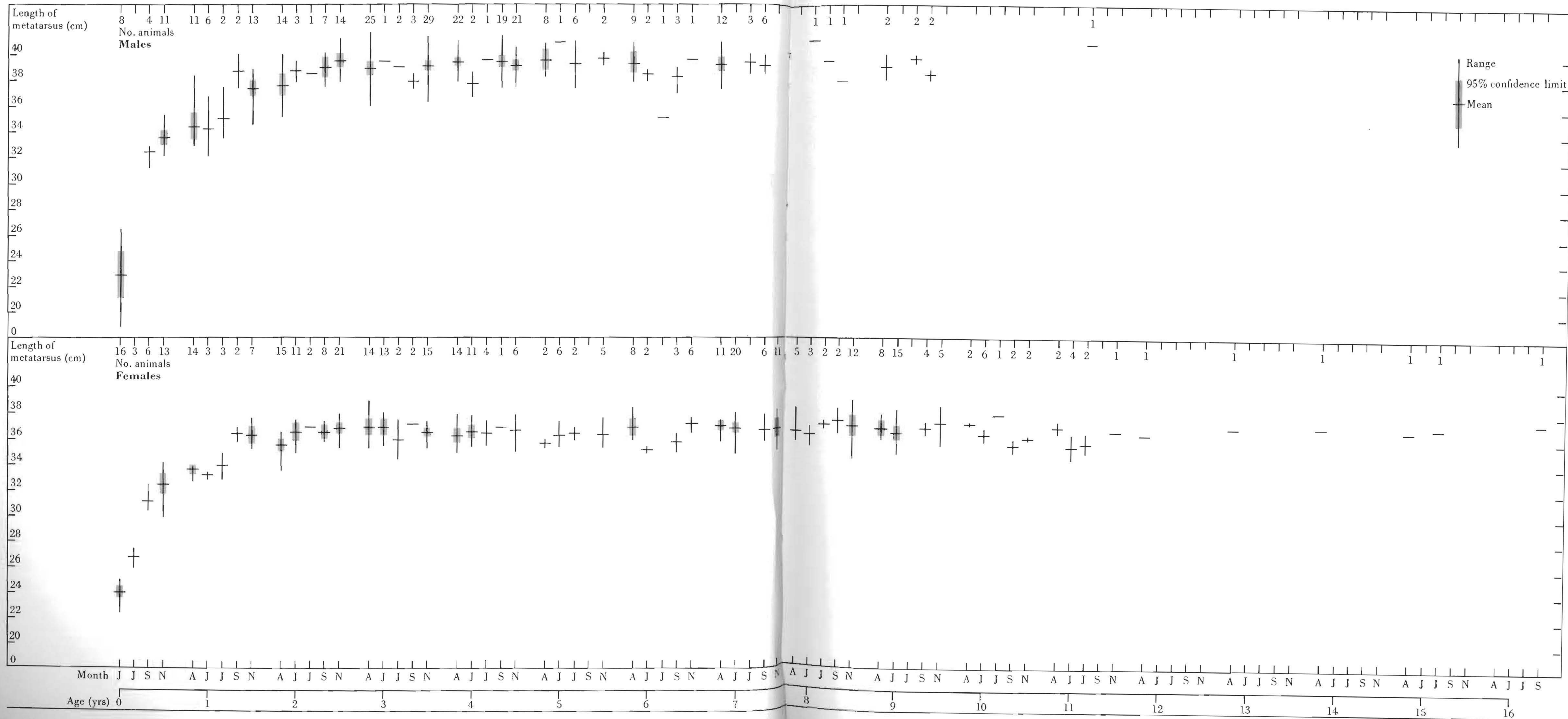
Figure 7

Figure 7
Mandible length of male and female barren-ground
caribou of each age collected from the Kaminuriak
population in April, June, July, September and
November of 1966, 1967, and 1968
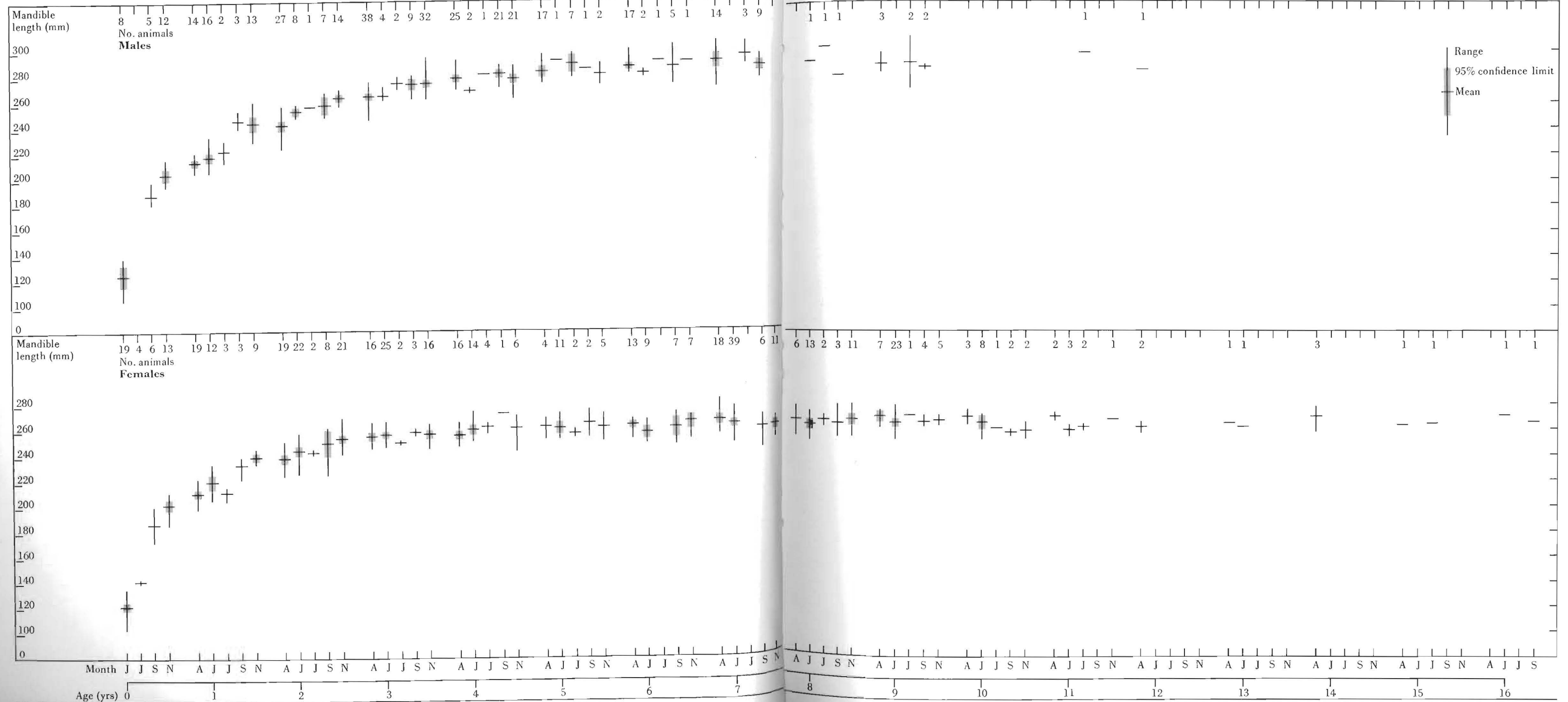
Figure 8
Shoulder height of male and female barren-ground
caribou of each age collected from the Kaminuriak
population in April, June, July, September and
November of 1966, 1967, and 1968
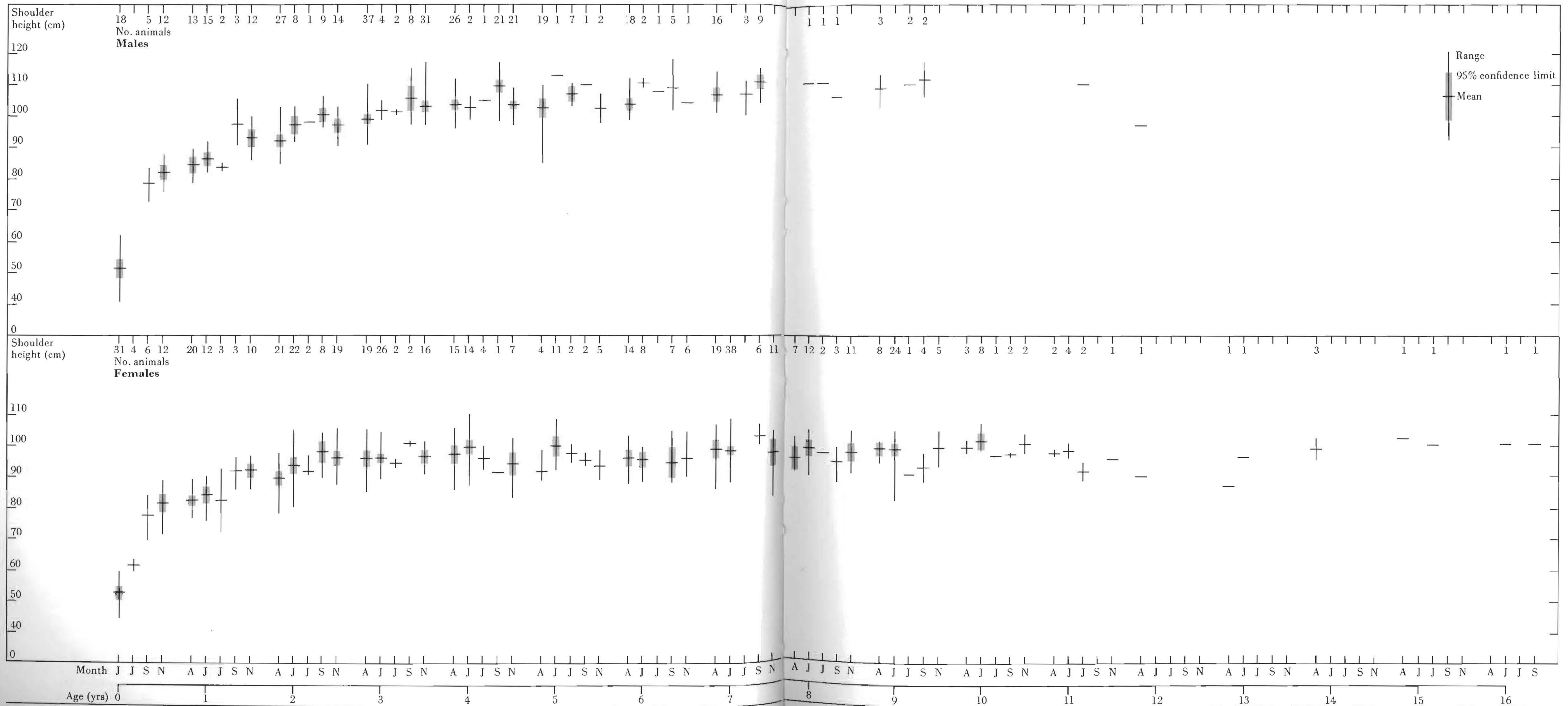
Figure 9

Figure 9
Total body length of male and female barren-
ground caribou of each age collected from the
Kaminuriak population in April, June, July,
September and November of 1966, 1967, and
1968

Figure 10
Heart (chest) girth of male and female barren-ground caribou of each age collected from the Kaminuriak population in April, June, July, September and November of 1966, 1967, and 1968
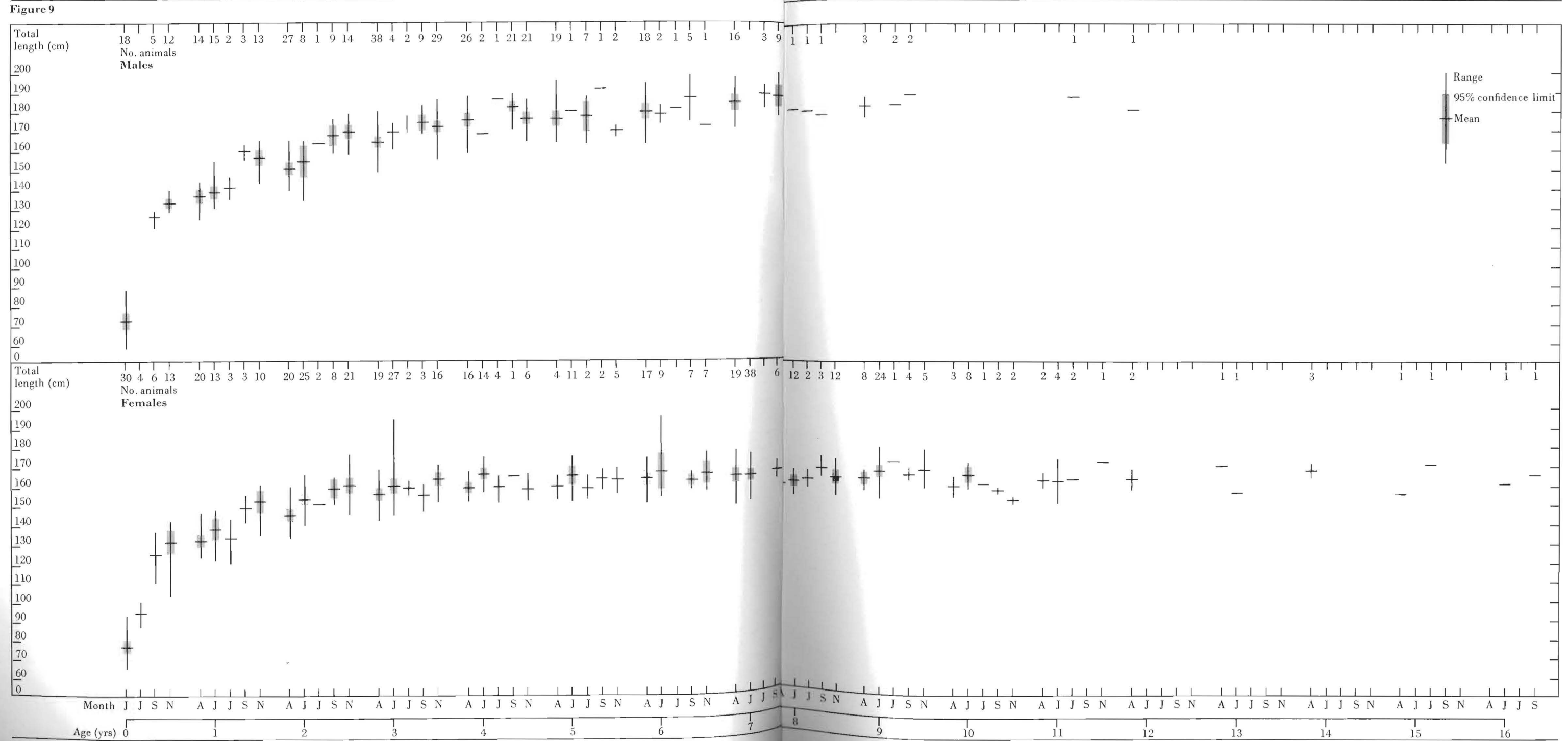
Figure 11
Body weight of male and female barren-ground caribou of each age collected from the Kaminuriak population in April, June, July, September and November of 1966, 1967, and 1968

