

by Donald B. Flook

**A study of
sex differential
in the survival
of wapiti**



**Canadian
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Causes and implications of an observed sex differential in the survival of wapiti

by Donald R. Flook

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Cover photograph shows bull at start of rut.
Velvet has been stripped from antlers, and
animal is in fat condition.
Photo by Darrell Eagles.

► **Errata**
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data on the population change and the numbers harvested in different years, Kelker's

► (1947) equation was expanded as follows:

First, for a situation in which there are two harvests between the initial and final population estimates,

$$P = [(Ar^{t_1} - H_1)r^{t_2} - H_2]r^{t_3}, \text{ or}$$

$$P = A(r^{t_1+t_2+t_3}) - H_1(r^{t_2+t_3}) - H_2(r^{t_3}),$$

where P and A are defined as above,

r = net annual productivity rate,

H_1 = number of animals in first harvest,

H_2 = number of animals in second harvest,

t_1 = number of calving seasons between initial count and first harvest,

t_2 = number of calving seasons between first and second harvest, and

t_3 = number of calving seasons between second harvest and final count.

Then in the general situation,

$$P = Ar^{t_1+t_2+\dots+t_n+t_{n+1}} - H_1r^{t_2+t_3+\dots+t_{n+1}}$$

$$- H_2r^{t_3+t_4+\dots+t_n+t_{n+1}} - \dots$$

$$- H_{n-1}r^{t_n+t_{n+1}} - H_n r^{t_{n+1}},$$

where with the exception that

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Wapiti, often called elk* in North America, formerly occurred from New York State to Vancouver Island and from New Mexico to northern Alberta. They went through a period of scarcity in the late 1800's and early 1900's caused, in many areas at least, by overhunting. They have since increased under protection and now occur in many wildland areas in the four western provinces of Canada and in the western United States. Throughout most of their range outside of

National Parks they are hunted under regulation. They range in both forests and grasslands and feed on a variety of herbaceous and woody plants. As long as there are wildlands with adequate stands of natural forage, including wintering areas without excessive snow, the future prospects for wapiti populations appear good.

The natural increase of herds that survived in or near the parks and the release of animals in Banff and Jasper in 1918 and

1920 resulted in the re-establishment of wapiti in all suitable areas of the National Parks of western Canada. In several of the National Parks wapiti increased to such high levels that they damaged the stands of forage plants on the ranges where they gathered in winter. This resulted in food shortages and was probably the cause of declines in numbers of mule deer and moose. To prevent excessive damage to the vegetation and reduce competition with

Abstract

other hoofed mammals, since the early 1940's park wardens have shot numbers of wapiti in the parks. The meat has been provided to the needy.

The study reported here was made to help understand the problem of expansion of wapiti populations at the expense of other members of the plant-animal community. It was found that bulls tend to disperse more from the areas where they were reared and die younger than cows. There are thus fewer bulls than cows, particularly on the rearing areas. A number of factors contribute to shortening the life span of bulls, probably a major one being the depletion of their fat reserves during the breeding season in the autumn. This leaves bulls less well prepared to survive the winter. As one bull can breed many cows, the natural removal of bulls does not slow the rate of increase of the population. Rather, it helps maintain a high rate of increase by leaving more food and space for the cows and calves. This contributes to the ability of wapiti to increase their abundance and distribution.

*The name wapiti is preferred, because elk properly refers to the moose-like European elk, a quite different animal from the wapiti. The wapiti's closest European relative is the red deer.

This study was conducted to seek the causes of an apparent unbalanced sex ratio favouring females, observed in wapiti populations in the National Parks in western Canada and reported from elsewhere.

In the mountain parks the sex ratio of wapiti older than calves counted in October and November was 37 males : 100 females. However, as the distribution of females coincided more closely with areas of low elevation and ready access to observers than did that of males, data on sex ratios from those areas are believed biased in favour of females. More reliable population data were obtained from an enclosed 50-square-mile area of uniformly low elevation in Elk Island National Park where wapiti were harvested at an average rate of approximately 21 per cent over a 19-year period. During that period the sex ratio in the net production, calculated from the sum of the total harvest and net population change, was 85 : 100.

The sex ratio of fetuses from all parks in winter was 113 : 100, and losses of males did not appear greatly to exceed those of females before 1½ years of age. The composition of harvests by park wardens instructed to shoot non-selectively indicates an abrupt decrease in the number of males at low elevations in the mountain parks between 1½ and 2½ years of age. This decrease is believed to be caused by dispersal to other areas. This dispersal makes males less observable and probably also contributes to mortality of males by taking some of them into unfavourable habitats. A marked decline in the number of males after 7 years of age and continuing to 14 years, the oldest represented, is believed due to increased mortality. In contrast, the number of females in successive age classes declined less rapidly, the oldest examined being 21 years of age.

Males grew more rapidly in absolute rate, and for about one year longer than females. In three of the four parks, tooth wear was more rapid in males and would thus adversely affect them at a younger age. Those findings suggest that males have a

greater food intake and greater food requirement.

Seasonal comparisons of adrenal weights and zona glomerulosa widths showed no evidence that males were subject to more stress than females as a result of the rut. However, fatty infiltration of the liver and decreasing perinephric fat deposits showed that during the rut adult males rapidly depleted their stored fat, in contrast to females, which did not. That was particularly marked in males older than 7 years, the age group in which the most intensive breeding activity apparently occurs. Males older than calves, particularly those older than 7 years, entered the winter, a period of potentially critical energy balance, with smaller fat reserves than females, and during the winter exhausted their fat reserves earlier than females. Therefore males, particularly older ones, are more vulnerable than females to death in late winter and spring, caused primarily by an inadequacy of energy.

Two factors are involved in unbalanced sex ratios observed in wapiti in the parks: firstly, a sex difference in distribution related to the dispersal of males; secondly, the natural mortality of males at a younger age than females, as substantiated by the data from Elk Island National Park. The removal of males from the population foci by these two agents leaves more food and space for females and young. This is believed to contribute to the ability of wapiti to sustain a high rate of increase. The extent to which this phenomenon occurs in other ungulates warrants further attention, in view of its significance to the ability of a species to increase its abundance and distribution.

This study was conducted under the auspices of the Canadian Wildlife Service with the co-operation of the National and Historic Parks Branch. The results were presented to the University of Alberta in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

Dr. W. A. Fuller of the University of Alberta gave guidance, particularly in planning the research, and with Dr. F. Zwickel of that institution provided valued advice on the presentation of the results.

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Populations of wapiti, *Cervus canadensis* (Erxleben), in several of the National Parks in Canada have increased in the past to levels at which they depleted the stands of winter forage plants. This has led to competition with mule deer (*Odocoileus hemionus*), moose (*Alces alces*), and bighorn sheep (*Ovis canadensis*) (Clarke, 1942; Cowan, 1947a; Mair, 1952; Love, 1955; Banfield, 1958; Flook, 1964). Resulting food shortages were probably the cause of declines observed in populations of mule deer and moose (Cowan, 1950). For these reasons, wapiti populations and winter range plant cover have been kept under surveillance, and slaughters by Parks Service personnel have been practised frequently to control the wapiti populations at levels within the carrying capacity of the forage stands. The success of wapiti as a competitor in the National Parks can, no doubt, be attributed at least in part to its ability to use a variety of habitat types and forage types (Cowan, 1947a; Murie, 1951: 188; Morris, 1956; Troyer, 1960; Flook, 1964; Blood, 1966b).

Cowan (1950) reported that during the period 1943 to 1946 when Jasper, Banff, Yoho, and Kootenay National Parks were overstocked with wapiti, the sex ratio among adult wapiti observed in those parks was 29 males : 100 females, whereas the sex ratios of the other species of ungulates present more nearly approached equality. Males were also in the minority among adult wapiti removed from Banff and Jasper Parks during that period, in slaughters in which the intention was to take animals without regard to sex and age.

A deficiency of males, provided it is not so great as to reduce the conception rate, does not lower the rate of increase in a population (for example, Kelker, 1947). As wapiti are polygynous (Murie, 1951: 126), a deficiency of males could, in circumstances where food is limiting, contribute to sustaining high rates of reproduction and female survival. A knowledge of sex ratios and the factors influencing them is therefore relevant to the problem of wapiti

management in the National Parks.

Kittams (1953) consolidated published and unpublished data on the sexes of wapiti fetuses from Yellowstone National Park and Jackson Hole, U.S.A., and Banff National Park, Canada, and showed that the sex ratio of the composite sample approximated 1 : 1. The sex ratio of samples of wapiti calves examined soon after birth also approximated 1 : 1 (Johnson, 1951; Picton, 1961). However, samples of adults observed in various wapiti populations have indicated a marked deficiency of males, usually greater than could be accounted for by selective shooting of bulls. A few examples follow.

The sex ratio of wapiti counted in winter in a lightly hunted population on an overstocked range in the Olympic Peninsula of Washington as reported by Schwartz (undated) and Schwartz and Mitchell (1945) was 14 males : 100 females among animals older than calves (computed from authors' tabulated data).

Murie (1951:275) and Anderson (1958) reported about three times as many cows as bulls among adult wapiti counted in winter in the Jackson Hole area of Wyoming. That area had a long history of overstocking with wapiti. The sexes were harvested in similar numbers. On the other hand, although only about one-third as many bulls as cows occurred on the National Elk Refuge in Jackson Hole during winter, males predominated among the known winter losses (Anderson, 1958). State-wide ear tag returns indicated that fewer bulls than cows reached old age (Anderson, 1958).

Miers (1962) tallied the sex of wapiti observed in three successive rutting seasons in an expanding population in the Stuart Mountains of New Zealand. Computed from his tabulated data, the sex ratio among wapiti older than calves was 71 : 100.

To equate the sex ratio of observed samples to that of the population of which they are part, it is necessary to assume that differences in the behaviour or distribution of males and females are not causing differences in the probability of observing them.

Schwartz (undated) mentioned that in the Olympic Peninsula the solitary tendencies and higher elevational distribution of bulls did reduce the probability of seeing males as compared to females. Similarly in the Canadian Rockies, Cowan (1950) noted the tendency of bulls and cows to segregate, many bulls occupying ranges at higher elevations both winter and summer. Even during the rut many bulls were separated from the cows at any one time. Murie (1951:275) remarked that some smaller feeding grounds in Wyoming had a preponderance of bulls, and both he and Anderson (1958) acknowledged that some adult bulls wintered at scattered, higher locations off the Jackson Hole feeding grounds. However, both writers considered the number of bulls missed to be too small to affect the sex ratio greatly.

Murie (1951:276) concluded, "On the whole, it appears to be fairly well established that among mature elk females greatly exceed males in numbers but the cause is hard to find."

The composition of samples of wapiti taken in some of the National Parks of western Canada during slaughters in which park wardens were instructed to shoot non-selectively suggested that the sex ratio remained about equal to at least 18 months of age, but that from 30 months of age males were in the minority.

Murie (1951:132) reported that wapiti entering the rut, particularly the bulls, are fat, but that, while the cows continue to eat regularly during the rut, the bulls eat less than formerly, and those engaged in breeding can be expected to expend energy very rapidly. As a result the condition of the bulls at the start of the winter is poor, whereas the cows are still fairly fat. It is logical to speculate, on the basis of Murie's observations, that if male and female adults were to lose condition at similar rates during the winter, the bulls would be the first to exhaust their energy reserves and as a result would be more prone to winter mortality.

According to Altmann (1960), during the rut the yearling male wapiti, unlike the

female of the same age, is driven from his accustomed group and from his dam by the harem bull, and is subsequently threatened by any bull that he encounters. During the rut adult bulls compete intensely for harems, and defend them against other males through threat and occasional combat. Christian (1959) and Christian, Flyger, and Davis (1960) have presented evidence for some other mammals that social pressures and intraspecific competition can, by stimulation of the pituitary-adrenocortical system, lead to lowered resistance to other debilitating agents in accordance with the general adaptation syndrome of Selye (1950). These considerations led to the hypothesis that the activities and social interactions of the rut might stress males older than calves to a degree that would predispose them to a higher mortality than occurs among females.

The objectives of the present study were to examine the population dynamics of wapiti in some of the National Parks of Canada, and to study from specimens collected in the wild some of the physical and physiological factors affecting the welfare of wapiti to learn how they are phased with the seasons of the year and how they affect animals of different sex and age. The factors studied were tooth wear, growth, the reproductive cycle, fat reserves, and adrenal activity.

Study areas

Figure 1. Map showing location of National Parks in which study was conducted.

Data were collected from wapiti in Elk Island, Jasper, Banff, and Waterton Lakes National Parks in Alberta, and to a minor extent from Kootenay and Yoho National Parks in British Columbia and the Ya Ha Tinda Ranch east of Banff Park. Hereafter the words "national park" will be omitted, the name Waterton Lakes, for example, referring to the park rather than the townsite within it or the lakes after which it was named. The locations of the five parks are shown in Figure 1. In Figure 2, Banff, Kootenay, and the Ya Ha Tinda Ranch are shown with the major drainages within them.

In the mountainous areas there are pronounced local variations in climate, and weather stations are few. The approximate mean annual total precipitation, and approximate mean daily temperatures for January, April, July, and October, for each park are shown in Appendix 1. The values are based on the Atlas of Canada (Canada Dept. Mines and Tech. Surveys, 1957) and each refers to the area within which most of the particular park is located.

Elk Island Park, with an area of approximately 75 square miles, lies on the Cooking Lake Moraine, which has knob and kettle topography, podzolic soils (Bowser *et al.*, 1962), and is assigned by Rowe (1959) to the Mixedwood Section of the Boreal Forest Region. Most of the park supports a *Populus* association in which aspen poplar (*Populus tremuloides*) dominates in the drier sites, and balsam poplar (*Populus balsamifera*) in the moister situations (Moss, 1955). Throughout the park are scattered grassy areas many of which, during the period 1959 to 1966, were being invaded by aspen poplar. Soper (1951) described the history of the park and its mammalian fauna. The wapiti are descendants of those native to the area when the park was established in 1906. They share the park with four other ungulates: moose, white-tailed deer (*Odocoileus virginiana*), mule deer, and bison (*Bison bison*).

The park is divided into two major enclosures separated by Alberta Highway 16. As the south enclosure has contained at

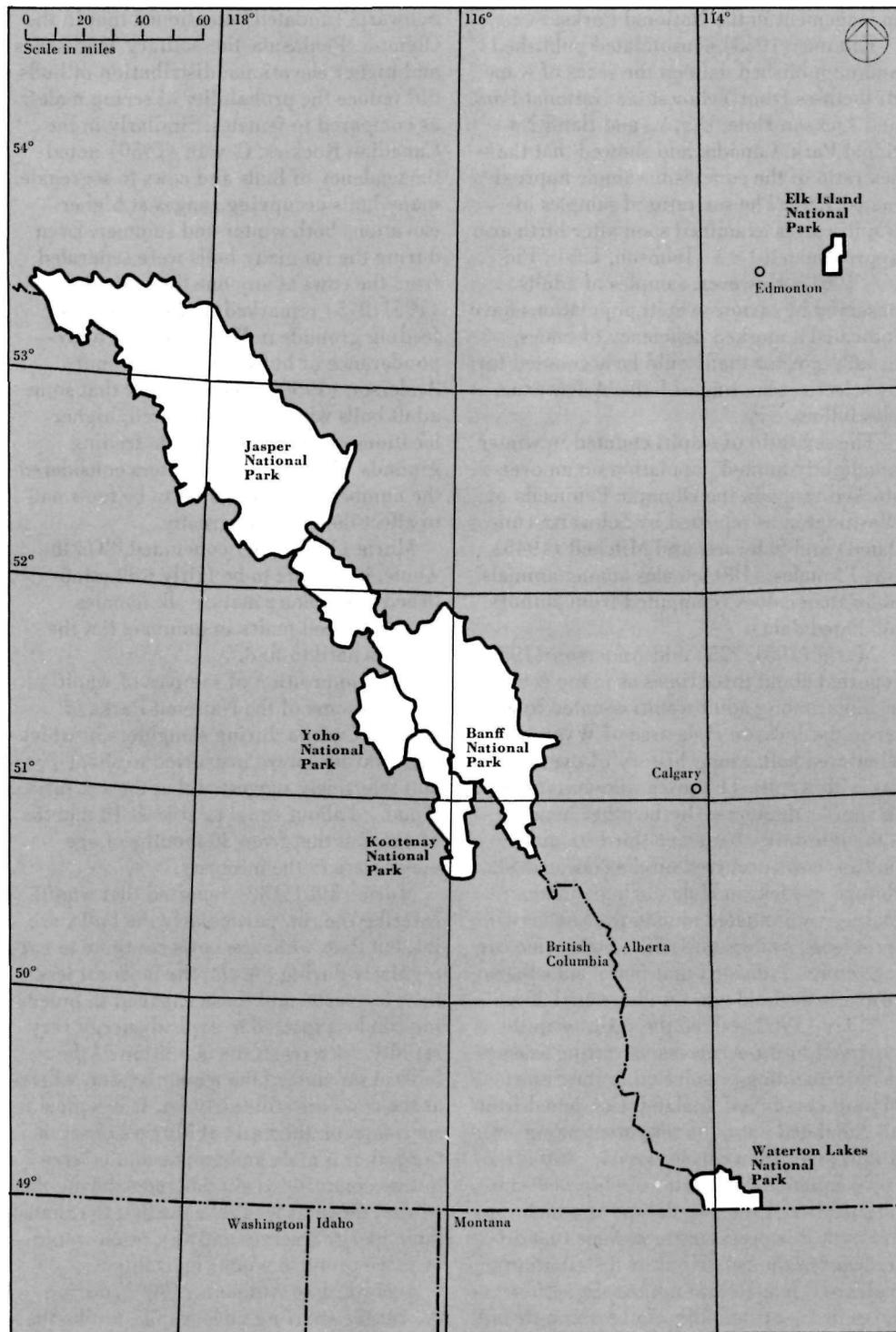
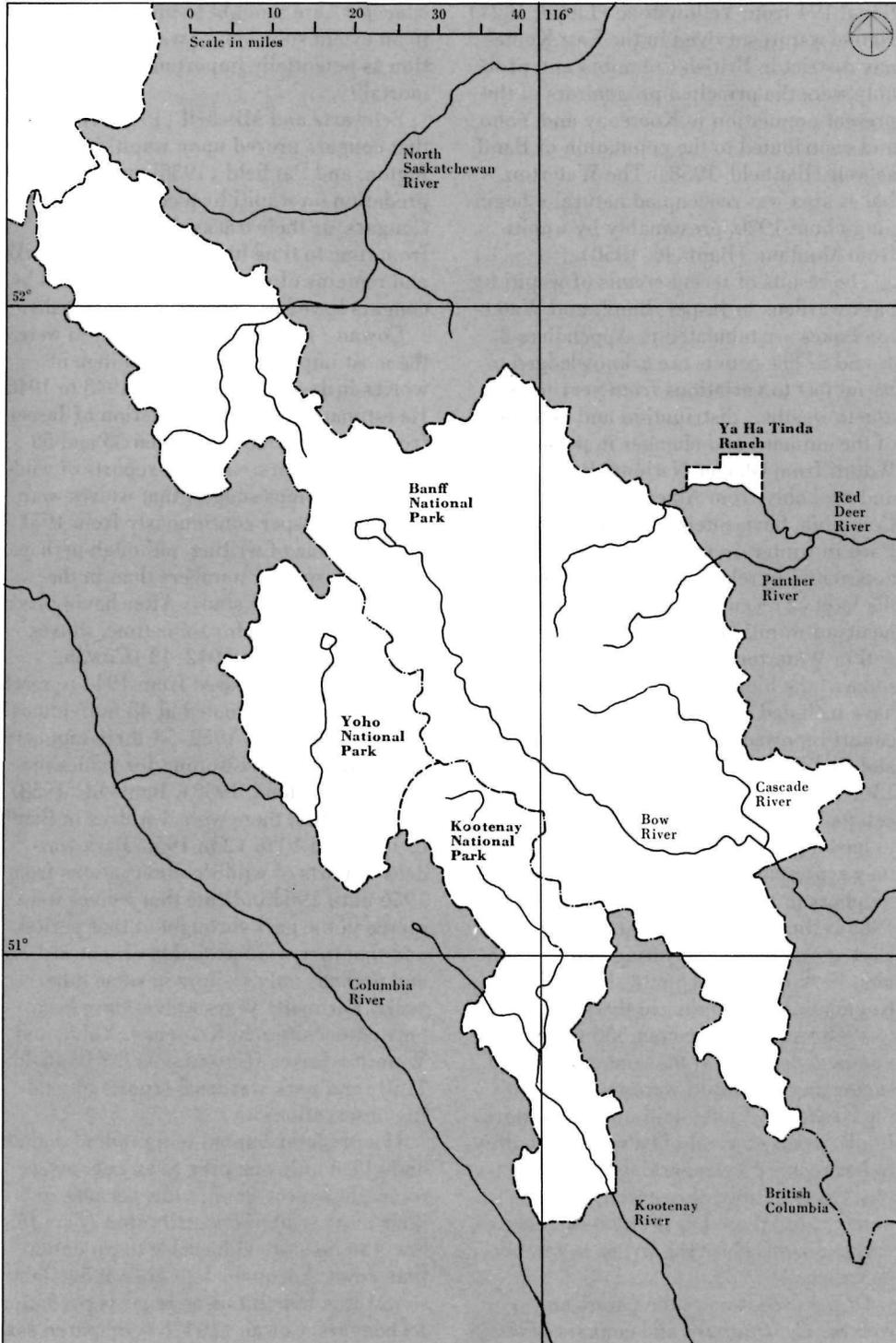


Figure 2. Map of Banff, Kootenay, and Yoho National Parks and the Ya Ha Tinda Ranch, showing major drainages.



most about 12 wapiti since it was added to the park in 1947, only the north enclosure of 50 square miles was considered in the study.

Estimates of numbers of wapiti, moose, and deer (species of deer not distinguished) in the north enclosure of Elk Island from aerial surveys from 1959 to 1966 are given in Appendix 2. Numbers of wapiti and moose removed in slaughters are shown, and pre-slaughter estimates computed from the numbers slaughtered and post-slaughter counts. While slaughters and recruitment have caused pronounced fluctuations in populations of wapiti and moose, there have been no indications of any large die-offs in recent years. Deer pass in and out of the park under the fence; and the park wardens report that moose occasionally slide over the fence during the rut. However, wapiti have never been reported to do either. From 1959 to 1966, the number of bison in the north enclosure as shown by park wardens' counts in the winter feeding lot has varied between approximately 400 and 700. Before 1966-67 bison were fed hay and oat sheaves in winter and in some years when stocking rates were high before 1960 a few wapiti, mostly bulls, were reported to have used the artificial food.

Jasper, Banff, and Waterton Lakes, all on the east slope of the Rocky Mountains, have areas of approximately 4,200, 2,585 and 204 square miles, respectively. Kootenay and Yoho, lying on the west slope of the Rockies, have areas of 543 and 507 square miles respectively. The Ya Ha Tinda Ranch, east of Banff, with an area of approximately 19 square miles, is crown land used by the Parks Service for grazing horses. The geology of the parks in the Canadian Rockies is described by MacKay (1952). The major areas of Jasper, Banff, and Kootenay are included by Rowe (1959) in the East Slopes Rockies Section of the Sub-alpine Forest Region. However, there are substantial areas of Alpine Tundra, and the lower portions of the Athabasca and Bow valleys in Jasper and Banff, respectively, are assigned to the Douglas Fir and

Lodgepole Pine Section of the Montane Forest Region. The lower part of the Kootenay Valley is assigned to the Southern Section of the Columbia Forest Region. Rowe assigns the Waterton Lakes area to three categories: Alpine Tundra, Douglas Fir and Lodgepole Pine Section of the Montane Forest Region, and Grassland. Moss (1955) discussed the plant associations of the east slope and their successional stages. Flook (1964) discussed the role of various vegetation types in Banff and Jasper as ungulate habitats. Grassy and shrubby stages which follow removal of forest cover by fire and other disturbances provide extensive range for wapiti and other ungulates in Jasper, Banff, and Kootenay. On valley floors and south-facing slopes there are areas of grassland and sparse tree cover with a grass-shrub understory. Those are relatively stable and apparently maintained in their present cover by an arid microclimate. They are the key winter ranges for wapiti. The Ya Ha Tinda Ranch is rolling grassland, which has been dominated by rough fescue *Festuca scabrella* in periods of high precipitation or less intensive grazing or both, and by shorter grasses in other periods. It is used in winter by wapiti, many of which range in Banff in the summer. In Waterton Lakes, extensive climax prairies dominated by rough fescue with groves of aspen poplar in the moister sites are of major importance as wapiti winter range. In all the mountain parks, the potential summer range for wapiti far exceeds the winter range, in both area and carrying capacity.