32

33
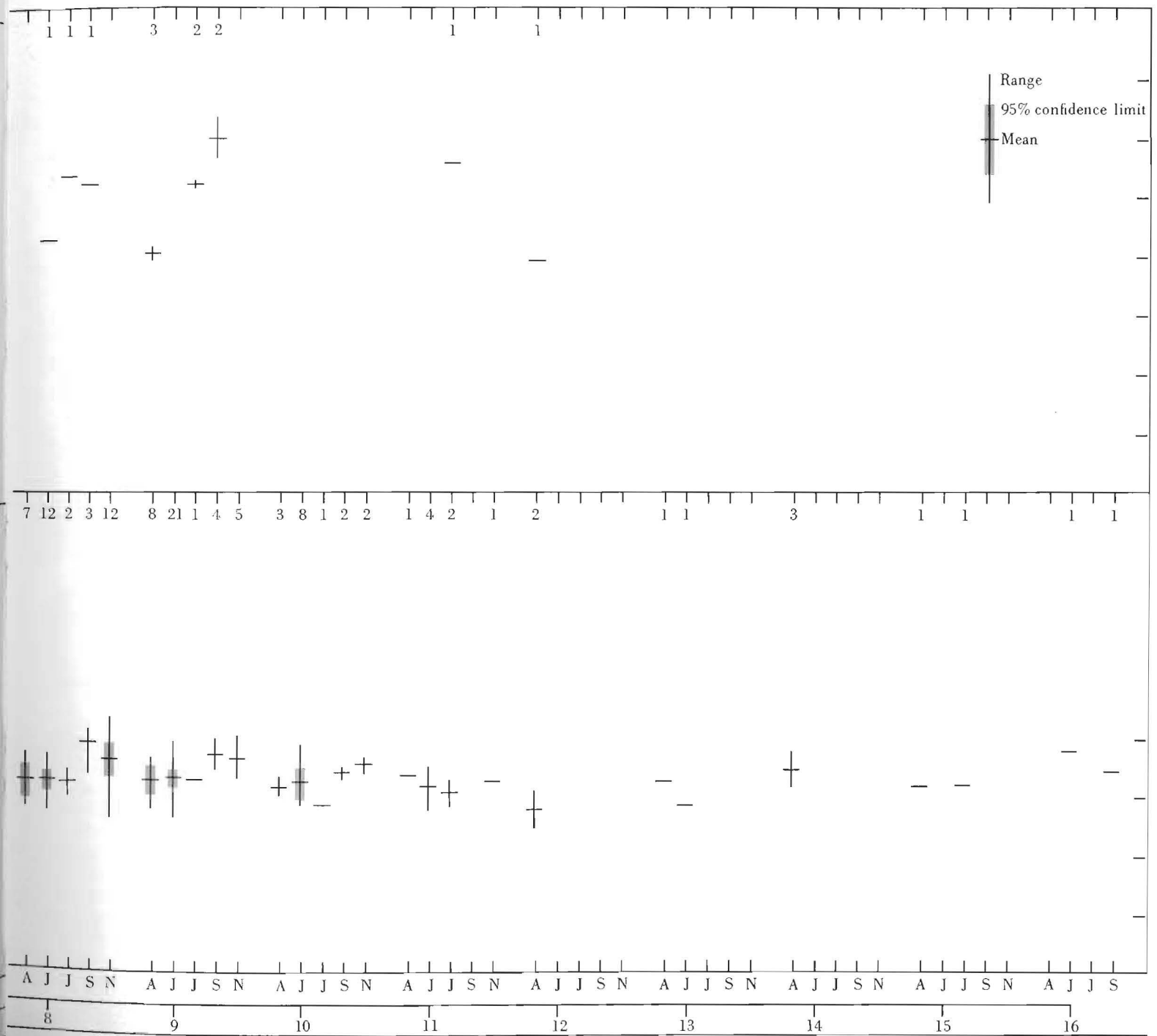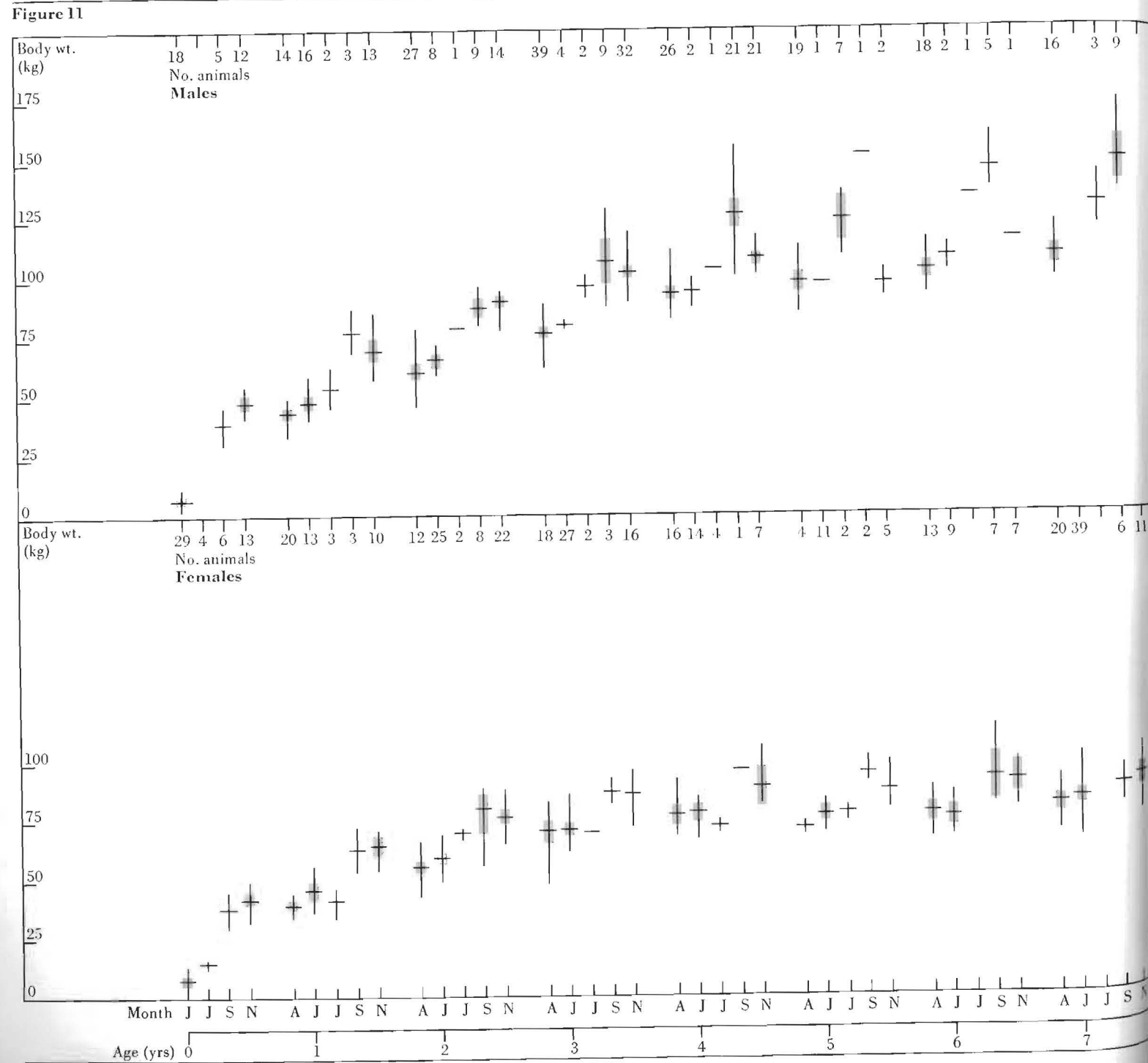
and April–June samples. The highest growth rate for all variables occurred during the first 6 months of life.

Body weight will be treated in detail in this report because it has been used most by other workers (Palmer 1934; Dobrotvorsky et al. 1938; Krebs and Cowan 1962; McEwan and Wood 1966; Preobrazhenskii 1968; McEwan 1968; Reimers 1972) to describe growth and body size in caribou and reindeer. The mean weight of male Kaminuriak calves was 6.4 kg in June and 47.4 kg in late November and early December, increasing by 641% during the 6-month period. Female calves increased from 7.3 to 42.4 kg or 481% over the same period. The average rate of increase was 6.8 kg/month for males and 5.8 kg/month for females. These values underestimate actual growth during the first 6 months because June means included weights of calves up to several weeks of age. McEwan (1968) reported mean birth weights of 5.2 and 4.7 kg for 24 males and 19 females respectively from the Beverly population, probably the most similar to the Kaminuriak in terms of genetics and physical size. If those birth weights are substituted in place of my June weights, the percentage increase for the first 6 months of a calf's life becomes 812 and 802 for males and females respectively.

Relative increases in body weight from the end of one summer growth period to the next are as follows for Kaminuriak males and females respectively: from calf to yearling, 46 and 51%; from yearling to 2-year-old, 28 and 18%; from 2- to 3-year-old, 14 and 12%; from 3- to 4-year-old, 15 and 6%; and from 4- to 5-year-old, 19 and 0%.

During the first 6 months, Kaminuriak caribou attain approximately the same rate of growth as captive caribou and semi-domestic reindeer but their later growth is slower and more protracted. The weight of reindeer calves may increase by over 900% during the first six months (Dobrotvorsky et al. 1938; Druri 1960), somewhat greater than the estimated growth

of Kaminuriak calves. McEwan (1968) also found growth of captive and wild calves to be similar during their first summer, a fact he attributed to the high nutrition available in the wild from milk and summer vegetation. However, at 6 months reindeer calves in the USSR usually attain 55 to 60% of their mother's (autumn) weight (Dobrotvorsky et al. 1938), but Kaminuriak calves attained only 52 and 46% respectively for males and females. In their second and later summers McEwan's captive caribou grew much more rapidly than wild caribou. McEwan and Wood (1966) estimated that a captive male barren-ground caribou reared on a highly nutritious diet attained the same body weight at only 2 years of age that wild individuals from the same population achieved at 6 years, and McEwan (1968: 1028) concluded that, "The difference in growth curves of wild compared with captive caribou is attributed to higher maintenance costs of wild caribou associated with their migration, feeding activities, and harassment from insects in summer."

The growth performance of Kaminuriak caribou in their second year was definitely less than that implied by Kelsall's (1968:197) statement that Beverly caribou "nearly double" their weight by their second autumn. During the summer, yearling Kaminuriak males increased from 47 to 76.4 kg or by 64%, and yearling females increased 42%, from 45 to 64 kg. The body weight gain was less than half of that attained during the first 6 months of life, and the gain in other measurements was less than 25% (Table 6). However, a captive male barren-ground caribou on a nutritious diet did attain, in its second summer, a rate of weight increase almost as high as in its first summer (McEwan and Wood 1966). Figures more similar to those for Kaminuriak caribou are given by Druri (1960) for male reindeer in the USSR as a 62% weight increase for yearlings and a 37% increase for 2-year-olds.

After the first 6 months of life, body weight of Kaminuriak calves followed alternating periods of positive and negative

growth which were simplified in Figure 12 by a curve A through the annual maximum ("prime") weights and a curve B through the annual minimum ("lean") weights (after Wood et al. 1962, McEwan 1968). The two curves are lines of "best fit" plotted through the sample means. They border the top and bottom edges of the sawtoothed curve (C, Fig. 12) which represents the actual weight change. In winter, both young and adult females lost between 6 and 11% of their prime autumn weight; consequently, curves A and B in Figure 12 are approximately parallel. However, the percentage of prime autumn weight lost by males in winter increased from about 9% the first year to 30% at maturity. This difference is reflected by the increasing separation of curves A and B in Figure 12. The fluctuations of body weight are largely attributed to the seasonal deposition and mobilization of fat reserves. The weights of the kidney and other visceral organs also undergo marked seasonal fluctuations (Dauphiné 1975). Therefore curve B (Fig. 12) represents growth of skeletal, muscle, organ and other "permanent" tissues and is perhaps the best growth indicator; curve A represents, in addition to these, the "temporary" growth of seasonal fat tissue and is an indicator of energy reserve.

Growth of Kaminuriak caribou ceased in winter because of either an inherent physiological rhythm or a decline in nutritive value of the diet, or both. That weight loss occurs in winter despite the availability of nutritious food has been demonstrated in captive caribou (McEwan 1968, McEwan and Wood 1966, McEwan and Whitehead 1970) and in many other ungulates (French et al. 1956, Wood et al. 1962, Silver et al. 1969, Caughley 1970, Bear 1971). However, in winter the caribou's natural diet is considerably less nutritious, particularly in protein content, than it is at other seasons (Scotter 1967, Steen 1968, Miller 1976) which leaves open the possibility that part of the seasonal weight and growth cycle may be exogenous. Exactly how much of

Figure 12

Table 7
The age of maturity and the mature size of six body measurements from male and female Kaminuriak caribou

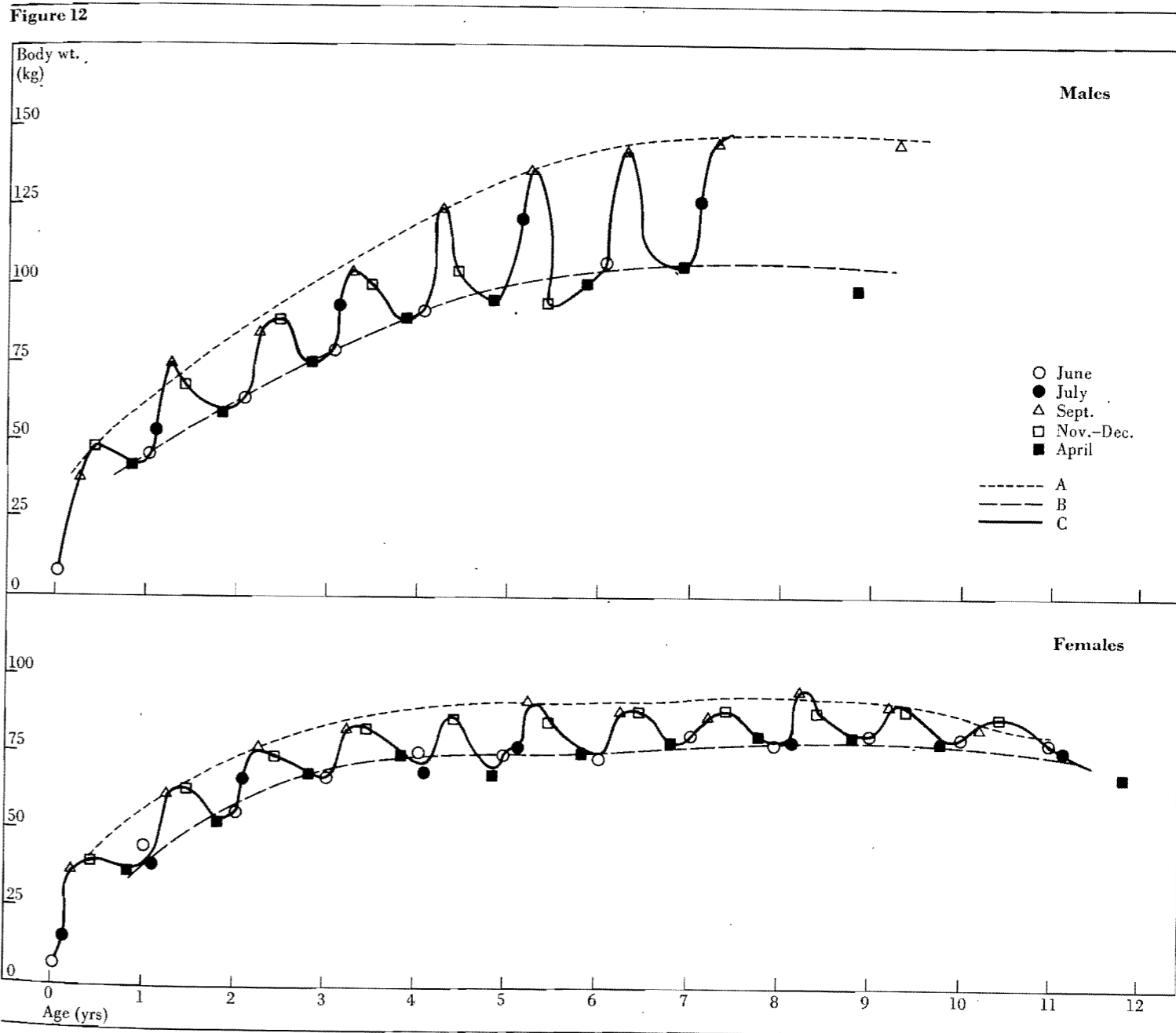| Body measurement	Sex	Age of statistical maturity* (mths)	Post-growth age group* (mths)	Post-growth statistics				
				n	$\bar{x}$	s	Range	95% conf. limit of mean
Metatarsus length (cm)	M	27 – 29	41+	158	39.2	1.0	35.0 – 41.5	39.0 – 39.4
	F	24	29+	269	36.7	1.2	34.5 – 39.0	36.5 – 36.9
Shoulder height (cm)	M	39	51+	139	106.3	5.7	85.0 – 118.0	105.4 – 107.2
	F	27	27+	378	97.0	5.0	82.0 – 110.0	96.5 – 97.5
Total body length (cm)	M	51 – 53	75+	46	183.8	7.4	170.0 – 198.0	181.6 – 186.0
	F	29 – 41	53+	258	164.2	6.7	149.0 – 195.0	163.4 – 165.0
Heart girth (cm)	M	39 – 41	51+	139	128.8	7.6	113.0 – 153.5	127.5 – 130.0
	F	17	41+	310	114.4	7.1	110.0 – 139.5	113.6 – 115.2
Average mandible length (mm)	M	51	70+	64	290.1	8.2	272.2 – 311.1	288.1 – 292.2
	F	48	65+	225	263.7	7.1	242.8 – 282.5	262.8 – 264.7
Lean whole body wt. (kg)	M	58	70+	38	104.4	8.0	91.6 – 122.5	101.8 – 107.0
	F	34 – 36	46+–48+	202	79.7	7.9	60.8 – 100.2	78.6 – 80.8
Prime whole body wt. (kg)	M	51	75+	17	146.6	10.8	129.7 – 171.9	141.2 – 152.0
	F	39 – 41	51+–53+	76	90.1	8.7	64.9 – 112.9	88.2 – 92.0

* See text on this page.

the weight loss was imposed on the animals by their environment during the years of this study is impossible to determine. Whatever the amount, it does not appear excessive or even unusual, as the cyclic growth pattern shown by the Kaminuriak data is similar to the pattern in other subspecies of *R. tarandus* on natural range. Dobrotvorsky *et al.* (1938:97) state, for example, that during the first winter of life of reindeer calves on average range, "...live weight begins to fall off and at one year of age the calves weigh less than at the age of five months . . . " Druri (1960) reported that after the reduction of body weight during the first winter, yearling reindeer weigh about the same as they did at the age of 3½ months. Thus, the 6 and 10% weight losses incurred by Kaminuriak calves between December and April (Fig. 11) appear typical. These losses are less than the maximum recorded, as Druri (1960) reported that during severe winters, reindeer calves lost 21% of their body weight of the previous October.

Information on seasonal weight trends of adult caribou and reindeer indicates that, except on the best ranges, it is characteristic that males lose weight during the rut, both sexes remain static or decline during the winter, and pregnant females lose weight during late gestation and lactation. The following body weight losses have been recorded: males during rut, 23 kg (Palmer 1934); females during gestation, 8–26% (Bergerud 1974); females pre- to post-partum, 15 kg (Palmer 1934) and 15% (McEwan 1968); males and females of all ages during winter, 10–15% (Steen 1968).

2.2. Age and size at maturity

In order to establish at what age growth ceased, the growth period was defined as that range of ages through which the increase between successive means was significant. Age of maturity was defined as the lowest age with a mean not significantly different from the combined means of all older ages (Table 7). Means with n ≤ 5 were omitted from individual comparisons because confidence limits based on such small samples were unreliable. However, visual inspection of the growth curves in Figures 6–11 suggested that some growth

occurred after the statistically calculated age of maturity had been reached. To obtain more realistic (though also more subjective) ages of maturity, therefore, I selected compromises between the statistical ages and the ages indicated by the growth curves and identified them as the beginning of the "post-growth" age groupings in Table 7.

Analyses of variance (Tables 4 and 5) indicate that the sizes of the mandible and metatarsus did not vary significantly with season in adult males and females. But some significant seasonal variation did occur in the four other variables in both sexes (Tables 4 and 5). Limited seasonal variation amounting to only 2 to 7% of annual maximum occurred in shoulder height, heart girth, and total length, so their mature sizes were expressed in Table 7 by combining all seasonal means. But the seasonal variation of body weight was so large, 30% in males and 11% in females, that it was more useful to express maximum and minimum body weights separately rather than to combine them into an overall annual average. Accordingly, a maximum "prime" body weight

was obtained from September means for males and September and November–December means for females (Table 7). Minimum or "lean" annual body weight was obtained from April means for males and April and June means for females (Table 7). These seasonal combinations were selected because the analyses of variance (Tables 4 and 5) indicated that, for adult males, mean body weight was highest in September, lowest in November, December, and April, and intermediate in June and July. For adult females, mean weight was highest in September and November–December and lowest in April, June, and July. Differences between means were significant for months at opposite ends of the annual scale but not for those at the same end of the scale. Only in September, before the rut, were both sexes at the same phase of their annual body weight cycles.

Each body measurement reached statistical maturity at a younger age in females than in males (Table 7). The differences between the sexes ranged from approximately 5 months for mandibular length to about 2 years for shoulder height, total body length, and both prime and lean body weight. The average mature size of each variable was significantly smaller in females than in males (Table 7), although the difference did not become apparent until the ages of 2 years for the mandible, 2½ years for total length, and 3½ years for shoulder height and heart girth (determined from 95% confidence limits in Figures 6–11). However, wide overlaps existed in the ranges of mature male and female metatarsus lengths and shoulder heights; in both variables, 99% of the females exceeded the smallest measurement obtained from an adult male. Heart girth was more discrete, having a 60% overlap, and mandibular length and total length were even more so (26 and 21% overlap respectively). Body weight was the most exclusive; there was only 8.4% female overlap with lean male weights and no overlap with prime male weights. Body weight,

mandibular length, and total length, the variables with the least amount of overlap, matured at a relatively late age; evidently the extended growth provided opportunity for males to outstrip most females.