Wapiti almost disappeared from the east slope of the Canadian Rockies about 1900 (Miller, 1916; Green, 1946; Cowan, 1947b; Banfield, 1950, 1958). The present population in Jasper originated from 88 brought from Yellowstone Park in 1920 and from about 35 native wapiti that had survived in the Brazeau Valley (Lloyd, 1927). The Banff population originated mainly from the release, in 1918, of 10 wapiti of mixed Manitoba and Wyoming ancestry and 41 from Yellowstone, and in 1920 of an addi-

tional 194 from Yellowstone (Lloyd, 1927). Native wapiti survived in the East Kootenay district in British Columbia and probably were the principal progenitors of the present population in Kootenay and Yoho, and contributed to the population of Banff as well (Banfield, 1958). The Waterton Lakes area was reoccupied naturally beginning about 1920, presumably by wapiti from Montana (Banfield, 1950).

The results of recent counts of wapiti by park wardens in Jasper, Banff, and Waterton Lakes are tabulated in Appendices 3, 4, and 5. The counts are acknowledged to be subject to variations from year to year due to weather, distribution and behaviour of the animals, and changes in personnel. Wapiti from Glacier National Park, U.S.A., and probably from Alberta and British Columbia, have entered Waterton Lakes Park in winter, in numbers which vary apparently in relation to snow depths. In the light of recent observations of movements of wapiti between winter ranges within Waterton Lakes, it is suspected that some of the higher counts in that park may have included duplications. Similarly, the counts reported for the Cascade, Panther, and Red Deer Valleys of Banff for 1962 to 1965 may be overestimates. All other counts in the mountain parks are believed to have been lower than the populations they represented. The apparent decline in numbers in the Bow Valley from 1963 to 1965 is thought to represent, in part at least, a real decline resulting from slaughters. Park wardens' counts of wapiti in Kootenay in November in the years 1962 to 1965 varied from about 350 to 480. The numbers declined as the winter advanced, suggesting the wapiti were moving down the Kootenay Valley and out of the park. In all parks, survival of calves is thought to have varied considerably from year to year depending on the severity of winter weather, but there has been no evidence of major die-offs since the writer began observations in 1955.

Of the predators in the parks, only wolves (*Canis lupus*) and cougars (*Felis*

concolor) are thought to prey on ungulates to an extent sufficient to warrant consideration as potentially important agents of mortality.

Schwartz and Mitchell (1945) reported that cougars preyed upon wapiti in Washington, and Banfield (1958) mentioned predation on wapiti by a cougar in Banff. Cougars, or their tracks, have been seen from time to time in all the mountain parks, and remains of wapiti apparently killed by cougars have been observed occasionally.

Cowan (1947b) found that wapiti were the most important single food item of wolves in Jasper and Banff in 1943 to 1946. He estimated the wolf population of Jasper from 1942 to 1946 at between 33 and 50 individuals. Park wardens' reports of wildlife observations suggest that wolves were present in Jasper continuously from 1951 until the time of writing, although perhaps usually in smaller numbers than in the period of Cowan's study. After having been absent from Banff for some time, wolves entered the park in 1942-43 (Cowan, 1947b). They increased from 1944 to reach a peak in 1947 estimated at 48 individuals (Green, 1951). In 1952-53 their numbers were reduced by poisoning for rabies prevention (Banfield, 1958). Banfield (1958) estimated that there were 4 wolves in Banff in 1953 and 10 to 12 in 1956. Park wardens' reports of wildlife observations from 1956 until 1964 indicate that wolves were scarce in the park throughout that period, and that they were probably absent in 1961 and perhaps only visitors in some other years. For many years wolves have been only rare visitors in Kootenay, Yoho, and Waterton Lakes (Cowan, 1947b; Banfield, 1950; and park wardens' reports of wildlife observations).

If a predator hunted in a random manner and killed only one prey at an encounter, we might expect wapiti bulls because of their more scattered distribution (data follows) to be more vulnerable to predation than cows. Adequate data are not available to test this hypothesis as regards predation by cougars. Cowan (1947b) compared sex

General methods

and age ratios of wapiti on wolf-inhabited and wolf-free areas and suggested that wolf predation had little or no effect on the composition of the wapiti population.

From 1957 to 1967 data on various phases of the study were obtained from wapiti shot in slaughters conducted for population control in Elk Island, Banff, Waterton Lakes, and the Athabasca Valley of Jasper. Most collection of data was done by park wardens. Other staff members of the Canadian Wildlife Service participated in slaughters at Banff and Jasper in 1966-67 and at Elk Island in several years. Zoology students from the University of Alberta also assisted in the latter park. The writer participated in data collection in all the parks at different times, demonstrated techniques to new observers, and checked the accuracy of the data collected.

To obtain detailed data at different seasons of the year, the writer autopsied 107 wapiti from July 9, 1961, to October 15, 1962. Initially the plan was to collect at intervals of 4 to 6 weeks two animals of each sex of each of two age-groups, yearlings, and animals 2 years old and older. In the first few months of collecting it became evident that 2-year-olds differed from older animals in a number of parameters, and it was found that 2-year-olds, particularly males, could be distinguished from older animals with fair success. Later collections therefore included three age groups: yearlings, 2-year-olds, and animals 3 years old and older. Forty animals in this series of 107 were taken November 1961 to January 1962 in the Bow Valley and in the Cascade, Panther, and Red Deer drainages in Banff. Most of the wapiti taken in the remainder of the collection period were shot in the last three mentioned drainages in Banff, but when animals of the appropriate sex and age were not readily available in those areas, wapiti were taken on the Ya Ha Tinda Ranch, in the Bow Valley, or in the Kootenay drainage. In addition, one specimen was examined on the Ranch in February 1963, and eight were collected in Banff in the autumn and early winter of 1965, to study changes in the liver during the rut. The total series of 116 specimens will be referred to hereafter as the research series. Complete data on

wapiti in this series are tabulated as appendices in Flook (1967).

There is thought to be little movement of wapiti between the Bow Valley and the Cascade, Panther, and Red Deer drainages. However, there are indications of movements among the last three areas. In the section on population dynamics, samples from Banff and the Ya Ha Tinda Ranch will be designated as having come from either of two areas, one being the Bow Valley and the other being the Cascade and Red Deer drainages, the latter including the Panther Valley and the Ranch.

A small series of skulls and skins of wapiti collected from Elk Island, Banff, and Waterton Lakes during the study was deposited in the National Museum of Canada, Ottawa.

Specific methods for each phase of the study will be discussed in the section of the paper dealing with that phase. In statistical comparisons 0.05 was the probability level at which the null hypothesis was rejected. Only in tests in which the probability of a larger value of t , F , or χ^2 is equal to, or less than, 0.01 will the probability be given.

Population dynamics

Data on the numbers of animals of each age and sex removed by the National Parks Service for population control, supplemented by the results of a few segregated counts of living wapiti, will be used to examine the population dynamics of wapiti in the parks.

Appendices 6 to 9 list the numbers of wapiti removed for population control from Elk Island, Jasper, Banff, and Waterton Lakes respectively, each year prior to the more detailed data collecting which was begun in the winters of 1957–58 in Banff and Jasper and 1958–59 in Elk Island and Waterton Lakes. In the data from Banff and Waterton Lakes, animals are classified as to sex and two age categories: calves and those older than calves. Early data from Elk Island cover the period from March 1, 1947, the earliest date records are complete. In that park some removals were made by trapping live wapiti for transport and some by shooting, and the method for each removal is indicated in Appendix 6. Henceforth the term shooting will refer to shooting free-ranging animals, and trapping will refer to capturing them in corrals baited with hay. Some of the latter animals were removed from the park alive and others were butchered. Data on removals from the other parks include all animals recorded from the time the parks were established until the start of this study. All such removals were by shooting.

The numbers of wapiti of each sex and year class removed each year during the

study from Elk Island, Jasper, Banff, and Waterton Lakes are presented in Appendices 10 to 14. The method of removal and whether or not intentional selection was practised are indicated. In Waterton Lakes, animals were taken by trapping and shooting, but they were not distinguished in the records. The methods by which age was assigned will be described in the section "Tooth wear and cemental deposition".

Numbers of wapiti of each sex produced in Elk Island

Certain circumstances make the wapiti population of Elk Island particularly useful for studying population dynamics of the species. That population is enclosed by a fence in a 50-square-mile area without entrance or exit. The population has been controlled by periodic removals for which records are available for a period of 19 years. An estimate of population size and sex ratio based on ground observations is available for the start of that period, and the results of a total segregated count are available for the close of the period.

In the slaughters in Elk Island before December 1958, shooting of calves was avoided as much as possible, and few were taken in that way. However, the wapiti removed by capture (Appendix 6) included calves in whatever proportion they entered the traps with the cows. Up to 1958, the slaughter quotas were apparently set so as to leave females in the majority. From December 1958 until the time of writing,

all removals from Elk Island were accomplished by slaughters in which the shooters were instructed to take animals without selection as to sex or age.

The total numbers of wapiti of each sex removed from Elk Island between March 1947 and January 1966, along with estimates of the numbers of animals of each sex present at the start and finish of that period, are shown in Table 1. The 1947 estimate was recorded by the late Dr. B. I. Love, Park Superintendent, on the basis of a ground count by the park wardens.

The 1966 estimate was obtained from an attempted complete count made by aircraft in January 20 of that year. A Helio Courier fixed-wing aircraft was flown systematically back and forth across the park on east-west lines at one-quarter mile intervals, at a height of about 300 feet above ground level and at speeds between 65 and 80 miles per hour. Two observers, D. A. Blood and J. R. McGillis, seated on opposite sides of the aircraft by the rear windows, recorded the species, number, and location of all wapiti, moose, bison, and deer (*Odocoileus* spp.) seen, on maps on which the flight lines had been previously drawn. A navigator seated beside the pilot assisted him in following the flight lines. The lines corresponded to the legal divisions of lands adjacent to the park, and at the start of each the pilot oriented his course from road allowances and fence lines. Most of the observers' attention was directed to searching for animals on a strip within one-eighth mile on each side, but when animals were seen farther out, as occurred particularly in open habitat, their location was plotted also. When such animals were sighted on the return flight along the adjacent line, they could be recognized because their location was already plotted on the map. A few animals were seen by different observers from lines one-half mile apart, but recognizable duplications were eliminated after the survey, when locations of animals plotted by the two observers were compared. Single wapiti and those in small groups were designated as calves, yearling males

Table 1
Net population change, total harvest, and net production of wapiti of each sex, Elk Island National Park, March 1947 to January 1966

Sex	Population estimates		Net population change 1947–66	Total harvest 1947–66	Net production* 1947–66
	March 1947	January 1966			
Male	254	132	–122	1091	969
Female	304	143	–161	1350	1189
Total	558	275	–283	2462†	2179†

*Total harvest minus net population change.

†Includes 21 harvested animals of unspecified sex.

(spike antlers), males older than yearlings (branched antlers), and females older than calves. However, as animals could be viewed only briefly during the flight, cows, calves, and yearlings in groups of six or more were recorded only as to number and location, and an additional procedure was followed to classify them. The writer met the observers from the Helio Courier when it returned to Edmonton to fuel, after the northern two-thirds of the enclosure had been surveyed. The location and number of animals in each group of unclassified wapiti were transcribed to a new map, and the writer proceeded immediately to the park as a passenger in a Bell 47B helicopter. Each mapped group was located and the members identified as to sex and age category.

The maximum interval between the time a group was initially observed in the strip survey and the time its members were categorized from the helicopter was six hours. Each group was found near the location where it was first sighted, and was recognized by the number of animals in it. Animals scattered among the aspen trees were gathered and herded into an opening where they were more readily identified and counted. The pilot flew slowly behind and to the left of each larger group, gradually coming alongside of it so that the observer in the right-hand seat could view the animals in profile. In the second flight of the strip survey which covered the southern one-third of the enclosure, the only large groups encountered included only bulls, and the observers in the Helio Courier succeeded in classifying all wapiti seen. In arriving at the estimate of numbers of wapiti of each sex present (Table 1), the sex ratio of the 34 calves was assumed to be 1 : 1.