Although the literature is vague regarding the age when growth is completed in *R. tarandus*, there is some evidence that Kaminuriak caribou reach full development somewhat later than caribou in many other populations and that they attain, at best, small to intermediate size. Dobrotvorsky *et al.* (1938) state that female reindeer attain their characteristic body size on the average by the age of 2½ years. However, growth in body weight in Kaminuriak cows continued to approximately 3¼ years (Fig. 6). According to Palmer (1934), Alaskan reindeer attain full size at 4 to 5 years. His findings would apply to Kaminuriak females, but Kaminuriak males grew for at least another year. Banfield (1961) maintained that skull growth ceases in *R. tarandus* at approximately 4 years of age, but the mandible of Kaminuriak specimens continued growing until 5½ years for females and 6 years for males, and possibly beyond (Table 7 and Miller 1974). The Kaminuriak data are in closer agreement with those of Steen (1968), who reported that growth (body weight) of Swedish reindeer continued for 5 years or more, even up to 8 years. Similarly, dressed weights of wild male reindeer on both good and poor ranges in Norway increased for the first 6 years of life (Reimers 1972).

Kelsall (1968:29), referring to Banfield's (1961) data, states, "Measurements, as well as weights, indicate barren-ground caribou are medium-sized animals . . .", being smaller than woodland caribou, Grant's caribou, and the domestic reindeer of the Mackenzie delta (of Siberian origin via Alaska), but larger than Peary caribou. Although Kelsall's statement probably applies generally to the Kaminuriak population, it is evident from my data that he underestimated the mature weight of Beverly caribou. The mean weights he presented (108 kg for males and 78 for females) were

Table 8
Analysis of variance tests for four measurements of fat reserves in female caribou (27 months and older) collected from the Kaminuriak population

Source of variation	Back fat depth (mm) F* (d.f.)		Log kidney† fat weight F (d.f.)		Log abdominal† fat weight F (d.f.)		Marrow fat content (%) F (d.f.)	
Collection			29.00	(10)§	21.10	(10)§	17.40	(10)§
Season			61.70	(4)§	52.70	(4)§	31.00	(4)§
Sept. and Nov. vs. others	81.6	(1)§	85.72	(1)§	58.92	(1)§	37.00	(1)§
April vs. June and July	35.4	(1)§	14.32	(1)§	20.33	(1)§	45.51	(1)§
June vs. July	n.s.‡		2.50	(1)	1.00	(1)	2.25	(1)
Sept. vs. Nov.–Dec.	0.17	(1)	0.63	(1)	1.41	(1)	0.95	(1)
Year (within season)			7.22	(6)§	3.18	(6)§	8.37	(6)§
Aprils			9.75	(2)‖	4.69	(2)*	0.84	(2)
Junes			9.60	(2)§	4.85	(2)§	23.68	(2)§
Septembers			2.97	(1)	0.20	(1)	1.10	(1)
November–Decembers			0.89	(1)	0.03	(1)	0.14	(1)
Age			2.57	(5)‖	1.79	(5)	5.30	(5)§
2 years vs. older			0.44	(1)	1.88	(1)	0.88	(1)
3 years vs. older			6.63	(1)‖	2.63	(1)	3.10	(1)
4–9 vs. 10+			8.14	(1)§	3.38	(1)	19.93	(1)§
4–5 vs. 6–9			1.26	(1)	1.13	(1)	0.00	(1)
10–11 vs. 12+			4.86	(1)‖	1.17	(1)	0.63	(1)
Age and season			0.65	(12)	0.33	(12)	1.67	(12)
Other			0.98	(55)	1.05	(55)	1.01	(59)
Within-group standard deviation			0.167		0.264		12.67	
Degrees of freedom for error			201		186		210	
No. of animals			284		269		297	
Overall mean			1.67		2.32		64.00	

* Calculated as χ^2 test of number of animals above the median value of the combined groups.
† Transformed to logarithms because of its skewed distributions and heterogeneous variances.
‡ Sample size inadequate for χ^2 test, so a binomial test of the proportions above median value was used to test for a significant difference.
§ $P < 0.01$.
‖ $P < 0.05$.

Table 9
Analysis of variance tests for four measurements of fat reserves in male caribou (58 months and older) collected from the Kaminuriak population

Source of variation	Back fat depth (mm) F* (d.f.)		Log kidney† fat weight F (d.f.)		Log abdominal† fat weight F (d.f.)		Marrow fat content (%) F (d.f.)	
Collection			9.72	(8)§	4.27	(8)§	2.11	(8)‖
Season			14.50	(4)§	7.55	(4)§	2.12	(4)
September vs. others	20.0	(1)§	32.50	(1)§	17.30	(1)§	6.09	(1)‖
April and Nov.–Dec. vs. June and July	8.9	(1)§	8.08	(1)§	7.58	(1)§	3.61	(1)
June vs. July	n.s.‡		1.03	(1)	2.00	(1)	0.13	(1)
April vs. Nov.	n.s.‡		3.96	(1)	16.00	(1)§	10.35	(1)§
Year (within season)			4.18	(4)§	1.01	(4)	2.08	(4)
Aprils			8.32	(2)§	0.37	(2)	0.75	(1)
Septembers			0.29	(1)	2.78	(1)	0.08	(1)
November–Decembers			0.01	(1)	0.56	(1)	6.69	(1)‖
Age			1.75	(2)	0.55	(2)	0.35	(2)
5 years vs. older			3.37	(1)	1.04	(1)	0.21	(1)
6 years vs. older			0.17	(1)	0.11	(1)	0.42	(1)
Age and season			0.67	(4)	1.03	(4)	0.24	(4)
Other			0.89	(16)	1.12	(15)	0.35	(16)
Within-group standard deviation			0.1493		0.2395		10.45	
Degrees of freedom for error			47		49		62	
No. of animals			78		79		93	
Overall mean			1.88		2.56		72.6	

* Calculated as χ^2 test of number of animals above the median value of the combined groups.
† Transformed to logarithms because of its skewed distributions and heterogeneous variances.
‡ Sample size inadequate for χ^2 test, so a binomial test of the proportions above median value was used to test for a significant difference.
§ $P < 0.01$.
‖ $P < 0.05$.

calculated from measurements of sub-adults (between 2 and 4 years old) as well as adults and are comparable to Kaminuriak adults only during the low period of the latter's annual weight cycle.

Some other populations of *R. t. groenlandicus* appear to attain larger size than Kaminuriak caribou. For example, the lengths of mandibles from Alaska's arctic herd (Skoog 1968) are 1 to 4% larger respectively than mandibles from comparably aged males and females of the Kaminuriak population. Male caribou on Coats Island in Hudson Bay (62° 30'N, 83° 00'W) attain mean body weights which range from 30 to 40% heavier than prime Kaminuriak males of comparable age (Parker 1975).

2.3. Declines in old age — senescence

Analyses of variance were conducted to determine if any variables declined in old age, particularly those which included fat and muscle tissue. The means for combined female age groups for each variable (4–9 vs. 10–15 and 10–11 vs. 12 years) were tested for differences. Heart girth declined significantly after 9 years of age and total length after 11 years of age. The means of other variables were homogeneous from the age of maturity through old age. However, as with determining the age of maturity, statistical tests may not reveal subtle trends with age, and Figures 10 and 11 indicate that a slight decline occurred in the heart girth and body weight of females after 10 or 11 years of age. Similar testings for males did not reveal a decline in any variable, but there were few specimens older than 9 years.

3. Changes in fat reserves associated with age, sex, and season

The fatness of each caribou specimen was determined by measuring subcutaneous fat on the back, perirenal fat, abdominal fat attached to the mesenteries and omentum, and fat in the femur marrow.

Measurements of fat deposits have been used as indices of energy reserves and general nutritive condition in deer (Harris 1945, Cheatum 1949, Ransom 1965, Anderson et al. 1972), red deer (*Cervus elaphus*) (Riney 1955, Caughley 1971), elk (*C. canadensis*) (Flook 1970), antelope (*Antilocapra americana*) (O'Gara 1968, Bear 1971), caribou (McEwan and Wood 1966, McEwan 1968), and other wild ungulates (Smith 1970, Caughley 1970).

Some adjustments to fat data were necessary before they could be analysed for the effect of season. Because analyses of variance (Tables 8 and 9) revealed that age contributed significantly to variation in kidney and marrow fat measurements of females 2⅓ years and older, each deposit's measurements for females in that age group were pooled by co-variate adjustments and then tested for the effect of season.

Results of tests of differences in fat reserves between collection years (Tables 8 and 9) were significant for kidney fat in April and marrow fat in November for males, and kidney, abdominal and marrow fat in April and June for females. Differences were not detected between 1966 and

Figure 13
Unlike the other three fat deposits, subcutaneous
back fat was completely utilized during the low
portion of the condition cycle in many caribou

Figure 14
Seasonal variation in mean back fat depth in
relation to age in male and female Kaminuriak
caribou. Sample sizes are given in Tables A. 1
and A. 2

Figure 13

Figure 14

1967 in animals of either sex shot in September or November. As explained previously, because the differences were not consistent, they were ignored in the analysis of seasonal variation. The development of fat deposits with age, and the effect of season on the growing and matured deposits will be described and compared for males and females. Statistics on the means of each fat measurement are given in Appendix 2 (Tables A.1–A.8).

3.1.   Back fat
Back fat was the only deposit to disappear completely in most individuals (particularly males) during part of the annual cycle (Fig. 13). It varied from universal abundance in some seasons to almost complete absence at others. The trend in mean thickness of back fat with age and season is shown in Figure 14.

During the first 3 years of life, males accumulated little back fat except in late summer and early autumn (Fig. 14). In males 4 years and older, however, substantial accumulations of back fat were also present in April, June and July. The seasonal trend of back fat during and after completion of body growth in males was accumulation in summer and early fall, almost complete utilization in October and early November, a recovery of 25% by April and of 75% by July. The September peaks of back fat thickness increased rapidly with age, approximately doubling each year during the first 4 years. Males 5 years and older had a mean back fat thickness of 40.5 mm (range = 16.5–64.4 mm, n = 18) in September.

The absence of back fat from many caribou precluded the use of the standard parametric tests used for other deposits. Therefore, to analyse seasonal variation in the depth of back fat of adult caribou, x^2 tests were conducted between the proportions of caribou in each season that had fat thicknesses which exceeded the median level (without adjustment for age differ-
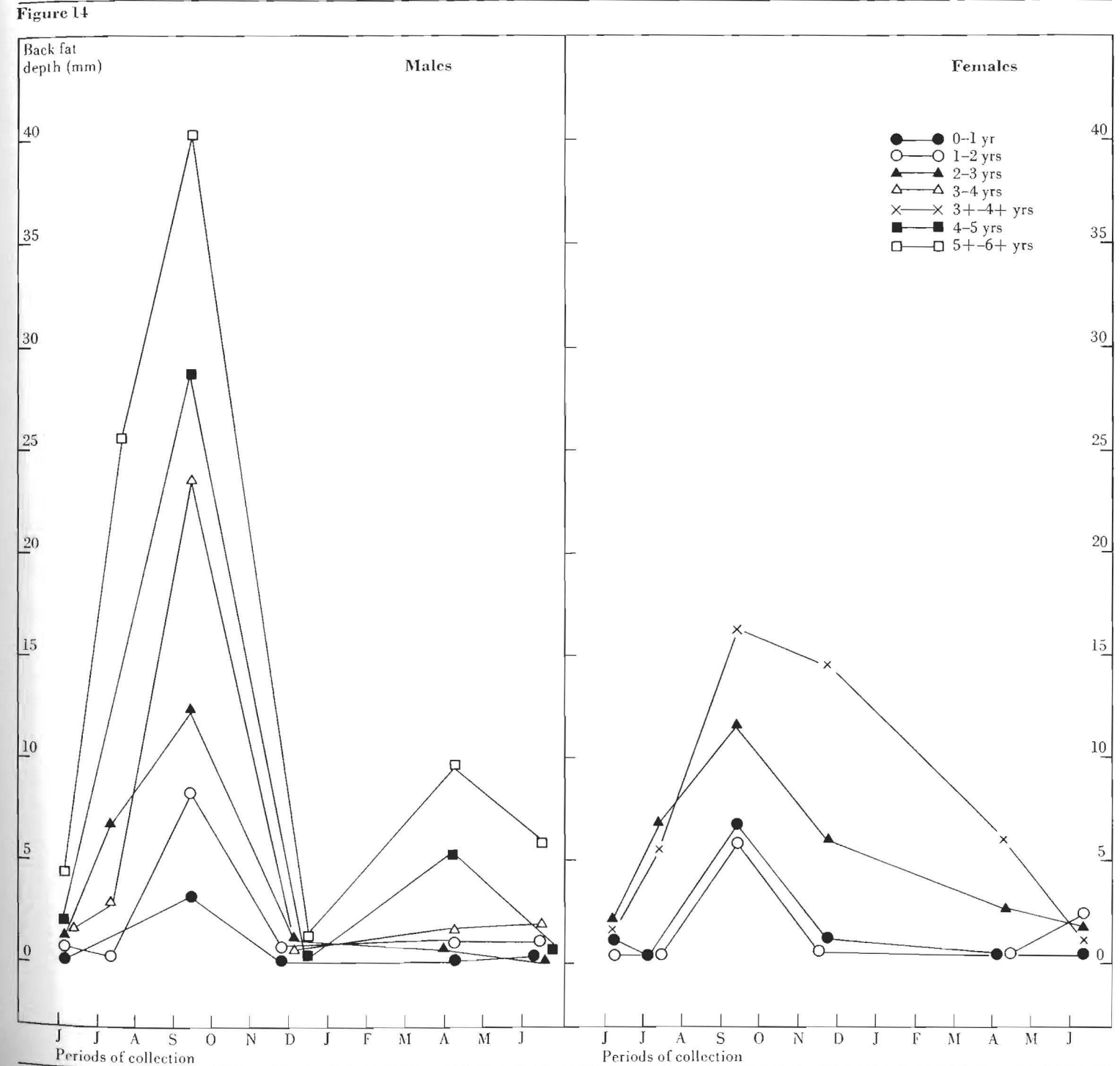
Table 10

The percentage of specimens with back fat in various age and seasonal samples of Kaminuriak caribou. Sample sizes in parentheses

Sex	Age class (yrs)	Season of collection				
		June	July	Sept.	Nov.–Dec.	April
Males	<1	0 (9)	—	60 (5)	8(12)	0(14)
	1	9 (11)	0 (2)	67 (3)	15(13)	8(26)
	2	29 (7)	100 (1)	78 (9)	21(14)	18(39)
	3	0 (3)	100 (1)	100(9)	10(30)	31(26)
	4	—	—	85(20)	0(21)	61(18)
	≥5	50 (4)	100(14)	100(15)	33 (3)	84(38)
Females	<1	20 (20)	0 (4)	83 (6)	38(13)	6(18)
	1	18 (11)	0 (3)	67 (3)	63 (8)	11(19)
	2	50 (2)	100 (2)	88 (8)	55(22)	37(19)
	≥3	30(134)	53(15)	90(29)	74(74)	63(78)

ences). The results for males (F values[1] in Table 9) confirmed that the mean depth of back fat was significantly higher in September than at all other seasons; that it was significantly higher in June and July than in November–December and April but that no significant difference existed between June and July or between November–December and April.

In young females, as in young males, the only substantial accumulation of back fat during the first 2 years of life occurred in early autumn (September), with little difference between the sizes of the deposit in each year. Between 2 and 3 years the deposit approximately doubled in size, and in older females it was present in all months sampled.

Fluctuation of back fat with season showed a difference between adult females (2½ years and older) and adult males (Tables 8 and 9). In females depths of back fat for September and November–December combined were significantly greater than for the other months, and a significant decline occurred between December and June (Fig. 14).

In both males and females the proportion of specimens with measurable (>0.1 mm) back fat paralleled seasonal

trends in the thickness of the deposit (Table 10 and Fig. 14). The proportion of females which carried back fat during the high part of the annual cycle declined in old age, as did mean thickness (Fig. 15). In September and November–December, 89% of 79 females from 4 to 9 years of age had back fat, compared to 67% of 15 females 10 years and older.

In September, the month of greatest back fat accumulation in both sexes, the mean thickness of the back fat layer in females (15.4 mm) was about one-third that of males. The greatest individual thickness in a female (36 mm) was half the largest measurement recorded among males.

3.2. Kidney fat

Kidney fat was present in all specimens, ranging from 2 to 189 g in females and 3.5 to 310 g in males. The amount of kidney fat varied with season in males and females of all ages.

A significant increase in the mean weight of kidney fat occurred between seasonal peaks (September) of male calves and yearlings. Subsequent increases in the mean weight of kidney fat with age were more gradual (Fig. 16) and differences between successive September means for males older than yearlings were not significant (Appendix 2, Table A. 3). The same seasonal pattern, with highest fat levels occurring in

the autumn samples, was repeated during the first four years. Figure 16 shows that the September to November declines in the mean weight of kidney fat increased in steepness with age. The decline became significant at 4 years of age (Appendix 2, Table A. 3). The amount of fat lost in autumn was even greater in males 5 years and older. In winter (November to April) young males mobilized fat while adult males slowly accumulated it (according to the data in Appendix 2, Table A. 3).

Analysis of variance[2] revealed that the mean kidney fat weight of males 5 years and older was significantly ($P<0.01$) higher in September than in other seasons combined. June and July weights were intermediate, being significantly different from higher and lower seasons but not from each other, and November–December and April weights combined were significantly lower than those of June and July but not from each other (Table 9).

Female caribou exhibited a seasonal change in kidney fat weight which did not change with age and was similar to that of young males. The characteristic female kidney fat pattern was a peak in autumn and early winter and a gradual decline during winter to a minimum in June and July (Fig. 16). Most year-to-year growth in the kidney fat deposit occurred during the first 2 years; significant differences existed between successive November–December means until 2½ years, between successive April means until 3 years, and between successive June means until 2 years (September means could not be tested because sample sizes were inadequate) (Appendix 2, Table A.4). Weight of the kidney fat deposit in females declined after approximately 10 years of age. Mean seasonal weights of females 10 years old and older were significantly ($P<0.01$) lower than corresponding mean weights of 4- to 9-year-old females (Fig. 15). Little difference existed

[2]To test for seasonal differences the measurements of kidney fat weight were transformed to logarithms because of skewed distributions and heterogeneous variances.