The term net production is adopted here to signify the absolute number of wapiti harvested during a given period plus the population increase or minus the population decrease during the same period. From 1947 until 1966, 2,462 wapiti were harvested from Elk Island and the population

apparently declined by 283 animals to give a net production of 2,179 wapiti (Table 1). If 21 wapiti of unknown sex harvested are disregarded, the net production was 969 males and 1,189 females. If it is assumed that an equal number of males and females were born during the period, then 220 more males than females must have been lost to non-harvest mortality. The sex ratio in the net production was 85 : 100 and was significantly different from a ratio of 100 : 100 and from the observed foetal sex ratio of 113 : 100 ($P < 0.005$).

The possibility that the higher non-harvest loss of males, as compared to females, was the result of the effects of harvests on the composition of the population should be considered. If rates of non-harvest mortality of the sexes were equal at equal ages, but males were harvested at lower rates (as a proportion of those living) than females, then a greater number of males would have reached old age, when death from natural causes must be expected. In order for that to have occurred, there should have been more males in the population at most times during the 19-year period. The following items of evidence indicate that such was not the case. Firstly, the Park Superintendent estimated that there were fewer males than females in the population in 1947. Secondly, the composition of a sample comprising 64 per cent of the population shot without deliberate selection, November 1959 to January 1960 (Appendix 10), indicated that among animals 3 years of age and older in the population, males were in a minority. Finally, although each slaughter since December 1958 removed more females than males, the aerial census in January 1966 showed fewer males than females among animals older than calves. Therefore it is concluded that the sex difference in non-harvest losses was not caused by the harvests having allowed more males than females to reach a common age of senility. Rather, within certain age classes a greater proportion of males than females must have been lost to non-harvest mortality.

To consider the rates of productivity and harvest of the population during the period in which production of males and females was compared, the period was divided into two parts, of high and low densities, respectively: March 1947 to February 1960, and February 1960 to January 1966. (From November 1959 until January 1960, 410 wapiti and 141 moose were slaughtered in Elk Island. On February 26, 1960, an aerial census carried out in the same manner as that of January 20, 1966, except that age and sex were not identified, gave counts of 233 wapiti and 83 moose. Sprouts of aspen, previously suppressed for many years by heavy use by wapiti and moose, responded to the reduction in browsing pressure with a marked increase in height, and throughout the remainder of the study period continued to encroach on grassed openings.)

Leopold (1933:22) defined productivity as "the rate at which mature breeding stock produces other mature breeding stock, or mature removable crop", and stated that it "differs from rate of increase in that it includes increments to the removable crop as well as to the breeding stock". Leopold later (1933:171) omitted the word "mature" from the definition of productivity and also stated, "The unit of productivity, where the increase is removed, is the ratio or percent which can be removed yearly without diminishing the capital." Robinette (1956:415) applied Leopold's latter definition to the term net productivity. Net annual productivity rate will be used in that context in the following discussion, and animals of both sexes and all ages will be treated together in the population base, the harvested segments, and the population increases and decreases.

For the rate of increase of a population, Kelker (1947) derived the equation, $P = Ar^t$, in which "P" equals the number of animals resulting when an initial population of "A" animals increases at a rate "r" for a period of "t" years. To compute the net annual productivity rate of the population in Elk Island Park from the

data on the population change and the numbers harvested in different years, Kelker's (1962) equation was expanded as follows:

First, for a situation in which there are two harvests between the initial and final population estimates,

$$P = [((Ar^{t_1}) - H_1)r^{t_2} - H_2]r^{t_3}, \text{ or}$$

$$P = A(r^{t_1+t_2+t_3}) - H_1(r^{t_2+t_3}) - H_2(r^{t_3}),$$

where P and A are defined as above,

r = net annual productivity rate,

H_1 = number of animals in first harvest,

H_2 = number of animals in second harvest,

t_1 = number of calving seasons between initial count and first harvest,

t_2 = number of calving seasons between first and second harvest, and

t_3 = number of calving seasons between second harvest and final count.

Then in the general situation,

$$P = Ar^{t_1+t_2+\dots+t_n+t_{n+1}} - H_1r^{t_2+t_3+\dots+t_{n+1}}$$

$$- H_2r^{t_3+t_4+\dots+t_n+t_{n+1}}$$

$$- H_{n-1}r^{t_n+t_{n+1}} - H_n r^{t_{n+1}},$$

where with the exception that

t_3 = number of calving seasons between second and third harvest, the above definition of symbols apply, and

H_n = last harvest prior to final count,

t_n = number of calving seasons between next to last harvest and last harvest, and

t_{n+1} = number of calving seasons between last harvest and final count.

In applying the equation for rate of increase, Kelker (1947) adjusted the number of males in the initial population so that the sex ratio was 1 : 1. In the present situation, as the sex ratios at the various stages between the initial and final count were not known, no such adjustments could be made. The computed productivity rate applies to the circumstances that prevailed, and does not represent a potential for the species at a 1 : 1 sex ratio. It is an average annual value for the period, in the sense that it is based on the assumption that it was constant from year to year, which was of course not so. The equation was applied by substituting three-digit numbers for " r "

until the one that most closely balanced the equation was found.

When the equation was applied to the data for the period March 1947 to February 1960, a net annual productivity rate of 1.21 or 21 per cent was obtained. However, the 1947 estimate and the 1960 count indicated a decline in the population from 558 to 233. Using the same equation it can be shown that a net annual productivity rate of 22 per cent would have been needed for the population to have sustained the harvests without declining. Because the rates of productivity and harvests would be equal in a stable population, it can be concluded that the harvests over the period March 1947 to February 1960, while varying from year to year, had an effect equivalent to a removal of 22 per cent of the population annually.

When the equation was applied to the data for the period February 1960 to January 1966, a net annual productivity rate of 22 per cent was calculated. The 1960 and 1966 counts showed an increase in the population from 233 to 275. The harvests

Table 2
Distribution and grouping of wapiti according to sex and age group, aerial survey of main enclosure of Elk Island National Park, January 20, 1961

Portion of enclosure	Type of group*	Sex, age, and numbers				Group size		Wapiti/sq mi
		Males 1 year	Males ≥ 2 years	Females ≥ 1 year	Both <1 year	Mean	Range	
North (33 sq mi)	Bulls		30			2.7	1-6	0.9
	Cows	10	2†	120	33	6.3	1-46	5.0
	Total	10	32	120	33	5.3	1-46	5.9
South (17 sq mi)	Bulls	2‡	70			1.7	1-13	4.2
	Cows	1		6	1	1.6	1-3	0.5
	Total	3	70	6	1	1.7	1-13	4.7
Entire enclosure (50 sq mi)	Bulls	2	100			1.9	1-13	2.0
	Cows	11	2	126	34	5.6	1-46	3.5
	Total	13	102	126	34	3.2	1-46	5.5

*Group characterized by most numerous sex among members older than calves.

†Each of the two bulls was a member of a separate cow group.

‡Two yearling bulls formed a single group.

during that period had an effect equivalent to a removal of 20 per cent of the population annually.

Buechner, Buss, and Bryan (1951) studied a population of wapiti in Washington State using aerial counts and numbers killed by hunters over a 6-year period. They computed a "rate of increase" of 24 per cent, using that term in the context that net productivity rate has been used here. They suggested that the numbers counted were probably lower than the actual population, and that therefore the estimated rate of increase was somewhat higher than the actual rate. Murphy (1963) reported a rate of increase of 28 per cent over an 8-year period for a small, enclosed population of wapiti in Missouri. In his computations he evidently adjusted the sex ratio of the wapiti initially stocked in the enclosure to 1 : 1.

Distribution of the sexes and classified counts

In slaughters conducted without deliberate selection, differences in distribution and behaviour of the animals associated with age and sex, and subconscious selection by the shooters, could cause samples to be unrepresentative of the populations from which they were taken.

Park wardens in Elk Island consistently reported that, during slaughters, most wapiti encountered in the southern part of the main enclosure were bulls older than yearlings, whereas most of those in the northern part were cows and followers.* Inspection of the observations made in the aerial count of January 20, 1966, showed that the area in which bulls predominated could be separated from that in which cows predominated by an east-west line. The area south of that line, which contained most of the bulls, covers 17 square miles, and the area north, 33 square miles. The numbers and grouping of wapiti of each sex-age category counted in each of those two divisions of the park are given in Table 2. In the south-

*The term cows and followers is used to designate cows accompanied by calves and yearlings of both sexes.

Table 3

Numbers of wapiti of each age group and sex, counted by park wardens in survey of Banff National Park, October 28 to November 1, 1963

Age, years	Sex	Bow Valley	Red Deer and Cascade drainages	Other areas*	Total
<1	♂ & ♀	159	109	96	364
1	♂	36	64	19	119
≥2	♂	83	75	49	207
≥1	♂	119	139	68	326
≥1	♀	291	431	166	888
≥1	ratio ♂ : ♀	41:100	32:100	41:100	37:100
Unidentified		45	436	71	552
Total count		614	1115	401	2130
Total estimate†		804	1380	495	2679

*Drainages of North Saskatchewan, Clearwater, and Spray rivers.

†Sum of district wardens' population estimates for the districts occupied by wapiti.

ern part of the park the trees are smaller and the grassy and shrubby openings more extensive than in the north.

In the mountain parks, wapiti have been removed only from those areas which supported high numbers of wapiti in winter and were accessible by vehicle. They consisted of interspersed grass, shrub, and forest habitats and, except for parts of the Cascade and Red Deer drainages where wapiti were shot early in winter, are at low elevations and accumulate only a moderate depth of snow. Although some wapiti were present in these areas during the entire year, many were there only in winter, dispersing to higher elevations in summer. In the slaughters there, some bulls were taken in the same general areas as cows and followers, but certain localities tended to be more commonly occupied by either bulls or cows and followers.

Data on sex-age composition are available from a special survey of wapiti in Banff, conducted October 28 to November 1, 1963, by park wardens. The wardens travelled the valleys of their districts by

truck, by horseback, and on foot, and with binoculars counted all wapiti seen. When possible they identified them as to one of four categories: yearling males, males older than yearlings, females older than calves, and calves. Each warden also supplied an estimate of the total number of wapiti in his district, based on his survey and his previous experience in the district. Results of the survey are presented in Table 3. The sex ratio among 1,204 wapiti older than calves was 37 : 100.

V. Geist (pers. comm.), who studied bighorn sheep in the Cascade Valley from May 15 to August 16, recorded all his observations of wapiti, classified as to age and sex. He made no attempt to exclude animals counted on previous days. The sex ratio of his total of 1,254 observations of wapiti older than calves was 38 : 100, although it varied by month between extremes of 65 : 100 in June and 14 : 100 in July.

Among the wapiti observed in certain habitats in the mountain parks and adjacent areas, bulls have outnumbered cows.



In December 1966 and January 1967, J. G. Stelfox (unpub.) of the Canadian Wildlife Service conducted a census of bighorn sheep by helicopter in parts of Jasper and Banff known or suspected to support sheep in winter. He also counted all wapiti observed on the high, treeless or sparsely treed slopes and ridges. He identified 49 antlered and 15 antlerless wapiti in Jasper, and 53 antlered and 26 antlerless wapiti in Banff. Most were observed near the upper limit of trees. That survey did not cover all potential winter ranges for wapiti at high elevations and, on the ranges surveyed, some animals are thought to have been overlooked among the conifers just below tree-line. Picton (1961), writing of wapiti in the Sun and Judith river areas, Montana, described the tendency of bulls to range in small groups at higher elevations and in areas of greater snowfall than cows and calves. Lowe (1966) reported partial sexual segregation among red deer (*Cervus elaphus*) on the island of Rhum off the west

coast of Scotland, particularly in winter. Stags tended to occupy lower areas than hinds and followers in winter and spring and higher areas in late summer. Similarly, Peek and Lovaas (1968) found in the Gallatin drainage in Montana that adult bulls comprised a larger proportion of wapiti observed in winter on ranges at low and high elevations than on a range at intermediate elevation.