Figure 15
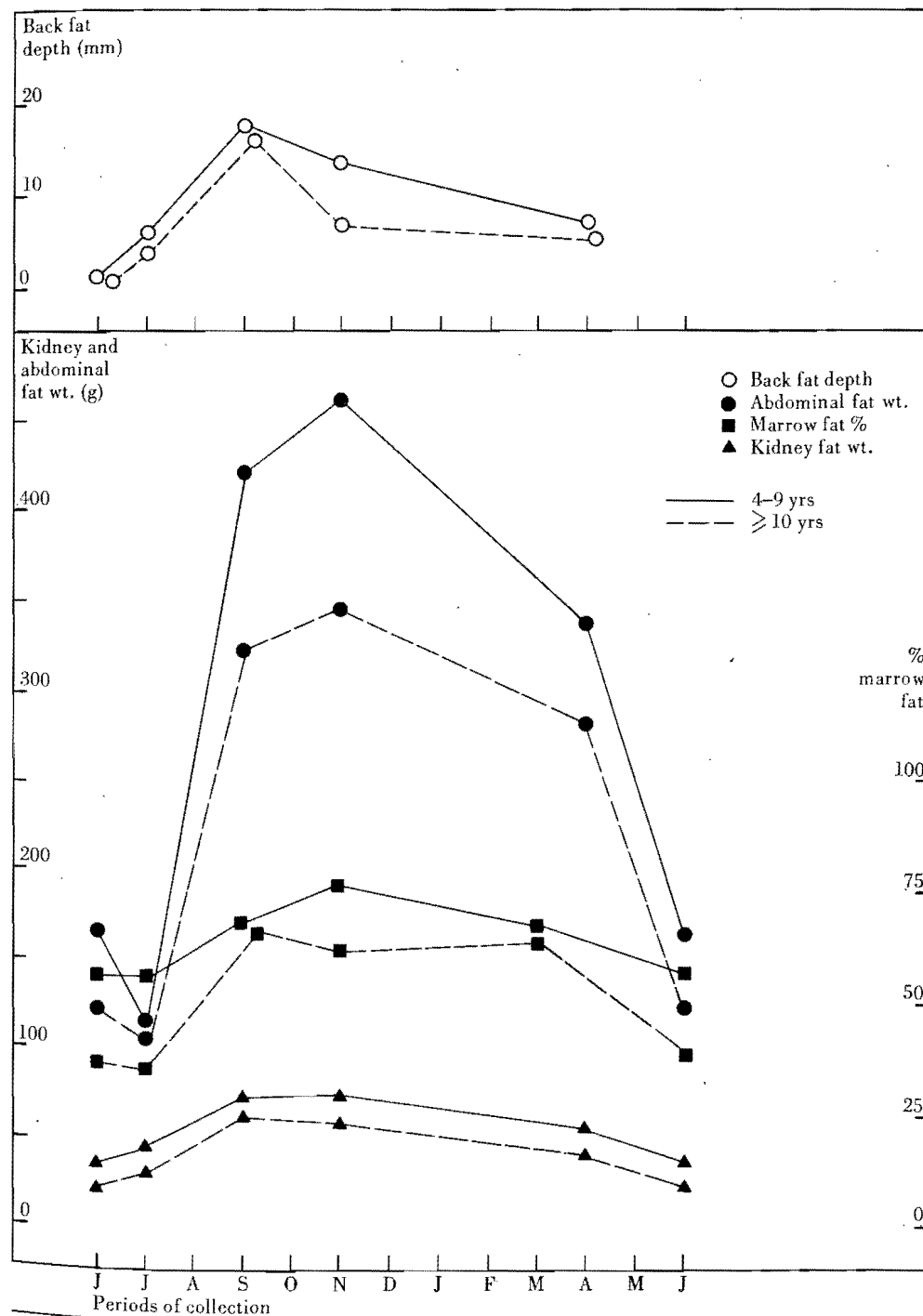
between the two age groups in September, but in November, June and July the older group had approximately 16% lower mean kidney fat weight than the younger.

The highest seasonal mean of kidney fat weights in adult females amounted to approximately half the peak seasonal mean in adult males. But, at the lowest point in their respective seasonal cycles, the mean amount of kidney fat in both sexes was approximately equal (37.6 vs. 36.0 g in Fig. 16). The fluctuation amounted to 72% of the annual seasonal maximum in males and 50% in females.

3.3. Abdominal fat

Abdominal fat showed variations similar to kidney fat in relation to sex, age and season. It was present in all individuals collected, ranging from 2 g in some calves less than one month old to 1652 g in a 4⅓-year-old male, and 991 g in a 5½-year-old female.

Mean weights of abdominal fat increased by 25 to 75% each year in males between 2 and 5 years of age for all seasons except November–December (Fig. 17). In November–December, the period with the lowest means, very little increase occurred after 1½ years of age. Where sample sizes permitted testing (Appendix 2, Table A. 5), significant differences in mean weights of abdominal fat existed between calves and yearlings in June and November–December but not between 2- and 3- or between 3- and 4-year-olds in September.

Analysis of variance[1] of mean weights of abdominal fat for males 5 years and older revealed approximately the same seasonal pattern as back and kidney fat deposits (Table 9), with the exception that abdominal fat increased significantly ($P<0.01$) from November to April. Loss of abdominal fat between September and November (during the rut) became significant at 2 years of age and was increasingly

[1]To test for seasonal differences in adult caribou, the mean abdominal fat weights were transformed to logarithms because of skewed distributions and heterogeneous variances.

[1]Significance level for χ^2 with one degree of freedom is identical to that for the F distribution with one: infinity degrees of freedom.

Figure 16

Figure 16
Seasonal variation in mean kidney fat weight
in relation to age in male and female Kaminuriak
caribou. Sample sizes are given in Tables A. 3
and A. 4

Figure 17
Seasonal variation in mean abdominal fat weight in
relation to age in male and female Kaminuriak
caribou. Sample sizes are given in Tables A. 5
and A. 6

Figure 16

Figure 17
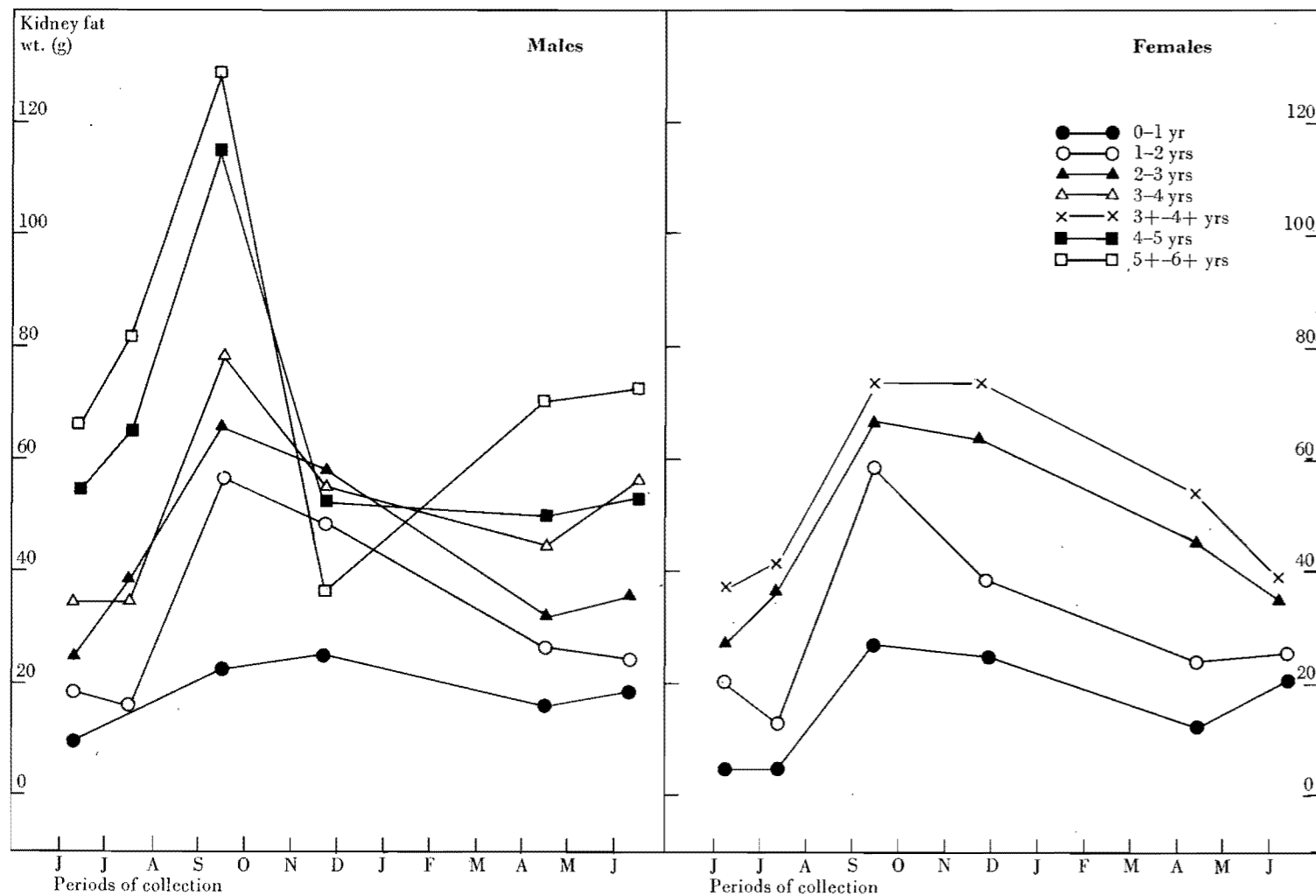
prominent thereafter. Young males did not
recover abdominal fat between November
and June, whereas during that period males
4 years or older recovered almost half of
the loss sustained in autumn (Fig. 17).

Abdominal fat weight increased with
age in females until at least 3 years; means
approximately doubled each year in all
seasons except June (Fig. 17). Significant
differences in mean weights of abdominal
fat existed in June between calves and year-
lings and between 2- and 3-year-olds and

in November–December between yearlings
and 2-year-olds and between 2- and 3-year-
olds.

As with kidney fat, size of the ab-
dominal fat deposit at its annual peak de-
clined after 10 years of age by approxi-
mately 25% from the peak attained by the
4–9 year age group (Fig. 15).

Analysis of seasonal variation in
mean abdominal fat of adult females gave
a result similar to that observed for kidney
fat and is summarized in Table 8. There

were no striking changes in pattern with
age; September and November–December
were highest, April was intermediate and
June and July were lowest for all age groups.

Male and female calves under one
month of age had similar amounts of ab-
dominal fat (means of 8.7 and 6.6 g respec-
tively). Among adults, however, the maxi-
mum mean weight of fat (641 g in Septem-
ber) in males was 55% higher than the
corresponding maximum weight in females
(417 g in November–December). The sex-

related difference in abdominal fat deposit
was less than that displayed by the kidney
fat. The minimum weight of abdominal fat
in adult males (65 g in November–Decem-
ber) was smaller than the minimum weight
in females (124 g in July). The overall
seasonal fluctuation of abdominal fat weight
in adult males and females amounted to 90
and 71% respectively of the maximum
seasonal mean weights recorded in each sex.

3.4. Femoral marrow fat

Percentage marrow fat exhibited less
variation with age and season than other
fat deposits, particularly in males. The lack
of variation with age occurred partly be-
cause this variable was expressed as the
percentage of fat in a standard 2-g marrow
sample, not as the total fat in the whole
marrow tissue. Seasonal variation aside,
the total amount of fat is directly corre-
lated with the quantity of marrow deposited
in the medulla of the femur and the size of

Figure 18
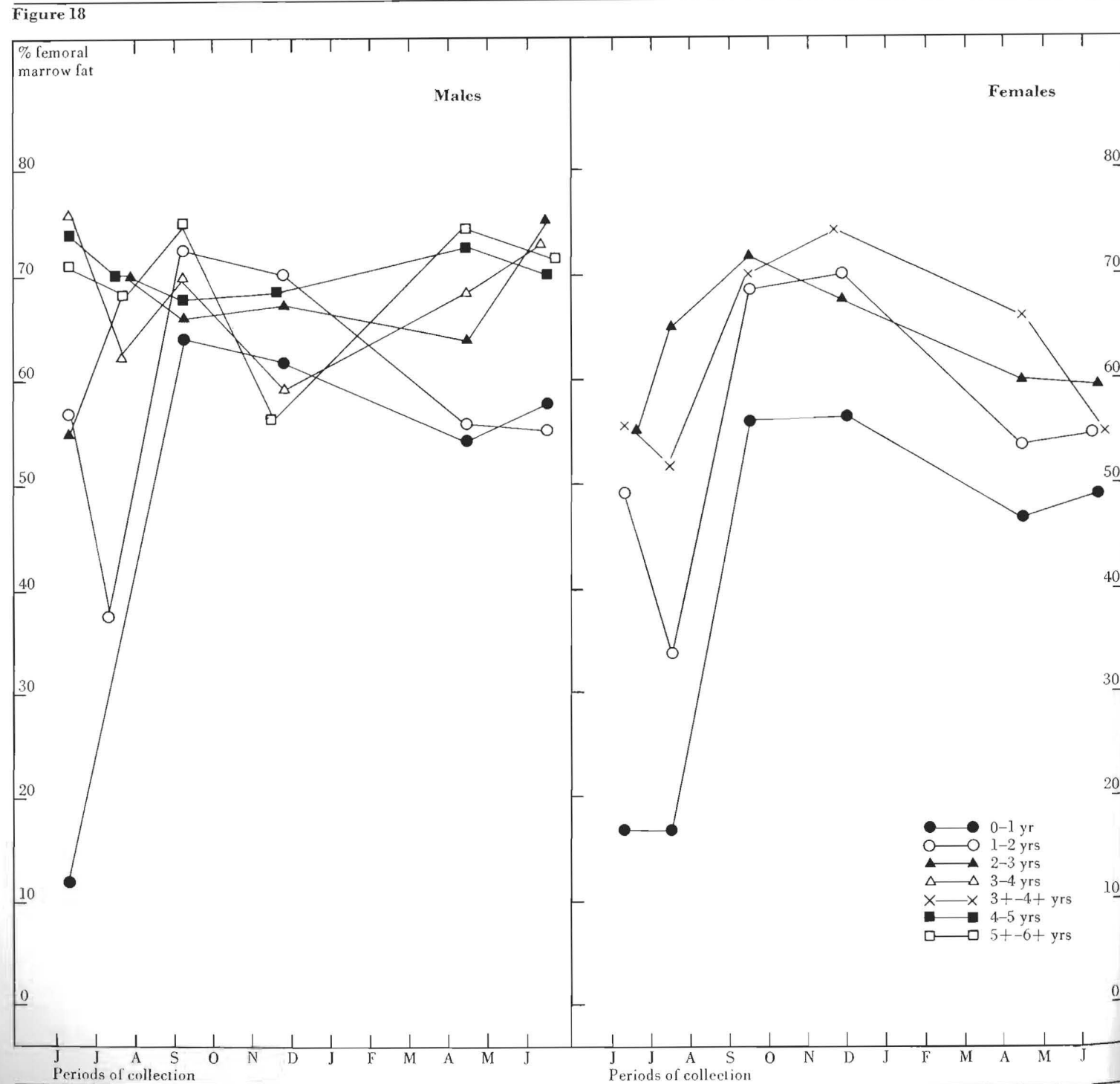
Figure 19
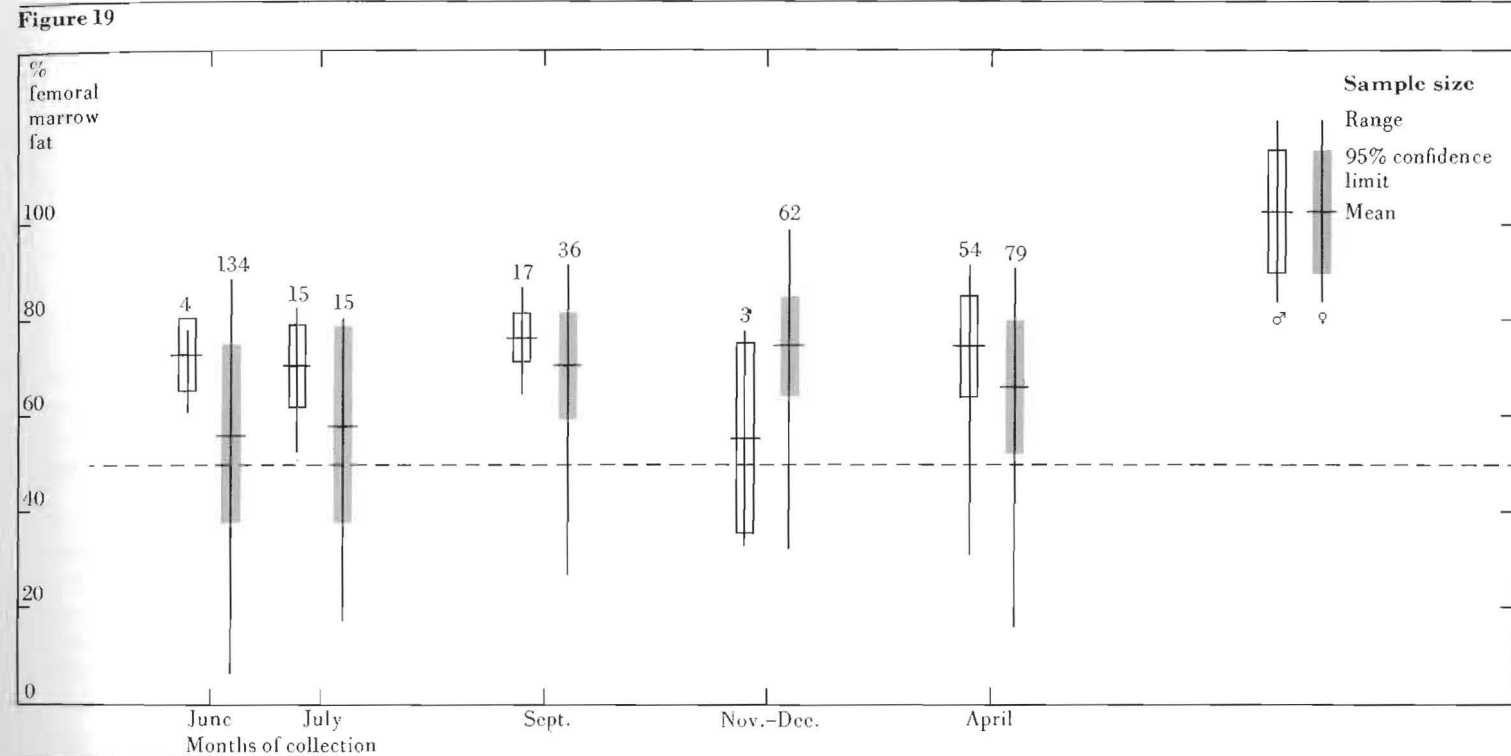
the bone. Fat was present in the marrow
of all caribou regardless of age and season,
ranging from 1% in some calves to 97% in
a male 8 years old and 89% in a female 5
years old.