After the re-introduction of wapiti in the Bow Valley in Banff in 1918 and 1920, the first reported sighting of wapiti on the Ya Ha Tinda Ranch was in 1933–34 (Cowan, 1944). In 1942–43, 50 to 60 bulls and no cows were reported to be wintering on and adjacent to the ranch (Cowan, 1944). M. Gilmar, foreman of the ranch for several years, reported (pers. comm.) that when he first worked there during the winter of 1945, the only wapiti seen were about two dozen adult bulls. He returned to the ranch in October 1950 and that winter saw between 80 and 100 cows and followers, but no

adult bulls. From then until the time of writing, bulls older than yearlings have rarely been seen on the ranch, but cows and followers have regularly wintered there in large numbers. Some have also ranged in the vicinity in summer, while others have migrated back up the Red Deer Valley to spend the summer in Banff. When the writer first visited the ranch in 1957, large, bleached shed antlers were still common, attesting to the previous abundance of bulls in spring.

R. Webb (pers. comm.), formerly of the Alberta Fish and Wildlife Division, in an aerial survey of wapiti on February 9, 1959, counted 603 cows and followers on the ranch and vicinity, and 21 bulls older than yearlings on the slopes above the ranch. In similar surveys on February 23, 1961, January 9, 1962, and January 26, 1963, Webb counted 516, 685, and 633 wapiti, respectively, on the ranch and vicinity. All were cows and followers.

Harrison Flats is a grass-shrub area on the floor of the Clearwater Valley north of

Table 4

Numbers of wapiti in samples removed* without deliberate selection from Jasper, Banff, and Waterton Lakes National Parks, including samples in which older animals

were assigned only to broad age groups, tabulated as to sex and age with animals 4 years old and older consolidated

Age, years	Jasper		Banff				Waterton Lakes		Total		Ratio ♂ : ♀
			Cascade & Red Deer drainages		Bow Valley				Number		
	Dec. '57–Jan. '67		Dec. '60–Dec. '66		Nov. '57–Jan. '64		Nov. '58–Feb. '63		♂	♀	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	
<1	21	40	35	33	81	65	32	49	169	187	90:100
1	48	33	24	21	74	71	64	35	210	160	131:100
2	16	41	5	26	43	91	23	36	87	194	45:100
3	19	43	10	23	32	73	12	43	73	182	40:100
≥4	40	167	29	200	150	296	44	134	263	797	33:100
?†	0	0	5	29	18	17	7	5	30	51	59:100
Total	144	324	108	332	398	613	182	302	832	1571	53:100
≥2 (no.)	75	251	44	249	225	460	79	213	423	1173	36:100
≥2 (ratio)	26 : 100		18 : 100		49 : 100		32 : 100		36 : 100		

*All animals removed in winter, most by shooting, but some in the Cascade and Red Deer drainages and Waterton Lakes by trapping.

†Age not known. Body size indicated age ≥1 year.

the ranch and east of Banff. Webb first noted wapiti there on his aerial survey of January 9, 1962, when he counted a single herd of 50 adult bulls. On a re-survey January 26, 1963, he observed a herd of 75 adult bulls and a separate group of 4 cows.

The history of wapiti on the Ya Ha Tinda Ranch, and probably also on the Harrison Flats area, conforms with Cowan's (1946) comment concerning wapiti in Jasper: "the vanguard of the penetration into new areas consists of bulls". Writing of red deer, Darling (1956:66) pointed out that typically when new ground is colonized stags are the first to use it. He described an example (1956:51) in which, when hinds took up winter occupancy on a ground that had in previous winters been occupied solely by stags, the latter abandoned it except during the rut. The sequence in which bull wapiti, after pioneering the ranch area, vacated it about the time cows took up occupancy, parallels the circumstances described by Darling. It is relevant that

Lowe (1966) reported that male red deer on Rhum dispersed farther from their places of birth than females.

Sex and age composition of samples of wapiti removed for population control

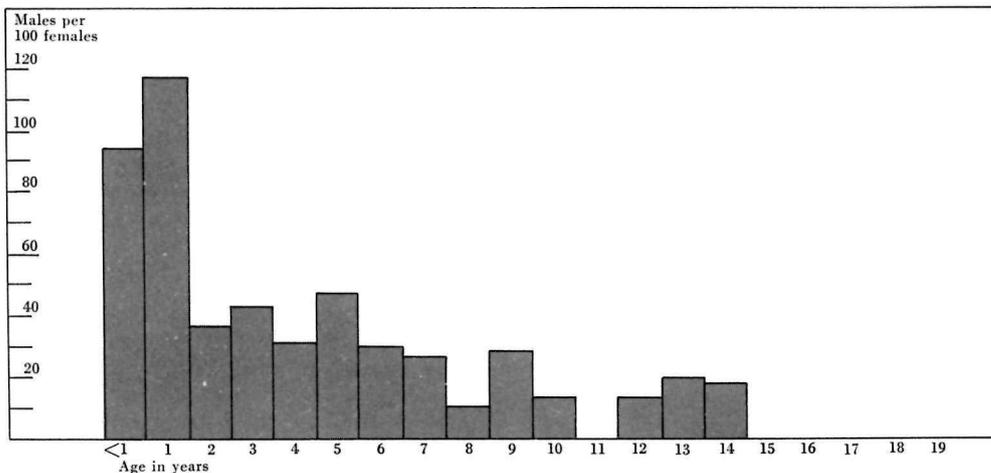
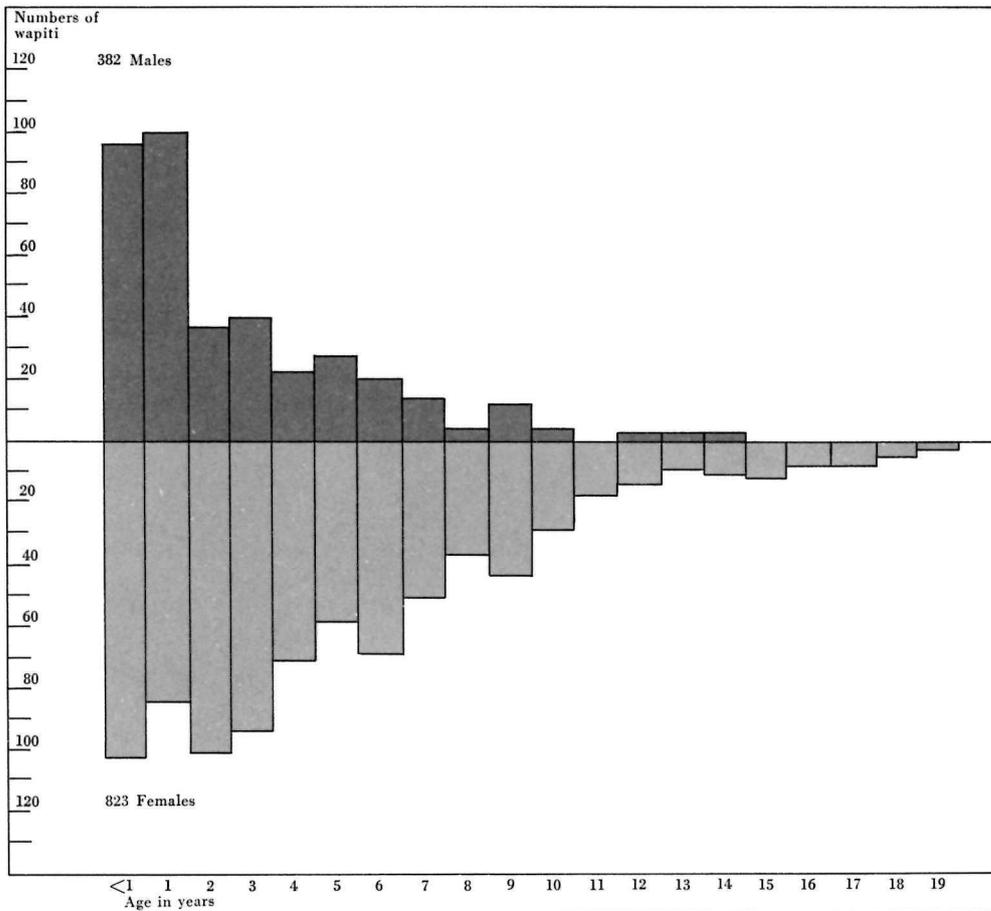
The numbers of wapiti of each sex and age removed from Jasper, Banff, and Waterton Lakes during the study are presented in Table 4, with animals taken in selective removals from Banff (Appendices 12 and 13) excluded. Animals 4 years old and older are treated as one group because data are included from slaughters in which the ages of animals with complete dentition were assigned by tooth wear only, in some cases to broad classes. Figure 3 shows the data combined from the mountain parks for those years in which specific ages were assigned on the basis of cemental layers, with each age class treated separately.

The numbers of yearlings exceeded the numbers of calves in the composite sample

removed from the mountain parks (Table 4), indicating either that calves were under-represented or yearlings were over-represented.

To test the possibility that calves were under-represented, the number of calves and the number of lactating cows shot in the slaughters were compared. The data available are all from the mountain parks. As animals taken in January are included in the samples, some cows would have ceased lactation because of weaning. Therefore, in order for calves and cows to have been represented in the slaughters in the same proportions as were present in the living populations, more calves should have been taken than lactating cows. As the samples contained 298 calves and 499 lactating cows, it can be concluded that calves were markedly under-represented in the slaughters. This was probably caused by both a subconscious preference of the shooters for larger targets and an aversion to shooting juveniles.

Figure 3. Numbers and age-specific sex ratios of wapiti removed from Jasper, Banff, and Waterton Lakes National Parks, 1960-67. All animals were taken in winter, most by shooting, but some in Banff and Waterton Lakes were trapped. Wapiti shot selectively for study are excluded.



Males exceeded females in the sample of yearlings removed in the mountain parks (131 : 100) and the difference was significant ($P < 0.01$). The shooting of slightly more female than male calves may have left more males than females available for shooting as yearlings. However, that effect would have been slight. Because the sex ratio favoured females in both calves and 2-year-olds, it seems improbable that there would have been substantially more male than female yearlings in the populations. More likely, some shooters subconsciously selected yearling males. Most yearlings of both sexes are with herds of cows in winter. The distinctive appearance of the yearling males may attract attention to them, causing them to be shot first.

Andersen (1953) presented data on the age and sex composition of a population of roe-deer at intervals during a period of 21½ months in which it was hunted to extinction. He showed that in all age classes males were more vulnerable to shooting than females.

The sex ratio of wapiti 2 years old and older slaughtered from the different mountain parks, while it consistently and heavily favours females, varies considerably (Table 4). Earlier data have shown that the winter distribution of bulls differs in part from that of cows and followers. In the mountains, more bulls than cows winter on high ranges inaccessible to vehicles. Because slaughtered animals must be salvaged, animals on such ranges are immune to slaughter. Variation among the four mountain areas in the degree to which road access coincides with the winter distribution of bulls is probably a major factor contributing to the variation in the sex ratio of the adults slaughtered. Also, shooters may subconsciously select for or against bulls.

In view of the evidence presented previously that males outnumber females on higher winter ranges, and that they tend to pioneer new ranges, the abrupt drop in the male : female ratio at 2 years old in the sample harvested in the mountain parks is thought to be partly attributable to dis-

persal of many bulls between their second and third winters from the ranges where they were reared to areas which were not accessible to slaughter. It is also partly attributable to over-representation of yearling males in the slaughters.

In the composite sample from the mountain parks (Fig. 3) the sex ratio remains fairly stable from 2 to about 7 years old, the ratio for the total sample of those six age classes being 36 : 100. The proportion of males in successive age classes then declines until males become extinct after 14 years of age. Perhaps the mortality rate of males is similar to that of females between 2 and 7 years old, as the data suggest. However, there is an alternative interpretation. During the rut there appears to be an influx of mature bulls to lower elevations. Some of the bulls coming from higher ranges may remain at low elevations to replace those that have been slaughtered or lost to natural causes. If this is the case, the mortality rate of bulls could exceed that of cows of equal age and the result still be consistent with the composition of the slaughtered sample. Lowe (1966) found evidence that among red deer on the island of Rhum older stags tended to occupy lower ground than those younger than 4 years. With the population data available it can be concluded only that the mortality rate of male wapiti became higher than that of females sometime after 1½ years of age. The data also suggest that after about 7 years of age the mortality of bulls increased markedly, relative to that of cows of equal age.