In male caribou, the most noticeable
effect of age on marrow fat content was the
rapid accumulation of fat to the adult level
of approximately 65% by 3 months of age
(Fig. 18). Marrow fat levels increased slight-
ly during the next 2 years, particularly in
September and April. However, significant
differences between successive ages could
not be demonstrated after the first year.
Calves, yearlings and 2-year-old males did
not mobilize much marrow fat in autumn,
whereas among adult males the mean mar-
row fat content declined from 75% in Sep-
tember to 56% in November–December.
(The November–December mean is based
on only three specimens and therefore the
significance of the difference was not test-
ed.) Analysis of variance did not reveal a

significant *overall* seasonal variation (Table
9). However, in common with the seasonal
trends of the other fat deposits, mean fat
content in September was significantly
higher than the mean of other seasons
combined, and the November–December
mean was significantly ($P < 0.01$) lower
than the April mean.

The percentage of fat in the marrow
of female calves and yearlings increased
rapidly with age. At the end of the second
summer it approximated that of adults, and
thereafter followed the adult seasonal cycle.
The only significant age difference within
seasons existed between female calves and
yearlings in June. As in males, the widest
divergence among age groups occurred in
summer. The percentage of fat in the mar-
row declined by up to one-third in old age
(Fig. 15); it was significantly ($P < 0.01$)
lower in specimens 10 years and older than
in those between 4 and 9 years (Fig. 15).
Overall seasonal variation in marrow fat

levels of adult females was significant
($P < 0.01$) (Table 8). Analysis of variance
showed that in females marrow fat exhi-
bited the same seasonal pattern as did kid-
ney and abdominal fat deposits; values
were equally high in September and Novem-
ber, and gradually declined through April,
June, and July (Fig. 18). The mean fat con-
tent in adult females ranged from 53% in
July to 73% in November; individuals
ranged from 3.8 to 97%.

Among seasonal mean values for mar-
row fat in both sexes there was an inverse
relationship between size of the standard
deviation and size of mean marrow fat con-
tent (Fig. 19 and Appendix 2, Tables A. 7
and A. 8). The opposite situation occurred
in the kidney and abdominal fat, where
standard deviations varied directly with
size of the mean. The difference may lie in
the fact that marrow fat was the last deposit
to be affected in the sequence of fat mobili-
zation (Dauphiné 1971). The back, kidney,

and abdominal fat deposits were mobilized earlier in the sequence of fat decline and all were utilized to some extent during the low portion of the annual cycle. Since not all females needed to mobilize marrow fat at low seasons, the range was expanded by low fat content in some specimens, increasing the variation of marrow fat content.

Although femoral marrow of most calves less than 2 months old was watery and red and did not appear as fatty as the solid white marrow of adults, it did contain appreciable amounts of fat. Fat comprised between 40 and 50% of marrow weight in many calves only 1 or 2 weeks old, and by autumn the mean marrow fat content of male calves (64 to 62%) was similar to the means of older males (Fig. 18). Evidently fat storage in marrow begins very soon after birth.

Adult males and females exhibited approximately the same amplitude in the seasonal variation of percentage fat in marrow. Males lost 26 and females 23% of their respective annual maxima. Yet, in the five seasonal samples drawn during the year, there was only one male sample in which the mean was below 70%, whereas the means of four female samples were below this figure. Females were also slower to attain the adult level of marrow fat than were males, 15 months compared to 3–5 months (Fig. 18).

The proportion of females with fat levels below 50% was also greater than the proportion of males (Table 11). The cause of the difference may be that, given the same energy demand, females have smaller fat deposits than males and would utilize marrow fat sooner.

3.5. Significance of annual fat cycle to condition

I have reported in detail (Dauphiné 1971) that mobilization of depot fat in caribou of both sexes occurred in the sequence, back fat, kidney fat, abdominal fat, and marrow fat. The exhaustion of the back fat, and the first use of the marrow fat, coin-

Table 11

Seasonal percentages of adult male and female Kaminuriak caribou with fat levels below 50% of the femoral marrow tissue. Sample sizes in parentheses

	June	July	Sept.	Nov.–Dec.	April
Male	0 (4)	0(15)	0(17)	33 (3)	2(54)
Female	31(134)	14(15)	3(36)	2(62)	13(79)

cided with the cessation of the decline in body weight and with a 50% decline in the two visceral fat indices. Kidney fat provided the most sensitive fat index of overall seasonal change. Both kidney fat and abdominal fat were effective indices over the full range of condition exhibited by our caribou. The sequence of fat mobilization applied more to the *rates* and less to the *start* of the decline because back, kidney and abdominal fat were mobilized together whenever body weight began to decline.

A similar sequence in deposition and mobilization of fat deposits occurs in mule and white-tailed deer (Harris 1945, Cheatum 1949, Taber *et al.* 1959, Ransom 1965), wapiti (Blood and Lovaas 1966, Flook 1970), red deer (Riney 1955), antelope (O'Gara 1968, Bear 1971), thar (*Hemitragus jemlahicus*) (Caughley 1970) and a variety of African ungulates (Smith 1970). Ransom (1965) reported that marrow fat in white-tailed deer was mobilized only when kidney fat had declined to approximately 30% of kidney weight.

The sequence of deposition and mobilization of fat deposits shown by Kaminuriak caribou also occurs in other populations of *R. tarandus*, according to qualitative descriptions by Jacobi (1931), Skoog (1968), and Kelsall (1968). There are few quantitative measurements available for exact comparison, however, and they largely concern the back fat deposit. Palmer (1934:9) observed back fat thickness of 2 to 3 in. (5.1–7.6 cm) in male Alaskan reindeer. Shaposhnikov (1955) reported back fat deposits up to 8 cm thick on wild reindeer in the USSR, and Jacobi (1931) recorded maximum fat thicknesses of 7.5 cm on Swedish reindeer. These thick-

nesses are slightly greater than our measurements from Kaminuriak males, but they probably represent upper extremes. However, Parker (1975) recorded an average back fat depth of 7.1 cm (range 4.1–8.0) for seven 4- and 5-year old males of *R. t. groenlandicus* killed in August on Coats Island. That mean is significantly greater than the peak mean (4.0 cm) attained by Kaminuriak males in September. Parker attributed the greater fatness of Coats Island caribou compared to those on the mainland to the absence of harassment from insects and predators, lack of migration, and possible use of marine plants as food.

Because of its large size, the back fat deposit has a larger effect on whole body weight than do the other fat deposits. A large male caribou examined by McEwan (1968) at the end of the summer growth period carried about 20 kg of back fat.

The fact that the mean fat content (by weight) of femoral marrow did not fall below 55% in Kaminuriak adults during the annual condition cycle indicated that the population did not suffer from extreme energy deficiency. Cheatum (1949) believed that the health of adult white-tails was not affected until the fat content of the marrow dropped below 25%. Klein (1968) found no marrow in the medullae of long bones from starved reindeer and took that as evidence that all fat was absent from the marrow at the time of death. Broughton (pers. comm.) found less than 10% fat in the marrows of starved Peary caribou, and Neiland (1970) encountered levels as low as 5% in Grant's caribou shot in Alaska.

Except for a small number of infant calves abandoned by their mothers, none

Figure 20

of the caribou we collected was debilitated and there was no evidence of mortality caused directly by malnutrition. The accumulation of snow was approximately equal during the winters when our specimens were obtained, and somewhat greater than the average of 16 winters between 1951 and 1968 (Fig. 20). Body weight and the size of fat reserves did not differ consistently from one winter to the next.

During this study there was no obvious relationship between snow depth (which may determine the availability of food) and the size of fat deposits in adult caribou. Males 5 years and older experienced a significant increase in marrow and

abdominal fat (Table 9) between December and April, despite the relatively deep snow present during that period (Fig. 21). The mean fat deposits of adult females (3 years or older) declined rapidly after April (Figs. 14, 16–18), although snow depth also lessened rapidly (Fig. 21). In younger males and females, however, the end of the winter decline in mean kidney, abdominal and marrow fat deposits occurred about April (Figs. 16–18), perhaps in response to lessening snow depth.

When snow accumulation is extreme, as in the winter of 1961–62 (Fig. 20), physical condition may be detrimentally affected. F. L. Miller (1974) found that

the 1962 cohort was almost completely missing from the population when this study began in 1966. He learned from eyewitness accounts that the females were in poor condition just before calving in 1962, and suggested that most of the cohort died shortly after birth. The survival of cohorts born in 1966, 1967, and 1968 was not unusually low. Therefore, I believe that the fluctuations in fat reserves observed during the study period were primarily the result of an inherent physiological rhythm, rather than of any nutritional deprivation posed by restricted availability of forage. In only one winter (1961–62) of 12 on the nearby range of Beverly caribou did snow depth

Figure 21
Average end-of-month snow depths recorded during
the winters of 1965–66, 1966–67, and 1967–68 at
three stations nearest the winter range and spring
migration routes of Kaminuriak caribou. Figure 1
shows the location of the stations. Snow data were
obtained from Monthly Records, Meteorological
Observations in Canada, Federal Department
of Transport

Figure 21
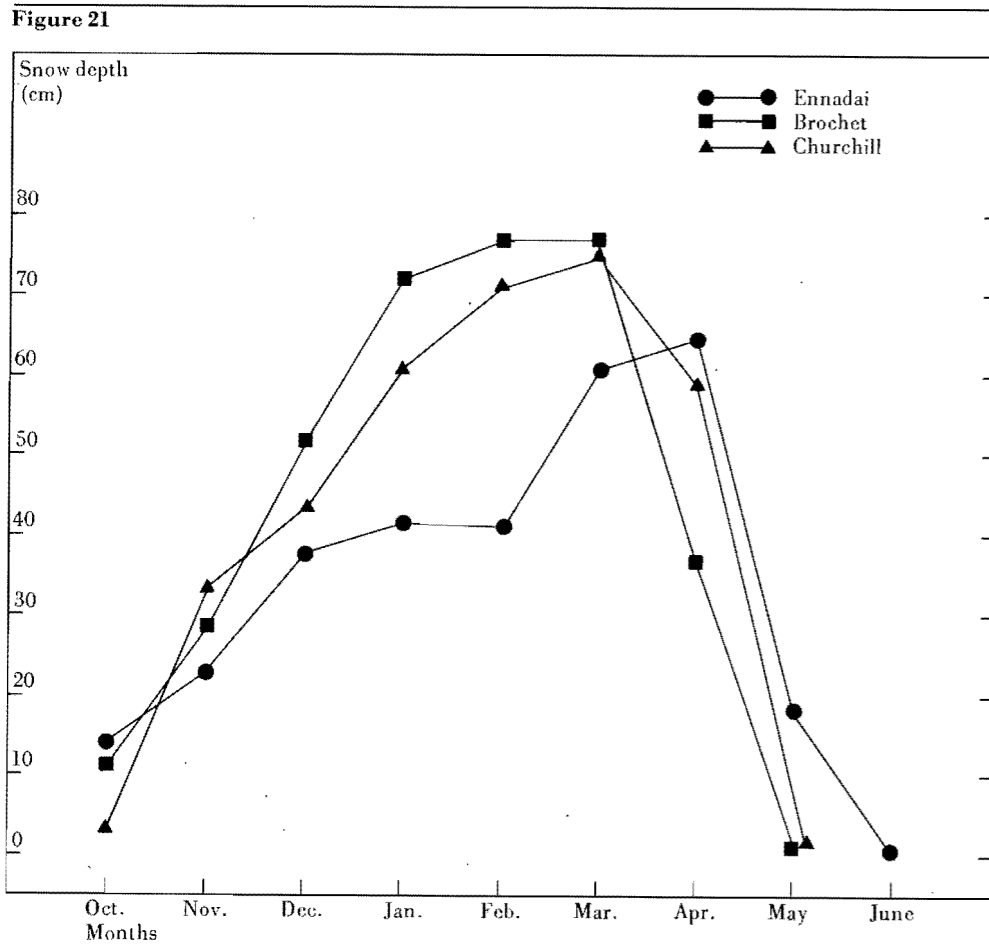
so restrict the availability of forage that
some starvation may have occurred (Kelsall
1968:237).

Captive caribou and reindeer may
voluntarily reduce their caloric intake by
30 to 40% in winter (Steen 1968, McEwan
and Whitehead 1970). A winter decline in
fat reserves need not be harmful if demands
do not exceed the reserve. Winter fat
reserves would not be adequate in the face
of unusual stress from such conditions as
very deep or hard snow, or continuous
harassment from predators or human activi-
ties. Males would be particularly vulnerable
from after the rut until April, and females
from late gestation until weaning, the

periods of the year when their respective
reserves are lowest.

4. Productivity

4.1. Age-specific rates of ovulation

Stained serial sections of the ovaries
from 94 caribou collected in November and
early December 1966 and 1967 were exam-
ined for ovulation structures formed during
the rut just passed. The structures enu-
merated were regressing corpora lutea of
estrus (non-pregnant cycles), functional
corpora lutea of pregnancy, and secondary[1]
corpora lutea of pregnancy. These three
structures comprised 62, 27, and 11%,
respectively, of the total ovulations. Age-

specific ovulation rates based on the oc-
currence of corpora lutea are presented in
Table 12. The female calves examined had
not ovulated, but at their second autumn
(age 1½ years) over half (57%) of the cows
ovulated. That proportion increased to
80% at the third rut (2½ years). Almost all
(96%) cows had ovulated when 3 years old
or older.

Age-specific ovulation rates have
not been determined for other populations
of *R. tarandus*, making an exact assessment
of the Kaminuriak data impossible. Accord-
ing to McEwan (1963), Beverly caribou
first ovulated at 1, 2, or 3 years of age, and
Michurin (1967) stated that most wild
reindeer on the Taimyr Peninsula first ovu-
lated as yearlings; these authors, however,
did not report the proportion ovulating
in each age group. In a Norwegian herd of
wild reindeer, ovulation was common
among calves since almost 50% conceived
at 4 months of age (Reimers 1972).

For the Kaminuriak sample, the
average annual number of ovulations per
ovulating female for all ages combined was
2.9. Ovulating yearlings produced an av-
erage of 1.5 ova each, about half the pro-
duction of older females. Age-related de-
clines were not apparent in either the pro-
duction of ova or the proportion of ovu-
lating females; however, the samples in the
10- and 11-year age groups were small. Of
the 73 ovulating cows examined, 11% had
ovulated five or more times in the current
year, including one female with a maximum
of seven ovulations.

4.2. Timing of ovulation

Forty-eight pregnant cows collected
between November 21 and December 12 in

[1] Defined here as a persistent corpus luteum from a
previous estrous cycle or from an additional ovu-
lation during the current cycle (Corner 1942,
Gibson 1957, McEwan 1963), or from a luteinized,
non-ovulated follicle (Robinette *et al.* 1955, Gibson
1957, McEwan 1963). A minor portion of second-
ary corpora lutea may not have been associated
with ovulation (accessory), as I could not dis-
tinguish positively between ovulated and non-
ovulated secondary corpora lutea.

Table 12
Age-specific ovulation rates based on counts of
corpora lutea in 94 Kaminuriak caribou collected
in November and December of 1966 and 1967

Age at rut (yrs)	n	Percentage ovulating	Ovulation rate*	Ovulations per ovulating female Mean	Range
< 1	12	0	0.0	0.0	—
1	7	57	0.9	1.5	1–2
2	20	80	2.4	3.0	1–6
3	15	100	2.9	2.9	2–4
4	6	100	3.7	3.7	2–5
5	4	100	2.2	2.2	2–3
6	4	100	2.0	2.0	2–2
7	8	100	3.4	3.4	1–6
8	10	90	2.6	2.9	1–5
9	5	100	2.6	2.6	2–4
10	2	100	6.0	6.0	5–7
11	1	0	0.0	0.0	—
0–11	94	78	2.3	2.9	1–7
≥ 1	82	89	2.6	2.9	1–7
≥ 2	75	92	2.8	3.0	1–7
≥ 3	55	96	2.9	3.0	1–7

* Rate for all females in age-group, including any
which did not ovulate.

1966 and 1967 had conceived between
October 19 and 29, according to the age of
their embryos (Dauphiné and McClure
1974). A count of functional and regressing
corpora lutea in their ovaries indicated that
during the breeding season these females
had produced an average of three ova each
and that eight had produced four to seven
ova. These ovulations probably occurred
within a 36-day span, because none of the
39 females collected between September
16 and 24 in those years had ovulated
(Dauphiné and McClure 1974). The dif-
ferent size and histological age of regressing
corpora lutea of estrus in the ovaries col-
lected after the rut indicated that corpora
were formed in different estrous periods.
Though the actual timing of the ovulations
could not be determined, they must have
occurred as single ovulations in a series of
estrous periods, as multiple ovulations
during one or more estrous periods, or as
ovulations shortly after conception. My
data and the observations of other workers

suggest that both of the first two possibil-
ities occurred.

4.2.1. Repeated estrous periods

Schmitt (1936), Bergerud (1961), and
McEwan and Whitehead (1972) have re-
ported that the estrous cycle (interval be-
tween estrous periods) is from 10 to 12
days in *R. tarandus*. Hence, in the time
between late September and the date of
conception in late October, two or three full
estrous cycles could have occurred. Ac-
cording to observations, reindeer are
capable of four or more estrous cycles a
year (Gorbunov 1939, Baskin 1970). Es-
trous periods which occurred before the
final fertile estrus in late October may have
been "silent heats" in which ovulation oc-
curred but the female did not exhibit es-
trous behaviour. Thomas (1970) reported
that black-tailed deer have a preliminary
silent estrus before the fertile estrus.
Bergerud (1961) believed that changes he
observed in the external genitalia of captive

Newfoundland caribou were the result of
ovulation without overt estrous behaviour.
Most Kaminuriak caribou mated synchro-
nously (Dauphiné and McClure 1974), and
one or more preliminary, silent estrous
periods may create a threshold condition
in the female's endocrine system which is
essential to synchronous mating. In the
wildebeest (*Comochaetes taurinus*), another
species which mates synchronously, first
estrus is not overt, and the presence of a
degenerating corpus luteum of estrus ap-
pears necessary for subsequent estrus and
conception (Watson 1969).

4.2.2. Multiple ovulation at estrus

The eight Kaminuriak cows which
ovulated four to seven times before con-
ceiving must have shed more than one
ovum during a given estrous period, since
they could not have cycled more than three
times before they conceived. McEwan
(1963) found two newly ruptured follicles
in each of a series of ovarian pairs he
collected during the rut from Beverly cows
and concluded that two ova were shed at
about 40% of all estrous periods. Twin-
ning, which has occurred in well-nourished
captive caribou (McEwan 1971), probably
results when two ova are shed and fertilized
at the same estrus.