The maximum age of any bulls to which precise age was assigned was 14 years, attained by two specimens taken in slaughters in Banff. The maximum age of cows among those from slaughters was 19 years, also attained by two Banff specimens. One older cow was examined, specimen 102 in the research series, taken in Banff at an age of 21 years. From records of 254 ear-tagged wapiti shot by hunters in Montana, Picton (1961) reported maximum longevities of 12½ years for one bull and 18½ years for two cows.

Table 5
Numbers of wapiti deaths caused by trains and highway vehicles, reported by park wardens, Banff and Jasper National Parks, 1958–65

	Sex and age of wapiti killed				Total
	Male ≥1 year	Female ≥1 year	Both <1 year	Not specified	
Train	23	60	12	20	115
Highway vehicle	10	28	16		54
Total	33	88	28	20	169

In addition to the removals of wapiti for population control, two other man-made causes of mortality are collisions with trains and highway vehicles, and recreational hunting on adjacent lands.

Reports by park wardens in Banff and Jasper during the period 1958–65 of wapiti struck by trains and highway vehicles and killed outright or injured so badly that they were shot, are presented in Table 5. The data are not thought to be a complete record of all vehicular deaths, but probably represent fairly the sex and age composition of the total mortality from that cause. The sex ratio of those older than calves was 37 : 100, the same as that of wapiti counted by park wardens in the survey of Banff in 1963 (Table 3) and of wapiti observed by V. Geist in the Cascade Valley in the same year. It supports the other evidence of a disproportionate sex ratio favouring females among adults in the valleys where the highways and railways are located, and indicates that vehicular deaths do not contribute to shifting the sex ratio in that direction. No deaths of wapiti from collisions with vehicles have been reported from Elk Island or Waterton Lakes.

For many years there have been open seasons for wapiti in those parts of Alberta adjacent to Jasper, Banff, and Waterton Lakes. Thus hunting has been a potential mortality agent for any wapiti moving outside the parks during open season.

The Bow Valley east of Banff has for several years been open to hunting of both sexes of wapiti with bow and arrows only,

during parts of the months of September through December, but according to W. Wishart of the Alberta Fish and Wildlife Division (pers. comm.) few animals have been killed. Of 51 wapiti ear-tagged in the Bow Valley inside the park in 1960 and 1961, none have been reported taken outside the park.

Throughout the other wildlife management zones bordering the mountain parks, there has been a season for rifle hunting of bulls only, in parts of September and October, followed by a season for either sex in parts of November and December. Although males have slightly exceeded females in the total harvests from those zones in recent years, females have been in the majority among those taken in November and December, when either sex could be shot (Wishart, 1966, and unpub.). Hunting in the latter season has probably removed more park animals than has the early season, because the herds which migrate from the parks to winter outside usually do so after the onset of winter weather. Even the late season does not usually result in a harvest of many wapiti near the park boundaries. Wapiti flushed by shooting during the slaughter operations in the parks have usually been observed to move uphill and into tree cover. Because the parks are located along the continental divide, such movement tends to keep the animals within the parks rather than drive them out. Because wapiti ranges adjacent to the parks are usually at lower elevations, we might expect hunting there to drive any wapiti

Tooth wear and cemental deposition

near the boundaries into the parks. In support of that supposition, since 1959, when hunting was first allowed on the Ya Ha Tinda Ranch, large herds have not become established there until after the season closed. In that year, a special season was opened in January on the ranch and vicinity, and about 200 wapiti were shot.

Occasionally, under conditions of heavy snowfall and north winds, wapiti have moved from Waterton Lakes Park to the ranchlands north of the park for short periods. Banfield (1950) reported that about 450 wapiti were shot there in the winter of 1946–47. During the present study, according to observations of park wardens and information obtained by G. Kerr and G. Armstrong of the Alberta Fish and Wildlife Division (pers. comm.), the numbers killed in that area have been small in spite of hunting of both sexes having been allowed from November until March 15.

Data are not available to assess the proportion of the wapiti born in the mountain parks that are harvested elsewhere. However, the limited information does not suggest that such harvests have been important in altering the sex ratio of the populations surviving in the parks.

The teeth were studied for two reasons. The amount of wear on the occlusal surfaces and the numbers of cemental layers provide alternative criteria for estimating age. Also, as deterioration of the teeth through wear could reduce the efficiency of food utilization, it is a potentially important feature of senescence.

Dentary bones were collected from all wapiti taken during the period of the study. They were assigned to age classes by criteria based on tooth replacement and wear (Quimby and Gaab, 1957). Up to December 1960, wear patterns of the molariform teeth were compared with the illustrations and descriptions published by Quimby and Gaab (1957). In 1960, Quimby kindly selected from a collection of dentaries from Waterton Lakes, a series showing conditions comparable to those represented in his collection of specimens of known age. The series comprised specimens representing each age class from calves to 9-year-olds and the inclusive groups, 10–15 years and 16–21 years. The series, supplemented by Quimby and Gaab's (1957) published illustrations and descriptions, was used in assigning age to wapiti shot in all subsequent slaughters. Quimby and Gaab showed that variation in tooth wear limits the precision with which individual age can be established, particularly as age increases.

Beginning with the specimens slaughtered in the winter of 1961–62, wapiti 2 years old and older were also assigned ages by counting seasonal layers in the dental cement by the method devised by Mitchell (1963, 1967) for red deer. A few yearling wapiti were included.

A lapidary saw was used to cut through the dentary between the cusps of the first molar, cutting through the thickest part of the cemental pad which lies between the roots (Fig. 4). Both surfaces exposed by the cut were examined under direct light at 16× magnification, using a stereomicroscope. No polishing was necessary, but the exposed surfaces were usually covered with a film of alcohol or water to facilitate clear viewing of the cemental layers.

Mitchell (1963, 1967) sawed the first lower molar through the cemental pad between the roots and found alternating translucent and opaque layers of cement. He found that the opaque cement was associated with summer/autumn growth and the translucent cement with winter/spring growth. In most red deer examined by Mitchell (1967), the first cement produced was a thin translucent layer deposited during the first winter of life, and that was followed by an opaque layer during the second summer. In 19 out of 22 red deer of known age between 1½ and 19½ years from the east Highlands of Scotland, Mitchell (1967) found that the number of opaque cemental layers corresponded to age in years. In each of the exceptions the disparity was only one year. Lowe (1967) found a wider range of discrepancies between numbers of cemental layers and known age of red deer from the island of Rhum. Mitchell (1967) suggested that the less marked seasonality of the climate of Rhum might make for a less consistent seasonal pattern in cemental deposition. Low and Cowan (1963) and Ransom (1966) demonstrated that in known-age specimens of pen-raised Columbian black-tailed deer (*Odocoileus hemionus columbianus*) and free-living white-tailed deer, respectively, each pair of alternating major light and dark layers of cement could be equated to one year of life after the onset of cemental deposition.

Since the mandibles of yearling and 2-year-old wapiti can be assigned to age classes with certainty on the basis of tooth replacement (Quimby and Gaab, 1957), they were used to ascertain the age at which cemental production begins under the first lower molar. A thin layer of opaque cement was present in all yearlings killed in early winter; and a thin opaque layer, a thin translucent layer, and a second opaque layer, thicker than the first, were present in 2-year-olds killed in early winter. A very few specimens had, in addition, adjacent to the dentine, a trace of opaque cement followed by a trace of translucent cement, evidently deposited in the first year of life.

Figure 4. Method of cutting dentary and first molar with lapidary saw to expose cemental layers.

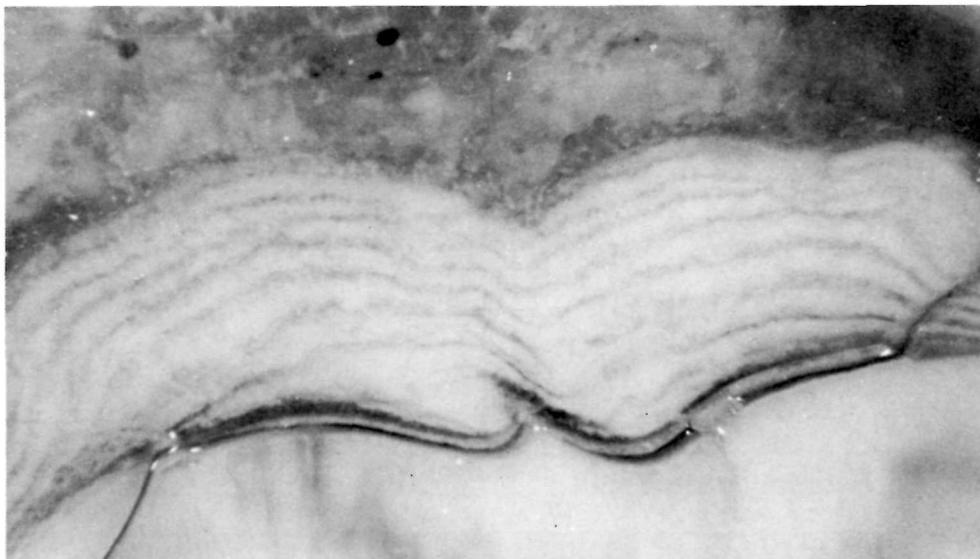


Those deposits were so small in thickness and area that there was no likelihood of mistaking them for the cemental layers produced during the second year of life.

Of 14 specimens of various ages taken between September 15 and February 21, all appeared to have opaque cement adjacent to the periodontal membrane. Of eight specimens taken between March 29 and July 9, one taken May 28 showed a trace of opaque cement adjacent to the periodontal membrane, and the remaining seven appeared to have translucent cement adjacent to the membrane.

On the basis of the above observations, ages were assigned from cemental layers by assuming that the first layer of opaque cement was deposited early in the second year of life, and thereafter a translucent layer was deposited annually in late winter and spring, and an opaque layer in late summer and autumn. The date of birth of all specimens was assumed to have been June 1, and each age assigned will refer to that of the previous birthday. The age in years of a specimen taken in December, for example, was estimated by counting the number of translucent layers enclosed between opaque layers and adding one year. Figure 5 shows the sectioned cemental

Figure 5. Cemental layers exposed by cut between roots of first lower molar of female wapiti shot in Jasper National Park, January 1967, at an estimated age of 9 years. Photomicrograph under direct light.



pad of the first lower molar of a wapiti of an estimated age of 9 years.

Ages given for specimens taken before December 1, 1961, were assigned from tooth wear, and those given for specimens taken after that date were assigned from cemental layers. In comparing age assigned from tooth wear to age assigned from cemental layers, the latter will be referred to as "actual age".

Complete permanent dentition is attained in wapiti at about 30 months of age (Quimby and Gaab, 1957). Thereafter, the enamel ridges which form the cutting edges of the molariform teeth become progressively abraded. The linear amount of enamel cutting edge becomes reduced as the lateral convolutions and the infundibula are worn away, particularly in stages beyond Quimby and Gaab's 7-year-old class. One might expect that tooth wear beyond a certain stage would reduce the efficiency with which the animal utilizes forage.

Assigning specimens to Quimby and Gaab's age classes provides an objective method of measuring the degree of tooth wear. To learn whether there were differences in the rate of wear of the teeth of wapiti populations in different habitats, and of males as compared to females, all spec-

imens 2 years old and older taken after December 1, 1961, were assigned an age by visual comparison of the teeth to the series assigned to age classes by Quimby. Ages were then estimated by counting the cemental layers, with no reference to the age previously assigned from tooth wear.

Using the resulting data, linear regressions of age estimated from tooth wear, on age estimated from cemental layers, were calculated for wapiti of each sex from each of the four parks: Jasper, Banff, Waterton Lakes, and Elk Island (Figs. 6 and 7). In samples from each park, specimens assigned on the basis of tooth wear to the broad categories 10-15 and 16-21 years old were excluded from the regression analyses, along with those of equal or greater "actual age". All specimens are plotted on the graphs, but each regression line includes only the range of actual ages which were used in the analysis. The regression coefficient can be considered an estimate of relative rate of tooth wear. It represents the average amount of abrasion that occurs in one year of life. It is represented in units that correspond to the amount of abrasion between Quimby and Gaab's (1957) successive age classes. Regression coefficients and actual ages corresponding on the re-

Figure 7. Linear regressions of age estimated from tooth wear on age estimated from cemental layers in wapiti of each sex from Waterton Lakes (above) and Elk Island (below) National Parks. Value beside each plotted point represents number of specimens.

tailed deer, respectively, and gave it the above interpretation. In the wapiti in which the condition described above was recognized, the secondary, opaque or semi-opaque layers were markedly thinner than the primary or summer layers, and were excluded from the count in estimating age.