4.2.3. Post-conception ovulation

Though reported for elk (Halazon
and Buechner 1956), ovulation during
gestation has not been reported for *R. taran-
dus*. I did not find any large or recently
ruptured follicles or new corpora lutea in
ovaries of Kaminuriak cows collected
during the 2nd, 6th, and 7th months of
gestation. Possibly some regressing corpora
lutea of estrus or secondary corpora lutea
in the ovaries of pregnant females collected
in November and December had formed
shortly after conception, *i.e.* at 10–12 days,
the length of one cycle. When cows were
collected 4 to 6 weeks after conception,
corpora from post-conception ovulation
would have been indistinguishable from
corpora formed before conception.

Table 13
Percentage occurrence by age (at breeding season), month, and year of pregnant and post-partum females in nine samples collected from the Kaminuriak population between April 1966 and July 1968. Sample sizes in parentheses

Gestation period	Age (yrs)	Percentage of females pregnant or post-partum				Ave. for period
		Nov.–Dec.	April	June	July	
1965–1966	< 1		0 (6)	0 (6)		0 (12)
	1		0 (6)	0 (10)		0 (16)
	2		80 (5)	25 (12)		41 (17)
	≥ 3		92(26)	90 (31)		91 (55)
1966–1967	< 1	0 (4)	0 (7)	0 (5)		0 (16)
	1	0 (1)	0 (9)	0 (12)		0 (22)
	2	55(11)	44 (9)	83 (6)		58 (26)
	≥ 3	100(36)	94(32)	83 (42)		92(110)
1967–1968	< 1	0 (8)	0 (7)	0 (2)	0 (3)	0 (20)
	1	0 (8)	17 (6)	0 (3)	0 (2)	6 (19)
	2	40(10)	40 (5)	56 (9)	0 (2)	46 (26)
	≥ 3	73(26)	88(26)	94 (50)	85(13)	87(115)
Months and periods combined	< 1	0(12)	0(20)	0 (13)	0 (3)	0 (48)
	1	0 (9)	5(21)	0 (25)	0 (2)	2 (57)
	2	48(21)	53(19)	48 (27)	0 (2)	48 (69)
	≥ 3	89(62)	92(84)	89(121)	85(13)	90(280)

Table 14
Age-specific pregnancy rates of females collected from the Kaminuriak population during or shortly after the 1966, 1967, and 1968 gestation periods[*]

Age at breeding season (yrs)	n	No. pregnant or post-partum	% Pregnant or post-partum
< 1	48	0	0
1	57	1	2 †
2	69	33	48 †
3	50	41	82
4	22	21	95
5	30	29	97
6	63	55	87
7	33	31	94
8	44	41	93
9	17	17	100
10	10	7	70
11	3	2	67
12	2	2	100
13	3	3	100
14	2	1	50
15	1	1	100
0–15	454	285	63
≥ 1	406	285	70
≥ 2	349	284	81
≥ 3	280	251	90

[*] Includes November, April, June, and July collections.
† $P < 0.01$.

4.3. Annual pregnancy rates

Pregnancy rates derived from nine samples of Kaminuriak cows obtained during and shortly after the gestation periods in 1966, 1967, and 1968 are presented by four age groups in Table 13. Pregnancy was identified by the presence of a corpus luteum and an embryo or fetus in 186 cows, by a functional corpus luteum in 12 cows (November–December samples only), and by a partially involuted uterus and regressed corpus luteum in 87 cows.

All combinations of pregnancy rates from seasonal samples drawn in the same year, and from samples drawn at the same season in different years, were subjected to χ^2 analyses[1] to determine the probability that deviations among pregnancy rates reflected real differences in the proportion of breeding cows. Inspection prior to testing revealed large differences in rates between age classes. Tests were therefore conducted

[1] The Yates correction for small expected frequencies in 2 x 2 contingency tables was applied when expected frequencies were below five (Maxwell 1961:21).

separately for cows 2½ to 3 years old and 3½ years and older. Samples of younger cows were too small for testing because of the low pregnancy rates encountered. The only evidence of a decline in pregnancy rate within any gestation period was a significant difference between pregnancy rates in November 1966 (100%) and June 1967 (83%) for cows 3½ years and older. The November rate was much higher than the other samples (Table 13), and the test may be misleading. I therefore assumed that pregnancy rates derived from females sampled early in gestation closely approximated the actual birth rate, and I combined samples taken at different times in each gestation period to estimate the pregnancy rate for the year (Table 13). Pregnancy rates in the 3 years were not significantly different.

4.4. Age-specific pregnancy rates

All females in each age class from the years 1966–68 and from different seasons of the year except September were combined to compute age-specific conception rates (Table 14).

Conception occurred in none of the calves, in less than 2% of yearlings, in 48% of 2-year-olds, and in 90% of cows 3 years or older.[2]

The differences between yearlings and 2-year-olds and between 2- and 3-year-olds were each highly significant ($P < 0.01$), but differences between cows of 3 and 4, 5 and 6, and 7 and 8 years of age were not significant. Furthermore, 9 (82%) of 11 females between 11 and 15 years of age conceived, indicating no decline in conception rate with increasing age within the limitations of the sample.

4.5. Age at first conception

Estimates of the approximate proportions of females that conceived for the first time as yearlings or 2-year-olds were obtained from the difference in pregnancy rates between age classes in Table 14; of 100 females, 2 first conceived as yearlings and 46 as 2-year-olds.

[2] Pregnancy rates given by Parker (1972:71) for the Kaminuriak population were misquoted.

The number of past pregnancies, assumed equal to the number of scars of regressing corpora lutea of pregnancy in the ovary, was also used to identify the age of first conception for females 2 and 3 years old. Regressing corpora lutea from pregnancies terminating 5 and 17 months before could be identified and were used to reveal the age of first conception. Of fifteen 3-year-old cows, 20% had first conceived as yearlings, 47% as 2-year-olds, and the rest (33%) as 3-year-olds. Twenty per cent of 20 females 2 years old experienced their first conception as yearlings, and 50% as 2-year-olds; the remaining 30% had not yet conceived. All 21 females that were 3 or 4 years old had conceived at least once. To summarize, regressing corpora lutea of pregnancy indicated that approximately 20% of a cohort first conceived as yearlings,

50% as 2-year-olds, and the remaining 30% as 3-year-olds. These rates, except for yearlings, are similar to those derived above from pregnancy rates in Table 14. The differences between the estimates of pregnancy rates for yearlings from fetal count (2%) and from regressing corpora lutea (20%) is significant. The former is more reliable as it is derived from the positive identification of pregnant females in a larger sample. The apparent excess in the number of regressing corpora lutea in 2-year-olds may be the result of pregnancies terminated early by resorption of embryos or of misidentification of corpora lutea of pregnancy.
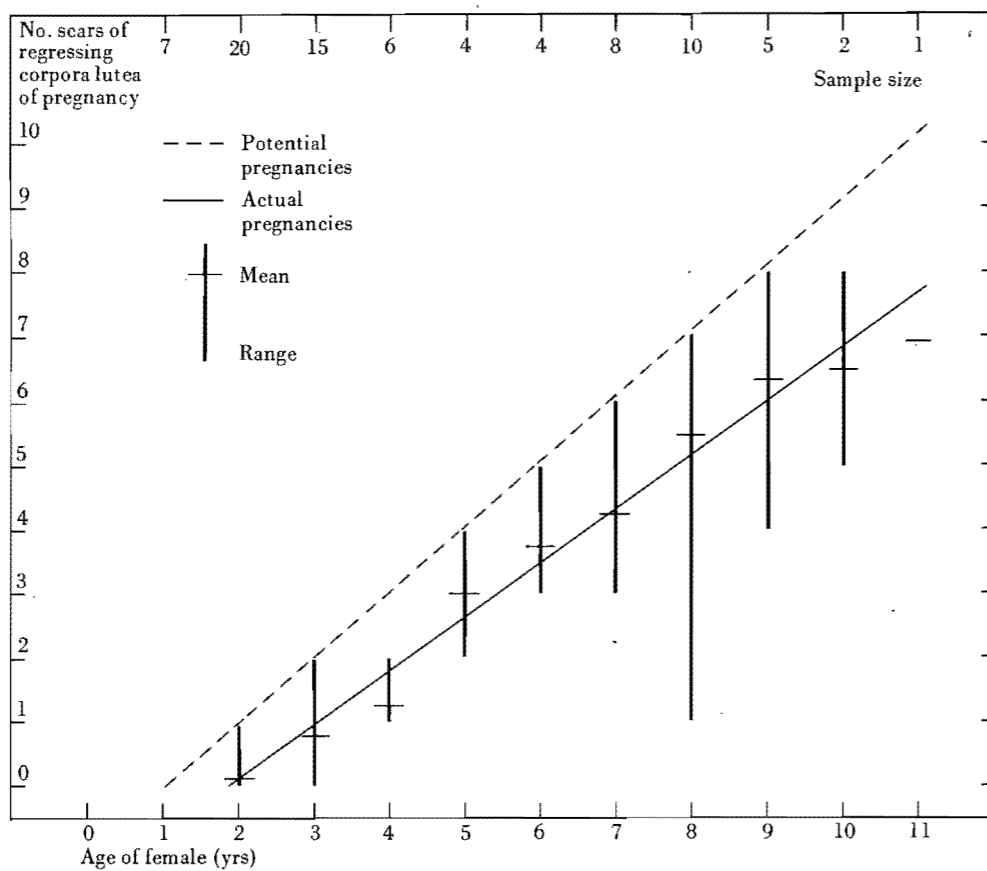
4.6. Continuity of conception during a female's lifetime.

The number of pregnancies experienced by a female during her lifetime was

estimated by counting scars of regressing corpora lutea of pregnancy. Cows pregnant during the previous season were identified by characteristic 5-month regressed corpora lutea of pregnancy, which were larger than older scars.

Pregnancy scars were used to make a comparison (Table 15) of the current pregnancy rate of females which had been pregnant the previous season with the rate of those which had not. All females 3 years or older which had not been pregnant in the previous year conceived in the year in which they were collected, whereas among females that had been pregnant the year before some of each age class failed to breed. Two- and 3-year-old females conceived at a lower rate in the rut following a pregnancy than did older females.

The linear regression of the number of regressing corpora lutea of pregnancy on age for 82 cows collected during November and December in 1966 and 1967 was highly significant ($P<0.01$, $r = 0.932$) (Fig. 22). The regression line (expressed by $y = 0.839x - 1.452$) indicated that after her first pregnancy the average cow became pregnant in approximately 4 of every 5 successive years.

The maximum potential number of pregnancies possible for a female first conceiving as a yearling is one less than the number of years that she has lived (Fig. 22). Fourteen (19%) of 75 cows between 2 and 11 years of age achieved that rate. The average number of pregnancies for each age group was between one and two below the maximum possible, since most females do not calve until 3 or more years of age and do not become pregnant every year. Only one cow, an 8-year-old, was far below the range expected for her age group, having produced only one calf. She was in her second pregnancy when collected and her reproductive tract, body weight and fat reserves were normal. She provided the only evidence that chronically infertile ("barren") females occurred in the Kaminuriak population. We found no completely barren females over 3 years of age.

Figure 22

4.7. Causes of reproductive failure

Non-breeding females were encountered in all samples, the proportion being relatively larger in those younger than 4 years (Table 14).

Non-ovulation was an important cause of infertility in young caribou, whereas non-conception after ovulation (or resorption of the ovum, blastocyst, or embryo soon after conception) was the usual cause in older cows (Fig. 23). Of the older non-pregnant cows examined in November and December, about 40% of the yearlings, 40% of the 2-year-olds, and 30% of the adults (3 years and older) had not ovulated; the remaining females had ovulated but either failed to conceive or resorbed their conceptuses within a few weeks.

Embryonic and fetal mortality, a possible cause of reproductive failure, was rare in the caribou examined. Four (7.5%) of 52 embryos collected in November were apparently not viable (although their deterioration may have been caused by incomplete fixation). All 126 fetuses collected in April and June 1966–68 were viable. Only one female, 14 years old, appeared to have aborted; when collected in April 1966, her uterus was non-gravid, but one ovary contained a corpus luteum of pregnancy in early regression. The surfaces of both her ovaries were covered with tiny (1–2 mm) wart-like projections. Although her serum was not tested, she may have had brucellosis, a bacterial disease of the reproductive organs in ruminants (Manthei *et al.* 1956);

its pathological effects may cause abortion. Broughton and Choquette (1969) found evidence of brucellosis infection in 4% of 200 Kaminuriak females collected during this study.

Because at the most only 2% of the fetuses and embryos examined were not viable, I conclude that prenatal mortality was not a significant cause of reproductive failure in Kaminuriak caribou. Instead, my results indicate that the major cause of reproductive failure in females above 1 year of age was failure of ovulating females to conceive, *i.e.* failure to copulate or copulation without fertilization, or conception with early death of the zygote. The question could be resolved only by examining ovaries from females collected at intervals during the rut, for which the occurrence of estrus and copulation were known. There is no comparable information on reproductive failure available for other *R. tarandus* populations.

4.8. Comparative fertility of Kaminuriak caribou

The age-specific pregnancy rates calculated for the Kaminuriak population (Table 14) are compared in Table 16 to rates of corresponding age classes in samples from the Beverly population (northern Canadian mainland) and the Nelchina population (central Alaska). Those were the only three caribou populations for which age-specific pregnancy rates were available. The comparison showed no significant differences with the exception that for cows 3 years and older, the pregnancy rate of the Kaminuriak sample was higher ($P<0.03$, $x^2 = 6.5$) than the Beverly's. However, the Beverly population's adult rate appears abnormally low compared to data from other *R. tarandus* populations.

The pregnancy rate was 94% in Newfoundland caribou cows 2 years or older at the breeding season (Bergerud 1969), in contrast to the 81% pregnancy rate for that age group in the Kaminuriak population. Between 80 and 95% of the females 2 years or older in a population of wild reindeer in

Figure 23
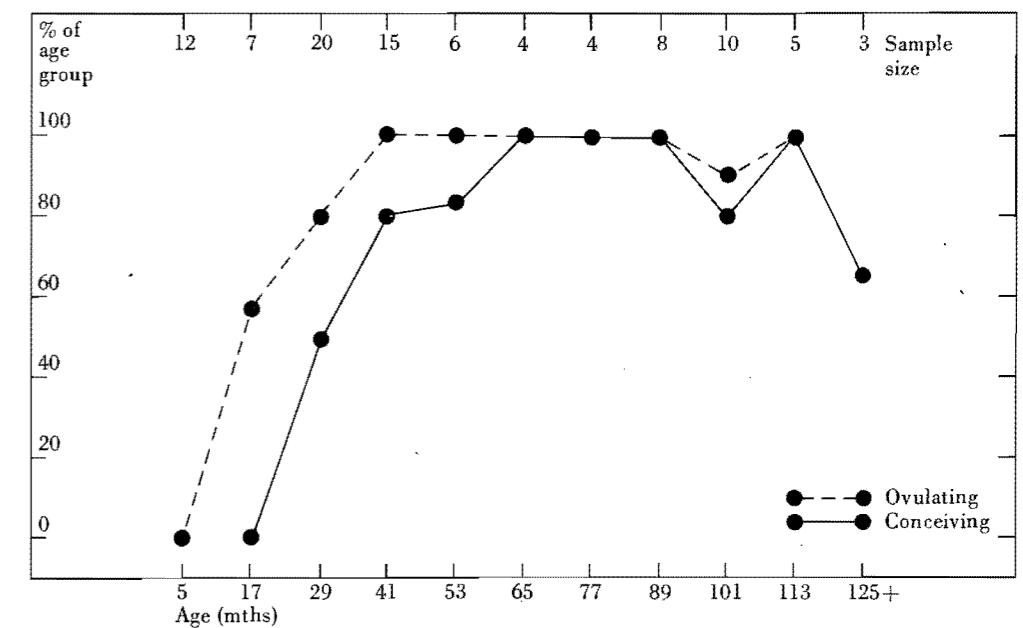
Table 15
Percentage pregnancy rates of female caribou according to whether or not they were pregnant in previous year. Sample sizes in parentheses

Age at breeding season (yrs)	Pregnant previous year	Not pregnant previous year
2	25 (4)	50(16)
3	67 (9)	100 (7)
≥ 4	89(35)	100(11)

Table 16
Percentage comparison of the age-specific pregnancy rates of the Kaminuriak, Beverly, and Nelchina caribou populations. Sample sizes in parentheses

Age at breeding season (yrs)	Kaminuriak population	Beverly population [*]	Nelchina herd Alaska [†]
< 1	0 (48)	—	0 (24)
1	2 (57)	33 (3)	13 (31)
2	48 (69)	50(16)	61 (46)
≥ 3	90(280)	78(69)	89(335)

[*] Data from McEwan (1963).
[†] Data from Skoog (1968).

Table 17
Comparison of mean body size and fatness measurements taken 4–6 weeks after the rut from reproductively active and inactive female caribou 1, 2, and 3 years of age

Age (yrs)	Reproductive status	n	Body size Shoulder height (cm)	Body length (cm)	Metatarsus length (cm)	Body weight (kg)	Fat deposits Back fat depth (mm)	Kidney fat wt. (g)	Abdominal fat wt. (g)	Marrow fat content (%)
1	Ovulating	3	92	152	36.1	62.8	1	40	115	70
	Non-ovulating	4	92	156	36.1	64.8	2	35	150	74
2	Pregnant	7	97	161	36.6	79.2*	10*	58	263	72
	Non-pregnant	10	94	158	36.7	73.2*	2*	58	157	65
3	Pregnant at both 2 and 3 years	6	97	168	36.4	86.0	23⎱	97⎱	613⎱	73
	Pregnant only at 3 years	6	95	160	36.6	86.0	19 †	82 †	475 *	70
	Pregnant only at 2 years	3	99	164	36.9	79.3	5⎰	46⎰	254⎰	69

* $P < 0.05$.
† $P < 0.01$.

the USSR become pregnant each year (Michurin 1967), far above the 70% rate indicated for that age group in the Kaminuriak population. Pregnancy rates of 70 to 90% were reported for Alaskan reindeer by Hadwen and Palmer (1922) and 80 to 90% for domestic reindeer in the USSR by Flerov (1952). Comparisons of the incidence of pregnancy in the Kaminuriak population with other populations for which the proportion of young females was not specified are not fully meaningful. Since young females usually have lower pregnancy rates than females over 3 years of age, population differences in pregnancy rates could be caused by differences in age composition.

There were no twin embryos or twin fetuses in 186 gravid uteri collected from the Kaminuriak population. Michurin (1967) found no twins in 300 gravid uteri from wild reindeer of the Taimyr Peninsula, and Skoog (1968) and Bergerud (1969) found no evidence of twinning in Alaskan and Newfoundland caribou respectively. Twinning has been reported for a captive barren-ground caribou (McEwan 1971) and free-ranging reindeer (Nowosad 1973), but not for wild caribou.

5. Relationship between breeding performance and fat reserves in female caribou

5.1. Female body size and fatness and the attainment of puberty

Approximately half of the 1½-year-old cows examined had ovulated (Table 12) and about half of the 2½-year-old cows had conceived (Table 14). Although no significant differences existed between the November–December means of the ovulating and non-ovulating yearlings in the four measurements of body size and four measurements of fatness (Table 17), sample sizes were too small for the result to be conclusive. Pregnant 2-year-old cows nevertheless showed a small but consistent superiority over the non-pregnant group in all variables except kidney fat and metatarsus length (Table 17). Differences were significant in body weight and back fat depth. On the basis of information from other species such as white-tailed deer (Verme 1967, 1969), domestic sheep (Clark 1934) and cattle (Joubert 1954), larger and fatter females in both age groups should be expected both to ovulate and to conceive at an earlier age than smaller, leaner females.

The reciprocity between breeding activity (conception, pregnancy, and lactation) and physical condition was also examined by comparing three categories of 3½-year-old cows: those conceiving at both 2 and 3 years; those conceiving only at 3 years, and those conceiving only at 2 years. Cows in the first two categories were similar and had higher mean body weights and fat deposits (except marrow fat content) than cows in the third category (Table 17). Females that became pregnant at both 2 and 3 years had the highest fat reserves. Cows that did not breed at 2 years, and that presumably possessed low fat reserves then, had about the same average levels of fat reserves when they reached puberty at 3 years as cows that bred in both years.[1] Lastly, the females which conceived at 2 but

[1]In April, pregnant 2-year-old females showed a greater superiority in body weight and fatness over non-pregnant females than in the previous November and December. There were significant differences in body weight, back fat depth, kidney fat weight and abdominal fat weight. However, in June at 3 years, the non-breeding females had means of the above variables which were equal to or slightly larger than those of the breeding females, though the difference was significant only in the case of back fat depth.

not at 3 years had lower mean body weight and fat reserves (except marrow fat content). To summarize, in November and December the breeding females in each cohort had consistently higher fat reserves than non-breeders and, conversely, those females that attained higher fat reserves in autumn experienced higher breeding success. In yearling females ovulation occurred regardless of, and with no effect on, condition whereas at 2 and 3 years of age pregnancy (with lactation) was influenced by physical size and fatness and in turn reduced the fatness of some individuals.

Many authors have stated that females in well-nourished *R. tarandus* populations ovulate and conceive at an earlier age than their counterparts in poorly nourished populations (Hadwen 1942, Klein 1959, Nikolaevskii 1968, Skoog 1968, Reimers 1972). Also, some caribou calves placed on highly nutritious diets in captivity have experienced estrus at 5 months of age (McEwan and Simard, pers. comm.), a feat not recorded for wild caribou. Kaminuriak females were typical in that differences in body size and fatness were associated with the age of first conception (Table 17). Several workers have remarked that pregnancy at a "premature" age may be undesirable in *R. tarandus* populations because the increased nutritional stress may impair further growth (Michurin 1967, Skoog 1968). Reimers (1972) found no difference in body weights and diastema lengths of females in two reindeer herds from a common origin, one better nourished than the other, whereas the males were different. Reimers postulated that because females in the well-nourished herd experienced puberty at an earlier age (47% at 4 months), they did not reach the full growth potential of males. Somewhat the same condition exists in the Kaminuriak population. Three of the nine 3-year-olds that had conceived at 2 years of age were smaller in body weight and fat reserves than any of the females that did not conceive until they were 3 years old. The majority of the females that conceived at 2 years, however,

were animals that had remained superior in weight and fatness despite their pregnancy at an early age (Table 17). Body growth was largely completed by the end of the third summer of life in most Kaminuriak cows (Figs. 6–10), yet only half of the cows bred that autumn (Table 14). The remaining cows did not breed until a year later at 3½ years of age (except for a few which bred as yearlings). The lag between body growth and sexual maturity in most cows may be of adaptive significance in that growth is given priority to ensure maximum development of the individual, which is then better equipped to bear and support calves.

5.2 Body size and fatness in breeding and non-breeding females

Body size and fatness of breeding and non-breeding females were compared at various intervals during the annual reproductive cycle to determine first, whether energy reserves of females prior to the breeding season influenced their breeding success, and second, whether pregnant cows suffered a greater drain on their fat reserves than non-breeders, and if so whether the drain affected subsequent reproductive performance.

Before analysing[1] differences in the condition of breeding and non-breeding females, specimens were grouped into homogeneous breeding and age combinations. Females aged 11 years or older were excluded from analysis because they were significantly smaller and leaner than 3- to 10-year-old females and because of inadequate sample size. Two-year-old cows were separated from 3- to 10-year-olds because the two groups differed significantly in pregnancy rates (Table 14).

[1]Student's *t* test was used for comparisons of kidney, abdominal, marrow fat, and body weight measurements. Body weight was adjusted by subtracting the weight of the uterus and its contents. At the low portion of the annual fat cycle, x^2 was used to test for differences between proportions of females with <0.1 mm back fat depth in each group. This was a more discriminate procedure than using the fat depth itself because many females had no fat in the deposit.

Table 18
Comparison of mean seasonal fat and body weight measurements from breeding and non-breeding female caribou aged between 3 and 10 years

Age combination (yrs)	Season of collection	Reproductive status	n	Body wt. (minus uterus) (kg)	n	Back fat depth (mm)	n	% with back fat	n	Kidney fat* wt. (g)	n	Abdom- inal fat* wt. (g)	n	Marrow fat content (%)
3–9	November and December	Breeding	38	89.8 †	39	16 †	39	90 †	35	78	36	458 †	37	77 †
		Non-breeding	7	76.4	7	3	7	57	7	45	7	203	7	68
3–9	April	Breeding	64	74.4	64	7 †	64	69 †	56	54	44	249 †	61	70 †
		Non-breeding	6	69.7	6	0	6	0	4	37	3	92	6	49
4–10	June	Breeding	100	76.4	92	1 †	92	24	99	32 †	97	125 †	96	55
		Non-breeding	10	81.2	9	4	9	44	10	60	10	22	10	64
4–10	July	Breeding	9	76.1	9	4	9	44	9	39	8	92	9	52
		Non-breeding	1	71.2	1	10	1	100	1	49	—	—	1	78
4–10	September	Post-partum	22	90.6 †	22	15	22	86	19	68	21	382	21	68
		Non-breeding	3	97.3 †	3	21	3	100	3	93	3	615	3	74
4–9	November and December	Pregnant this yr, and last	32	90.0	31	14	31	88	30	74	30	476	31	75 †
		Pregnant this yr, not last	4	95.9	4	19	4	100	4	85	4	468	4	81

* Geometric means.
† P < 0.05.

Figure 24

The means of body weight[1] and four fat deposits of breeding and non-breeding females were compared (Table 18) at six stages in the annual reproductive cycle; 1 to 1½ months gestation (November–December), 6 to 6½ months gestation (April), 7 to 7½ months gestation or less than ½ month post-partum (June), 1 to 1½ months post-partum (July), 3 months post-partum (September), and 5 months post-partum (November–December). The means are plotted against months in Figure 24.

In early gestation (November and December), mean body weight and fat measurements of pregnant cows were significantly higher than corresponding means of non-pregnant cows (Table 18). Superiority was as follows: body weight, 18%; back fat depth, 433%; kidney fat weight, 73%; abdominal fat weight, 126%; marrow fat, 13% (Fig. 24). Similar differences probably also existed during the rut 4 to 6 weeks earlier, as there were no significant changes between September and November–December means of body and fat measurements for females 2 years and older (Tables 4 and 8).
[1]Minus the weight of uterus and its contents (p. 15).

Between November–December and April, fat reserves and body weight dropped considerably, with the pregnant cows showing the greater loss. In April pregnant females still had greater fat reserves than non-pregnant females (Table 18). By June, non-breeders had already started to accumulate fat and exceeded breeders in all mean fat measurements except abdominal fat. The breeding cows did not begin to accumulate fat until after mid-July (Fig. 24). Figure 24 indicates that pregnant cows mobilized their fat reserves most rapidly between April and June, the last third of gestation. McEwan and Whitehead (1972) reported that during this stage of gestation captive caribou and reindeer voluntarily increased their energy intake by about 14%, apparently to meet the increased energy demands of their rapidly-growing fetuses. Kaminuriak cows apparently used their reserve fat to obtain the necessary energy because during late gestation their access to food was limited by deep snow (Fig. 21) and by the time required to migrate about 640 km (400 miles) to the calving grounds (Parker 1972).

The opposite trends in the use of fat reserves by breeding and non-breeding cows (Fig. 24) indicate that in June and July the energy demand created by pregnancy and lactation was so great that cows could not replenish fat reserves even though dietary energy in excess of maintenance requirements became available. A high demand for energy continues and may even increase during lactation; according to Moen (1973:362), the energy expenditure of female white-tails increases after parturition and, during peak lactation, it may exceed by 20 to 40% the amount of energy required during gestation.

Only small samples of cows which had not bred the year before were obtained in September and November–December (Table 18), making statistical comparisons with cows which had been pregnant inconclusive. However, the body weight and fat means of the former group were consistently larger (Table 18, Fig. 24), except for abdominal fat in November–December, and significantly so for body weight in September and marrow fat in November–December. The data strongly suggest a tendency to
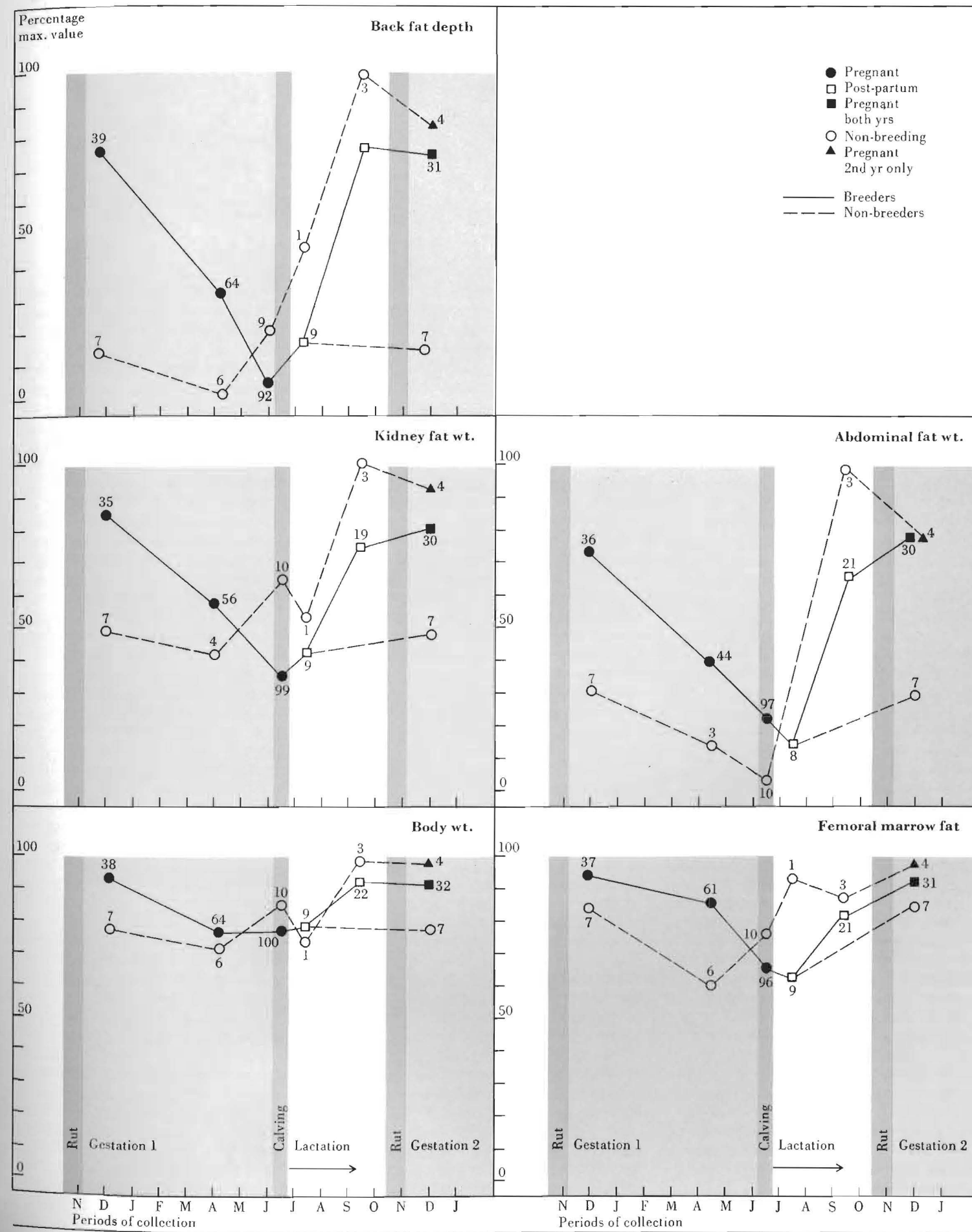
Conclusions and overview

greater fatness among cows that were not pregnant the previous year.

It may be that a cow's pre-rutting condition tends to decline from year to year with successive pregnancies and lactations until she fails to breed. The year's respite permits her to recover her condition and begin breeding again the following autumn. There would be obvious survival value to the cow and to her next calf. Failure to breed could be caused by low energy reserves before the rut. Poor physical condition is associated with the reduction or prevention of estrus and estrous behaviour in mule deer (Robinette *et al.* 1955, Julander *et al.* 1961), white-tailed deer (Verme 1967), domestic sheep (Clark 1934), and cattle (Wiltbank *et al.* 1962).

Loss of calves soon after birth may permit more complete recovery of condition in some cows. Parker (1972) reported that at least half of the calves born in 1967 and 1968 died before they were one month old. Death of the calf before the normal weaning age of 3 or 4 weeks (McEwan, pers. comm.) would relieve the dam of part of the stress of lactation. The relatively rapid summer fat deposition in non-breeding cows suggests that the sooner a calf dies after birth the more complete will be its dam's recuperation by the following rut and the better her chances of another pregancy. It is possible that the annual pregnancy rate of 90% exhibited by adult cows was partly maintained by the high infant mortality rate in those years. Had more cows successfully weaned their calves, perhaps the pregnancy rate would have been lower. Similar compensatory relationships have been identified in bison by Fuller (1966) and in white-tailed deer by Verme (1967, 1969). The question that remains is whether the dam's poor physical condition contributes to the early death of her calf; it is of key importance to explaining the relationship between nutrition and the regulation of numbers in barren-ground caribou populations.

Information presented in this report and in the companion reports by Parker (1972), F.L. Miller (1974), and Miller (1976) provides the basis for an overview of the biology of the Kaminuriak population and for an evaluation of the feasibility of its management.

During each of the two winters of our study, snow depth was above average but within the range of what the population had experienced during the previous two decades. Body growth and the deposition of reserve fat were restricted to the periods June to October for males and non-breeding females and July to October for nursing females. During winter, growth and energy demands were reduced as part of an inherent metabolic cycle. However, the extensive mobilization of fat reserves during reproductive activity, although it did not result in outright starvation, came at potentially critical times, *i.e.* for males preceding the period of greatest snow depths and for females preceding the period of highest energy demands of fetus and calf. Because females did not attain pregnancy rates typical for the species until 3 years of age, the productivity of the population as a whole was low. The evidence suggests a reciprocal relationship between physical condition and reproductive performance in females. Pregnancy and lactation, if repeated in a series of years, may reduce the condition of the cow. If she is unable to attain a certain level of condition by autumn she may not breed. During the ensuing idle year she recuperates to begin breeding again. The Kaminuriak population's high birth and neonatal mortality rates suggest that many cows may repeatedly produce calves that die before being weaned, partially recuperate, and breed again without attaining a high enough level of condition necessary to produce calves that can survive.

From 1966 to 1968 the size of the population remained stable, an annual increment of about 10% balancing approximately equal adult losses to hunting and predation (Parker 1972). Calf mortality was the greatest impediment to population

growth; only about one-fifth of the calves born lived to the age of 1 year. The direct causes of calf mortality observed in the Kaminuriak and other barren-ground caribou populations included predation, abandonment, hypothermia, disease, injuries, accidents, birth defects, and starvation (De Vos 1960, Hart *et al.* 1961, Pruitt 1961, Lent 1966, Kelsall 1968, Miller and Broughton 1974). Parker (1972) found that most calves died within 4 to 5 weeks of birth, during the period when they are dependent on milk (McEwan, pers. comm.) and when, as my results show, their dams have lowest energy reserves. Druri (1960) reported that when ice crusts or deep snow caused unfavourable grazing conditions for pregnant reindeer, their calves weighed less at birth and the percentage of calves that died at birth increased. According to Bergerud (1974:763), "Newborn calves in Newfoundland ranged in weight from 10 to 22 lb; however, newborn hand-reared calves of less than 14 lb seemed weak, and invariably died in captivity." Though the relationship between maternal condition and calf viability has not been investigated for barren-ground caribou, it seems reasonable to assume that survival of Kaminuriak calves must depend to some degree on the level of nutrition available to their dams during late gestation, as suggested by McEwan and Whitehead (1972), and during lactation. It has been shown in deer and domestic sheep that maternal energy deficiency during late gestation and lactation lowers birth weight and milk production, and leads to an increase in neonatal mortality (Thomson and Thomson 1953, Kitts *et al.* 1956, Alexander 1962, Verme 1963). My results indicate that during late gestation Kaminuriak cows received inadequate energy from their diet and had to mobilize their fat reserves. The question that remains is whether those fat reserves provided enough energy to meet the demands of their growing fetuses and nursing calves, since according to experiments with captive cervids (McEwan and Whitehead 1972, Moen 1973) such demands are very high.

The proportion of cows that could provide sufficient energy for survival of their calves would change from year to year according to the influence of several variables, including depth and hardness of snow on both the winter range and the migration route to the calving ground, wind-chill levels to which neonates are subjected, and the amount of activity required of calves to travel with their dams and to escape predators.