If each translucent cemental layer counted represented one winter of life after the first, then the differences in regression coefficients are attributable to differences in the rate of tooth wear. However, an alternative explanation is that the differences are due to the groups with the lower coefficients having had a higher frequency of extra-annual cemental layers which were inadvertently counted as annual layers. To test that possibility, samples from Jasper and Elk Island were re-examined. Those populations represented the two extremes, the regressions of males and females exhibiting no significant difference in Jasper but the greatest difference in Elk Island. If, in Elk Island, translucent cemental layers counted as annual layers were produced more frequently by females than by males, we might expect the average interval between succeeding translucent layers to be proportionately thinner in females than in males.

For each specimen 3 years old and older from Elk Island and Jasper, the greatest thickness of the cemental pad was measured, using a dissecting microscope at a magnification of 16X with a micrometer disc mounted in the ocular lens. The results of those measurements in relation to the age of the specimens are presented in Table 7. The Elk Island females do not exhibit a smaller mean interval between cemental layers when compared to males of the same population than do Jasper females when compared to males of that population. The data therefore do not support the hypothesis that the groups with the lower regression coefficients had a higher frequency of secondary cemental layers. The interpretation that the differences in regression coefficients represent differences in the rate of tooth wear is the more acceptable.

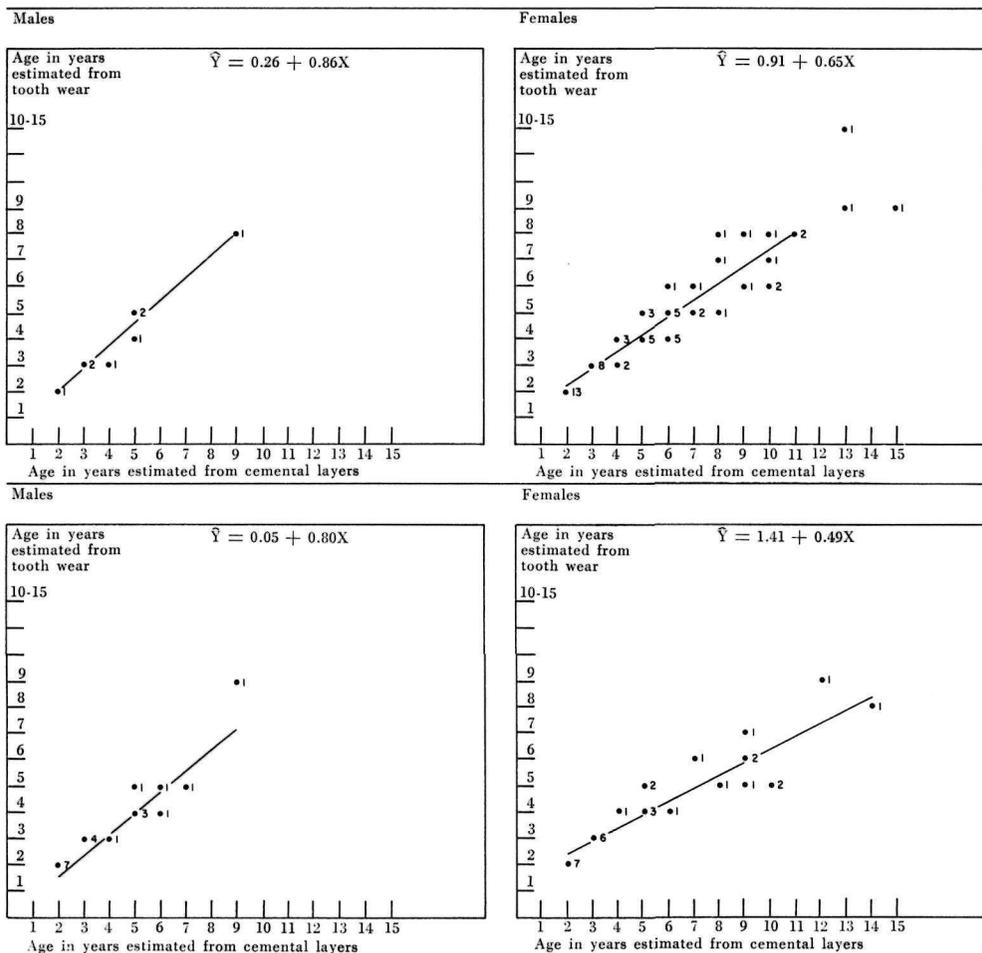


Table 6
Regression coefficients of "tooth-wear-age" on actual age and actual ages corresponding on regression line to 8 years' "tooth-wear-age"

	Regression coefficient		Actual age at 8 years' "tooth-wear-age"	
	Male	Female	Male	Female
Jasper	0.87	0.89	8.3	8.5
Banff	.81	.72	9.3	10.1
Waterton Lakes	.86	.65	9.0	10.9
Elk Island	.80	.49	10.1	13.4

Table 7
Average intervals between cemental layers counted in wapiti from Jasper and Elk Island National Parks

	Number of specimens	Average age, years	Average no. cemental layers	Average interval between layers, mm
Jasper				
Males	23	5.1	4.1	0.51
Females	80	6.0	5.0	0.42
Elk Island				
Males	11	5.3	4.3	0.46
Females	23	7.0	6.0	0.44

In attempting to explain the apparent differences in rates of tooth wear between males and females, it is pertinent to know whether males have a larger occlusal surface than females. In samples of mandibles of wapiti 4 to 9 years old from Elk Island and Banff Parks there were no significant differences between males and females in length of molariform tooth rows and crown widths of molariform teeth (Table 8), each measurement having been taken at the widest point. That would indicate that in the permanent dentition there is slight if any difference associated with sex in the area of occlusal surface available for mastication. The relationship of the rate of tooth wear of males to that of females varied considerably among the populations of the four different parks (Table 6). That seems to indicate that in at least some of those parks males have tended to use foods of different abrasive qualities than females.

The following hypothesis, offered to explain the indicated differences in rate of tooth wear between the sexes and among populations, while consistent with the available information, is still largely speculative. In Elk Island where the habitats used by the sexes were most similar, and presumably therefore the forage used was also most similar, the difference in rate of tooth wear between the sexes was the greatest among the populations studied. As data indicated that the occlusal surfaces of males and females are of equal area, it is suggested that the more rapid rate of tooth wear of males was caused by a greater annual food intake.

It is hypothesized that differences in the ranges used by wapiti in the four parks lead to the differences in tooth wear between populations. It is suggested that a sex difference in annual intake of forage is common to wapiti in all the parks, but that

in the mountain parks its effect on tooth wear is compensated to various degrees by differences in the distribution of the sexes and associated differences in the amounts of abrasive material eaten in or with their forage.

Grasses are the major component of the diet of wapiti in some areas (e.g. Cowan, 1947a). They are characteristically high in silica (Bonner and Galston, 1952:69), most of which is in the form of opaline phytoliths (Baker, Jones, and Wardrop, 1959). Healy and Ludwig (1965) found the content of opaline phytoliths in pasture grasses about ten times as high as that in clover. Baker *et al.* (1959) found that the hardness of opaline phytoliths exceeds that of the enamel of sheep's teeth. They considered the consumption of phytoliths in forage an important factor contributing to the wear of sheep's teeth in Australia.

Severinghaus and Cheatum (1956:94) found that the rate of tooth wear in white-tailed deer was approximately doubled in specimens foraging in areas where the vegetation carried quantities of abrasive material on the surface.

Healy and Ludwig (1965) showed a direct relationship between the degree of wear of sheep's incisors on three New Zealand farms and the amount of soil consumed. They demonstrated the abrasive qualities of the soil experimentally and concluded that differences in soil consumption were the cause of the observed differences in tooth wear. As the average incisor height of 5-year-old ewes on a high-wear farm was less than one third that of ewes of the same age on a low-wear farm, the contrast appears to have been greater than that observed in the populations of wapiti in the present study. The consumption of phytoliths varied little between farms. They made up only about one tenth of the abrasive material consumed on the high-wear farm but most of the abrasive material consumed on the low-wear farm. Thus, where tooth wear is light, differences in the consumption of phytoliths or extraneous sediment, or both, could be important in causing differences

in rate of wear. There are reasons to expect variations in the consumption of silica from both those sources among the populations of wapiti studied.

At low and medium elevations there appears to be a gradient in certain characteristics of the ranges from Jasper to Banff, Waterton Lakes, and Elk Island, in that order, the same sequence as the decreasing trend in rate of tooth wear. In the Athabasca Valley in Jasper, the grasses are shortest and sparsest, the soil most sandy, and the preferred forbs and browse plants the scarcest of the ranges of wapiti populations studied. Sediment from glaciers that feed the Athabasca River is deposited by the river where it passes through the major winter ranges. Winds frequently pick up sediment from the beaches and dunes along the river and other areas where plant cover is sparse and deposit it over the grassy areas. In contrast to Jasper, blowing sediment is negligible on ranges in the other parks. In Banff, grass stands have a higher proportion of tall species and are more dense, and browse is somewhat more abundant than in Jasper. Stands of grass in Waterton Lakes are much taller and fairly dense, and browse and forbs are fairly abundant. In Elk Island, grass stands are of moderate height and fairly dense, but limited in extent, and browse and forbs are abundant.

Data on food habits from the various parks indicate a close relationship between the relative abundance of grass, forbs, and browse, and their proportions in the diet of wapiti. Cowan (1947a) showed that the winter diet in the Athabasca Valley was almost exclusively grasses. Preliminary data from Banff (Flook, unpub.) indicate that grasses and sedges are the major component of the diet at most times of the year, but use of forbs in summer and of browse in summer and winter is substantial. Holsworth (1960) showed that in Elk Island browse comprised most of the winter diet, and browse and forbs together made up most of the summer diet.

Wapiti using browse, tall grasses, and forbs would be expected to consume less

Table 8
Measurements of mandibular molariform tooth row of adult wapiti

	Males (16)			Females (34)		
	Mean	Range	Standard error	Mean	Range	Standard error
Length of tooth row, mm	139.9	131-148	1.11	138.9	129-148	0.60
Crown width of P3*, mm	12.44	11.2-14.0	.152	12.29	11.0-13.8	.103
Crown width of M2*, mm	17.78	16.9-19.2	.202	17.55	16.0-19.5	.166

*Nomenclature follows that of Riney (1951).

extraneous sediment than those using short grasses, particularly where the latter are sparse and soil is exposed. Also a higher proportion of forbs and browse in the diet could be expected to be accompanied by a lower consumption of opaline phytoliths.

Males tend to spend more of their lives at higher elevations than females (Cowan, 1950, and data to follow). The writer suggests therefore that males in the mountain parks tend to use more forbs and browse than females, those plants being more abundant at higher elevations, and perhaps feed less on closely cropped grass stands, and therefore their diets contain lower proportions of abrasive material. That would be particularly so in Jasper where the areas farther from the Athabasca River would be less affected by blowing sediment.

Other factors being equal, animals that wear their teeth more rapidly can be expected to suffer the effects of inefficient food utilization at a younger age. In Quimby and Gaab's (1957) age classes, the 8-year-old class shows particularly marked reduction in enamel ridges as compared to the younger classes. Apparently, in Banff males reached that stage of tooth wear on the average almost one year earlier than females (Table 6). In Waterton Lakes, the indicated sex difference was almost 2 years, and in Elk Island more than 3 years. It will be shown in the Discussion that deterioration of the teeth is relevant to the question of longevity of the sexes.

Body growth

Little information concerning growth in wapiti is available in the literature.

Johnson (1951) reported a mean body weight of 32.5 pounds (14.7 kg) and a mean hind foot length of 15.46 inches (39.3 cm) in a sample of 23 wapiti calves measured in their first day of life in Montana. The mean weight of males was heavier than that of females by 4.41 pounds (2.0 kg).