The actual effect of malnutrition on mortality of Kaminuriak calves is difficult to demonstrate and if operative has largely been masked by more direct agents of mortality. Miller and Broughton (1974) found relatively few calf deaths resulting from malnutrition in 1970. However, favourable weather during that calving season and little snow accumulation the previous winter (less than in 12 of the 16 winters illustrated in Figure 20) may have combined to minimize nutrition-related losses. Indeed, these authors reported that calf mortality during the summer of 1970 appeared to be only about half as great as mortality in 1967 and 1968 measured by Parker (1972). I suggest that malnutrition rarely runs its full course to become a direct cause of death to Kaminuriak calves, but that instead it renders calves more vulnerable to other forms of mortality.

Although there is evidence that pre- and post-natal nutrition could be of major importance to the survival of calves in the Northwest Territories, that may not be the case in areas with different climate or predators. After studying calf survival in Newfoundland for 8 years, Bergerud (1971) concluded that the availability of forage in winter (snow depth) may have affected the birth weight of calves the following spring, but that their birth weight did not influence their survival rate. The weather on Newfoundland calving grounds was not severe enough to kill calves. Most calves that died were killed by lynx (*Lynx canadensis*) (wolves were absent). Lynx apparently selected calves (the healthiest and boldest) which wandered farthest from

their dams, and transmitted to all that they bit a bacterial infection that was fatal regardless of the calves' initial health. The amount of calf mortality varied from year to year with the abundance of lynx and with the availability of its major alternative prey, the snowshoe hare (*Lepus americanus*). The variation in both factors was independent of snow depth or calf viability. I conclude that neonatal mortality in Newfoundland was far less dependent on innate viability than in the Northwest Territories.

The adult caribou examined during our study were free of pathology attributable to malnutrition (Broughton and Choquette 1969), which supports my conclusion, from examining fat deposits, that malnutrition was not an important cause of death among adults. D. R. Miller (1974, 1976) reported that forage on the winter range grew faster than it was being used, and that because caribou varied their feeding habits they obtained amounts adequate for maintenance during the winters of our study.

A management plan for the Kaminuriak population will have to allow for uncontrollable annual fluctuations in population size which could amount to as much as 10%. According to historical records reviewed by Parker (1972), large fluctuations in size have been characteristic of the Kaminuriak population. F. L. Miller's (1974) analysis of the population's age structure indicates that such fluctuations have been the result of large differences in cohort size. Our evidence suggests that the birth rate has been more stable than the neonatal mortality rate. It follows that differences between cohorts were largely due to year-to-year differences in survival, not production. Neonatal survival may be governed by maternal condition, and that, in turn, by food availability each winter.

Males made up about 58% of the harvest during our study (Parker 1972). Walters *et al.* (1972) demonstrated with simulation modelling that if an even greater proportion of the harvest were taken from among males, more females would be left to

breed and the size and potential yield of the population would be increased. If shifting the sex ratio of the harvest could not provide enough caribou to meet the requirements, the only other management tool that appears practicable is predator control. Parker (1972) estimated that wolves killed annually about 5% of the caribou over 1 year of age, and Miller and Broughton (1974) found wolves to be a "principal cause" of calf mortality in 1970. However, before a sound decision can be reached regarding the merits of controlling wolves, it will be necessary to determine what proportion of their kill represents caribou that would otherwise remain available to the hunter.

As a final point, the results presented in this report suggest the key importance of summer forage to the reproduction, growth, and winter survival of the Kaminuriak population. Caribou are adapted to marginal subsistence during winter, but depend on full nutritional recovery during summer to prepare for demands of body maintenance and reproduction the following autumn and winter. Any disturbance to caribou on their summer range which decreases feeding time or increases energy demands is detrimental, especially preceding or following a winter of deep snow. Human activities that may disturb caribou on summer range should be carefully regulated.

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Appendix 1

Masson's Trichrome stain procedure for caribou ovaries

(Adapted from Galigher and Kozloff 1964)

For paraffin sections cut at 10 μ:

Xylene	5 min
Absolute ethanol	5 min
95% ethanol	1 min
70% ethanol	1 min
50% ethanol	1 min
35% ethanol	1 min
Distilled water	1 min

1. Mordant in Bouin's fixative overnight at room temperature or 1 h at 56°C.
2. Bathe in running tap water until clear of yellow colour.
3. Rinse in distilled water.
4. Place in Weigert's haematoxylin for 20 min.
5. Wash in running tap water for 10 min.
6. Place in distilled water to rinse.
7. Place in Biebrich scarlet – acid fuchsin solution for 15 min.
8. Rinse in 3 baths of distilled water.
9. Place in phosphomolybdic acid – phosphotungstic acid solution for 10 min (discard after each batch of slides is passed).
10. Place directly in aniline blue solution for 3½ min.
11. Rinse in 3 baths of distilled water.
12. Place in acetic water 1% for 3 min.
13. Dip in:
    70% ethanol
    95% ethanol
    Absolute ethanol — 2 changes
    Xylene — 3 minutes
    2nd xylene — leave here for mounting in Permount.

Table A.1.
Means and other statistics for the depth (mm) of back fat in male caribou, subdivided by age and season of collection

Table A.2.
Means and other statistics for the depth (mm) of back fat in female caribou, subdivided by age and season of collection

Table A.3.
Means and other statistics for the weight (g) of the kidney fat in male caribou, subdivided by age and season of collection

Table A.4.
Means and other statistics for the weight (g) of the kidney fat in female caribou, subdivided by age and season of collection

Appendix 2
Means, sample sizes (n), and other statistics for depth of back fat, weight of kidney fat, weight of abdominal fat, and fat content of femoral marrow grouped by age and season of collection. s is standard deviation

Table A.1.

Month of collection	Age (mths)	n	Mean	s	Range	95% conf. limit
June	<1	9	0.1	0.0	0.1– 0.1	0.1– 0.1
	12	11	0.2	0.3	0.1– 1.0	0.0– 0.4
	24	7	0.6	0.9	0.1– 2.0	–0.2– 1.5
	36	3	0.1	0.0	0.1– 0.1	
	48	2	1.8	2.3	0.1– 3.4	
	≥60	4	4.4	5.0	0.1– 9.6	
July	13	2	0.1	0.0	0.1– 0.1	
	25	1	7.0	0.0	7.0– 7.0	
	37	1	3.0	0.0	3.0– 3.0	
	≥61	14	25.2	6.9	10.6–33.6	21.2–29.2
Sept.	3	5	3.6	3.2	0.1– 6.0	
	15	3	8.4	7.2	0.1–13.0	
	27	9	12.5	8.0	0.1–25.8	6.3–18.7
	39	9	23.5	12.9	8.5–51.3	13.5–33.4
	51	20	28.1	16.3	0.1–59.7	20.5–35.7
	≥63	18	40.5	14.0	16.5–64.4	33.5–47.4
Nov.–Dec.	5	12	0.2	0.3	0.1– 1.0	0.0– 0.3
	17	13	0.6	1.5	0.1– 5.6	–0.3– 1.5
	29	14	0.8	1.6	0.1– 4.5	–0.1– 1.7
	41	30	0.4	0.9	0.1– 4.7	0.0– 0.7
	53	21	0.1	0.0	0.1– 0.1	0.1– 0.1
	≥65	3	0.9	1.4	0.1– 2.5	
April	10	14	0.1	0.0	0.1– 0.1	0.1– 0.1
	22	26	0.7	2.5	0.1–12.3	–0.2– 1.7
	34	39	0.4	0.9	0.1– 4.3	0.1– 0.7
	46	26	1.4	3.4	0.1–15.9	0.0– 2.7
	≥58	53	8.1	8.1	0.1–32.0	5.9–10.4

Table A.2.

Month of collection	Age (mths)	n	Mean	s	Range	95% conf. limit
June	<1	20	0.5	0.9	0.1– 3.0	0.1– 0.9
	12	11	0.3	0.4	0.1– 1.3	0.0– 0.6
	24	20	2.1	2.9	0.1–10.0	0.1– 3.4
	36	134	1.3	2.8	0.1–15.2	0.8– 1.8
July	2	4	0.1	0.0	0.1– 0.1	
	12	3	0.1	0.0	0.1– 0.1	
	25	2	6.6	0.1	6.6– 6.7	
	37	15	5.6	6.3	0.1–18.0	2.1– 9.2
Sept.	3	6	6.7	5.9	0.1–15.1	
	15	3	6.0	8.3	0.1–15.5	
	≥27	37	15.4	8.9	0.1–32.8	12.5–18.4
Nov.–Dec.	5	13	0.9	1.3	0.1– 4.1	0.1– 1.7
	17	8	1.0	1.0	0.1– 3.0	0.2– 1.8
	≥29	87	12.4	10.6	0.1–36.4	10.1–14.6
April	10	18	0.2	0.5	0.1– 2.4	0.0– 0.5
	22	19	0.4	1.3	0.1– 5.6	–0.2– 1.0
	≥34	97	5.4	7.0	0.1–27.7	4.0– 6.8

Table A.3.

Month of collection	Age (mths)	n	Mean	s	Range	95% conf. limit
June	<1	15	7.9	4.8	3.5– 20.0	5.3–10.5
	12	14	19.5	9.7	7.0– 38.5	13.9–25.1
	24	7	25.5	11.6	11.0– 40.8	14.8–36.2
	36	4	34.9	11.5	19.8– 45.0	
	48	2	55.8	3.9	53.0– 58.5	
	≥60	3	66.8	16.6	53.5– 85.5	25.5–108.2
July	13	2	16.5	5.1	12.5– 20.5	
	25	1	39.0	0.0	39.0– 39.0	
	37	2	34.8	23.0	18.5– 51.0	
	49	1	65.0	0.0	65.0– 65.0	
	≥61	14	82.4	16.1	49.0–104.0	73.1– 91.8
Sept.	3	5	23.2	9.2	17.0– 38.5	
	15	3	56.9	31.6	25.0– 88.1	
	27	9	66.8	15.5	47.7– 88.0	54.9– 78.7
	39	9	77.8	36.4	37.9–155.0	49.9–105.8
	51	20	115.1	57.0	34.0–310.0	88.4–141.8
	≥63	17	129.1	39.1	74.5–232.5	108.9–149.2
Nov.–Dec.	5	12	25.7	6.2	15.4– 38.0	21.8– 29.1
	17	13	48.6	14.4	27.0– 77.2	39.9– 57.3
	29	14	57.0	10.4	37.1– 73.2	51.0– 62.9
	41	30	53.6	15.7	28.0– 90.7	47.7– 59.4
	53	19	50.9	16.6	33.5– 88.0	42.9– 58.9
	≥65	3	36.0	5.6	32.5– 42.5	
April	10	11	17.6	15.0	8.5– 61.5	7.5– 27.6
	22	14	27.3	11.4	10.0– 56.5	20.7– 33.9
	34	33	31.5	7.8	19.5– 47.0	28.7– 34.2
	46	23	46.2	13.2	28.0– 76.5	40.4– 51.9
	≥58	41	65.3	29.4	19.9–148.5	56.2– 74.6

Table A.4.

Month of collection	Age (mths)	n	Mean	s	Range	95% conf. limit
June	<1	25	6.3	2.7	2.0– 14.5	5.2– 7.4
	12	13	20.7	9.6	9.0– 39.4	14.9–26.5
	24	25	26.7	10.7	12.5– 51.5	22.3–31.1
	≥36	138	37.6	22.7	9.2–183.2	33.8–37.6
July	2	4	6.6	3.7	2.0– 10.5	
	13	3	13.5	2.2	11.0– 15.0	
	25	2	37.0	4.9	33.5– 40.5	
	≥37	15	42.5	17.7	20.0– 77.5	32.7–52.3
Sept.	3	6	26.5	12.6	4.0– 38.7	
	15	3	59.9	13.1	49.2– 74.5	
	≥27	32	73.9	28.6	38.0–147.5	63.5–84.2
Nov.–Dec.	5	11	24.4	10.4	6.5– 45.5	17.4–31.3
	17	9	38.2	4.7	31.5– 47.0	34.6–41.8
	≥29	81	72.6	27.9	22.0–189.4	66.4–78.7
April	10	17	12.8	4.8	7.5– 20.5	10.3–15.2
	22	19	24.4	13.1	9.5– 59.0	18.1–30.8
	≥34	82	54.2	23.6	17.6–117.0	49.0–59.4

Table A.5.
Means and other statistics for the weight (g) of the abdominal fat in male caribou, subdivided by age and season of collection

Table A.6.
Means and other statistics for the weight (g) of the abdominal fat in female caribou, subdivided by age and season of collection

Table A.7.
Means and other statistics for the percentage fat content (weight) of femoral marrow in male caribou, subdivided by age and season of collection

Table A.8.
Means and other statistics for the percentage fat content (weight) of femoral marrow in female caribou, subdivided by age and season of collection

Table A.5.

Month of collection	Age (mths)	n	Mean	s	Range	95% conf. limit
June	<1	7	8.7	5.7	2– 20	3.5– 14.0
	12	14	48.2	22.6	25–103	35.2– 61.2
	24	5	45.8	23.3	25– 75	
	36	4	119.0	76.6	40– 211	
	48	2	222.0	19.8	208– 236	
	≥60	3	258.3	75.6	189– 339	70.4–446.2
July	13	2	38.0	35.3	13– 63	
	25	1	88.0	0.0	88– 88	
	37	2	210.0	26.9	191– 229	
	49	1	273.0	0.0	273– 273	
	≥61	14	427.1	159.9	214– 823	334.7–519.4
Sept.	3	4	87.5	31.4	44– 111	
	15	3	204.3	143.4	42– 314	
	27	9	288.8	105.2	161– 506	207.9–369.6
	39	9	392.3	192.9	181– 754	244.1–540.6
	51	21	582.6	327.1	67–1652	433.6–731.5
	≥63	18	641.9	328.6	220–1459	478.5–805.4
Nov.–Dec.	5	10	53.9	27.0	25– 107	34.6– 73.2
	17	11	140.1	58.0	61– 216	101.1–179.1
	29	14	114.9	69.5	32– 263	74.7–155.0
	41	24	116.6	60.0	8– 289	91.3–142.0
	53	18	153.1	64.8	44– 337	120.9–185.3
	≥65	3	94.7	65.3	55– 170	
April	10	11	58.3	123.8	12– 431	–24.9–141.4
	22	13	58.0	50.1	7– 149	27.7– 88.3
	34	24	106.7	64.0	27– 254	79.7–133.7
	46	20	175.5	133.9	44– 537	112.8–238.2
	≥58	41	388.5	206.2	49– 903	323.4–453.6

Table A.6.

Month of collection	Age (mths)	n	Mean	s	Range	95% conf. limit
June	<1	11	9.1	6.6	2– 25	4.6– 13.5
	12	11	67.7	46.3	15–181	36.6– 98.8
	24	20	72.2	46.6	20–169	50.4– 94.1
	≥36	136	155.1	106.4	30–629	137.2–173.0
July	2	3	12.7	7.8	4– 19	
	13	3	46.3	26.7	18– 71	
	25	2	77.5	2.1	76– 79	
	≥37	13	123.8	60.0	46–213	87.5–160.0
Sept.	3	5	111.0	45.0	61–168	
	15	3	165.7	27.8	134–186	
	≥27	36	380.8	183.0	32–706	318.9–442.7
Nov.–Dec.	5	9	65.8	56.3	8–185	22.5–109.1
	17	9	127.4	36.5	76–204	99.4–155.5
	≥29	77	416.7	218.1	45–991	367.2–466.3
April	10	15	19.8	13.3	3– 47	12.4– 27.2
	22	12	57.1	57.0	15–224	20.8– 93.3
	≥34	66	274.4	194.1	15–745	226.6–322.2

Table A.7.

Month of collection	Age (mths)	n	Mean	s	Range	95% conf. limit
June	<1	10	12.6	11.4	1.0–38.4	4.4–20.7
	12	12	58.1	15.0	20.2–82.5	48.6–67.6
	24	5	55.0	11.9	37.4–70.4	
	36	3	74.9	9.7	64.3–83.3	
	48	2	73.7	0.3	73.5–73.9	
	≥60	4	71.6	8.4	60.4–78.4	58.3–71.6
July	13	2	37.8	17.1	25.8–40.9	
	25	1	70.0	0.0	70.0–70.0	
	37	2	63.1	1.0	62.5–63.8	
	49	1	70.0	0.0	70.1–70.1	
	≥61	15	69.8	9.1	52.0–81.3	64.7–74.9
Sept.	3	5	64.1	18.8	42.3–88.2	
	15	3	72.7	11.7	59.3–81.1	
	27	9	66.6	9.4	55.1–79.2	59.4–73.8
	39	9	69.6	9.3	51.3–81.1	62.5–76.8
	51	20	68.3	11.7	33.5–83.6	62.8–73.8
	≥63	17	75.7	5.1	66.5–84.7	73.1–78.4
Nov.–Dec.	5	11	62.0	14.6	37.8–81.8	52.5–71.9
	17	13	70.3	13.8	31.6–83.0	62.0–78.7
	29	14	67.1	14.2	36.6–83.2	58.9–75.4
	41	30	59.5	17.3	27.5–83.1	53.0–66.0
	53	20	67.4	8.6	53.4–84.8	63.4–71.4
	≥65	3	56.4	21.8	34.1–77.6	
April	10	12	54.2	14.8	33.2–75.1	44.8–63.6
	22	25	55.5	17.8	12.2–83.0	48.1–62.8
	34	38	63.8	13.7	24.7–84.7	59.3–68.3
	46	25	68.4	11.4	44.0–88.6	63.7–73.1
	≥58	54	73.3	10.4	30.9–89.4	70.6–76.2

Table A.8.

Month of collection	Age (mths)	n	Mean	s	Range	95% conf. limit
June	≥1	17	17.6	16.3	1.2–48.6	9.2–26.0
	12	11	49.7	14.9	14.8–67.9	39.7–59.7
	24	20	56.0	16.4	24.5–88.1	48.3–63.7
	≥36	134	55.9	17.9	3.8–87.8	52.9–59.0
July	2	4	16.8	5.4	11.1–22.0	
	13	3	35.7	24.7	12.5–61.6	
	25	2	65.2	11.0	57.4–72.9	
	≥37	15	53.1	19.9	17.2–77.6	42.1–64.1
Sept.	3	6	57.3	8.3	47.0–69.1	
	15	3	69.3	8.8	63.7–79.4	
	≥27	36	69.7	11.2	28.4–88.4	65.9–73.5
Nov.–Dec.	6	13	57.8	19.8	9.0–79.7	45.9–69.8
	17	10	71.1	3.1	65.7–74.0	68.9–73.3
	≥29	82	73.1	10.4	34.6–97.0	70.8–75.4
April	10	19	48.4	23.1	13.8–89.5	37.8–59.5
	22	21	55.0	15.4	28.4–79.6	48.1–62.0
	≥34	94	66.4	13.9	14.8–88.9	63.5–69.2

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