Blood and Lovaas (1966) summarized data published by a number of authors on weights of entire and dressed carcasses of wapiti, as well as data on animals they had weighed in Riding Mountain National Park, Manitoba. In each study the number of animals weighed in one area at one season of the year was small, and only the data collected by Blood and Lovaas (1966) included specific ages of all specimens.

Greer and Howe (1964) presented weight measurements of eviscerated carcasses of 271 male and 856 female wapiti of five age groups: calves, yearlings, 2-year-olds, 3- to 7-year-olds, and 8-year-olds and older, slaughtered in winter in Yellowstone National Park. They concluded, "A levelling off in weight [of males] appears to occur between the 3-thru-7-year group and the 8-year-and-older group but the data do not permit a reliable estimate for the age of maximum weight", and, "Females classified in the 3-thru-7-year group appear to have reached a maximum weight."

In the slaughters held in Banff in 1960-61, 1961-62, and 1962-63, entire carcasses were weighed to the nearest pound with viscera and antlers intact. Before being weighed, all animals were bled by having the throat cut, but the weight lost in bleeding varied because some animals bled internally more than others. Antlers were later sawn off, weighed to the nearest 0.05 pound, and their weights subtracted from the total weight to give body weight. Both body and antler weights were converted to metric units.

Chest girths and hind foot lengths were also measured. Bandy *et al.* (1955) pointed out that chest girth provides an indication of the bulk of an animal and relates closely

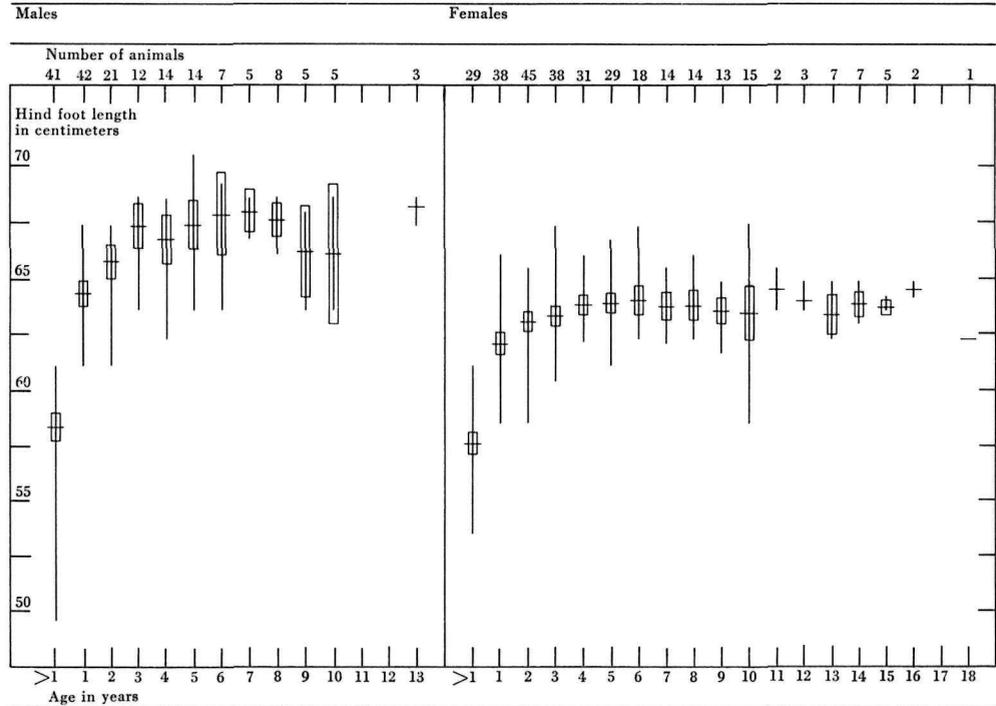


Figure 8. Hind foot length of wapiti of each sex and age slaughtered in winter in Banff National Park. Median horizontal lines represent means, vertical bars represent 95 per cent confidence limits, and vertical lines represent ranges.

to body weight, whereas hind foot length is a measure of skeletal size and is unchangeable once it has reached its maximum. Measurements were taken to the nearest one-quarter inch using a steel tape and were later converted to millimetres. Chest girth was measured immediately posterior to the axilla. The hind foot was measured from the proximal end of the calcaneum to the tip of the hoof, with the hock joint flexed enough to locate the proximal end of the calcaneum but not so much as to cause flexing of the toes.

Measurements of hind foot length, chest girth, and body weight are summarized in Figures 8 to 10. Among the 73 males and 198 females 3 years old and older on which data are included, 25 males and 84 females were taken in the 1960-61 slaughter, and their ages were assigned from tooth wear. The remaining 58 males and 114 females were taken during the two subsequent slaughters, and their ages were determined from cemental layers.

For each measurement it is useful to learn the age at which growth ceased and whether there was a reduction in size following the attainment of maximum size. Therefore, each graph was inspected and mean and sum of squares were determined for the group of age classes which appeared homogeneous and of adult size. That group was then compared with younger and older age classes or groups of age classes by analyses of variance. If the difference between the selected group of age classes of maximum size and the next youngest age class was not significant, then the latter was grouped with the former and the resulting group was compared to the next younger age class, until a significant difference was detected. The results of the analyses were considered evidence that, on the average, growth in the particular measurement continued at least to the age of the youngest class which was found not significantly smaller than older classes.

The indicated curve of means shown in

Figure 9. Chest girth of wapiti of each sex and age slaughtered in winter in Banff National Park. Median horizontal lines represent means, vertical bars represent 95 per cent confidence limits, and vertical lines represent ranges.

Figure 10. Body weight of wapiti of each sex and age slaughtered in winter in Banff National Park. Median horizontal lines represent means, vertical bars represent 95 per cent confidence limits, and vertical lines represent ranges.

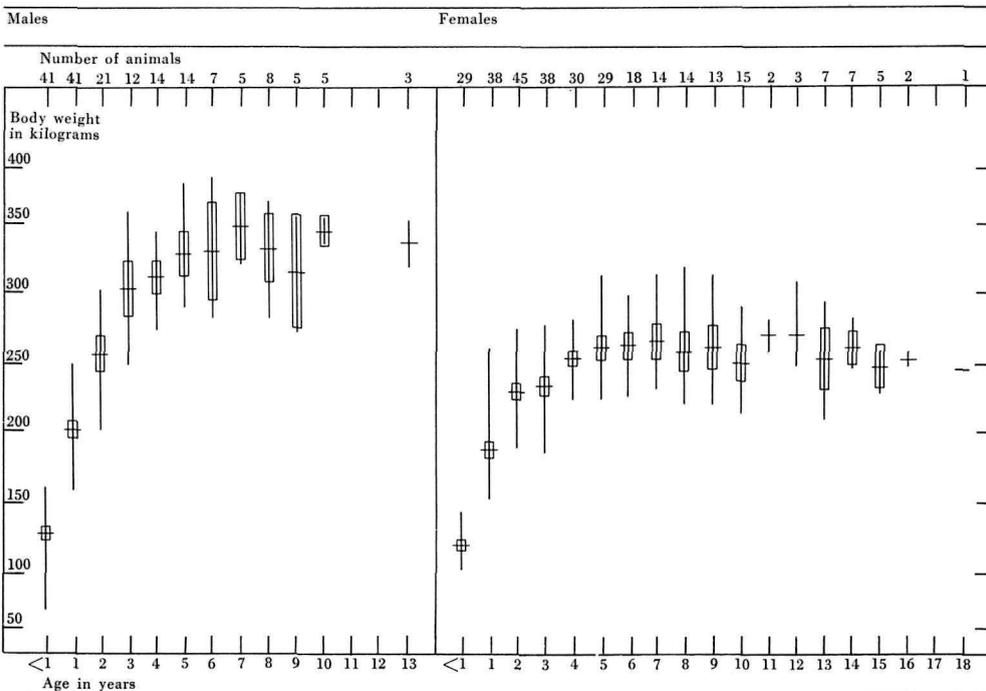
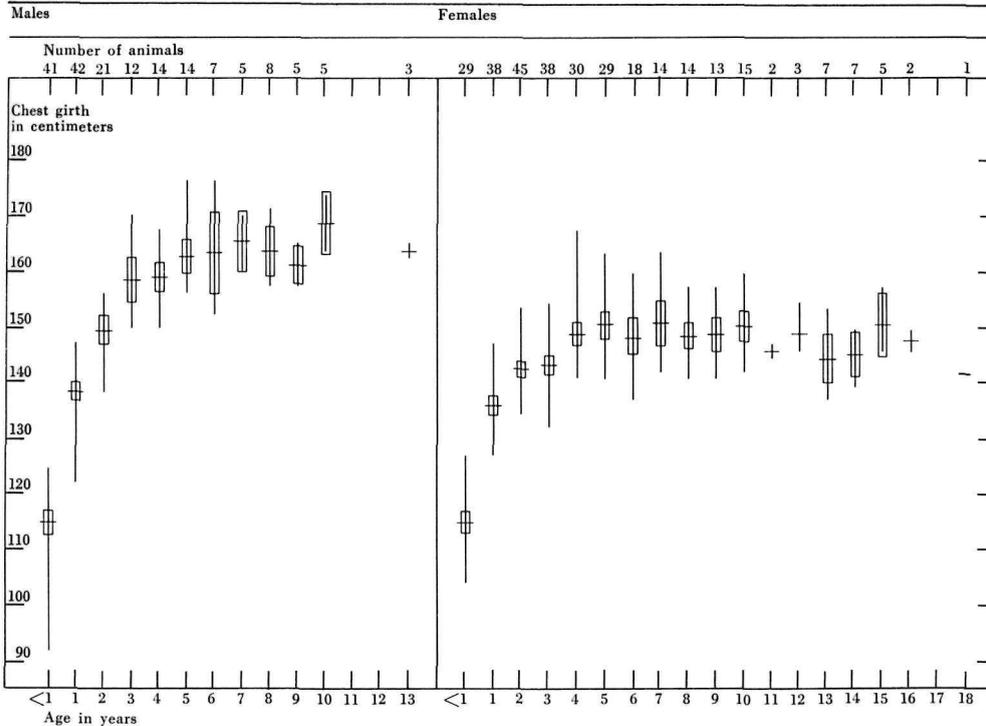


Figure 8 suggests that among males hind foot length may have continued to increase until 6 years of age. However the 3-year-old class was not significantly smaller in hind foot length than older males as a group. The mean hind foot length of the 2-year-old class was significantly smaller ($P < 0.01$) than that of the group 3 to 13 years old.

In the females also, the configuration of the graph in Figure 8 suggests that slight increase in hind foot length may have continued to 6 years of age. However, the 4-year-old class was the youngest which was not significantly smaller in hind foot length than all older females as a group. The mean hind foot length of the 3-year-olds was significantly smaller than that of the group 4 to 18 years old.

Inspection of the mean hind foot lengths and confidence limits reveals that for all ages represented by four or more animals, mean values of males were significantly greater than those of females of the same age. The mean hind foot length of males 3 years old and older was 67.3 cm as compared to a mean of 63.7 cm for females 4 years old and older.

The data in Figure 9 suggest that in males chest girth may have continued to increase to an age of 10 years. However, the 5-year-old class was the youngest which was not significantly smaller in chest girth than all older animals as a group. The mean chest girth of 4-year-old males was significantly smaller ($P < 0.01$) than that of the group 5 to 13 years old.

Among females the mean chest girth values of different age classes suggest a decline with advancing age after 10 years of age. The mean chest girth of females 11 to 18 years old was significantly smaller than that of the group 4 to 10 years old. The configuration of the graph suggests that in females maximum chest girth was not reached until 7 years of age. However, the 4-year-old class was the youngest which was not significantly smaller in mean chest girth than those older in the group 4 to 10 years old. The 2-year-olds and the 3-year-

olds did not differ significantly in chest girth. However, both individually and grouped together they were significantly smaller ($P < 0.01$) in mean chest girth than the group 4 to 10 years old.

The confidence limits for mean chest girth of calves show no significant difference between males and females. However, for all other age classes represented by four or more animals, mean values of males were significantly greater than those of females of the same age. The mean chest girth of all males 5 years old and older was 163.9 cm as compared to a mean of 149.2 cm for females 4 years old and older.

Mean body weights of males (Fig. 10) suggest that body weight continued to increase to a maximum at 7 years of age and then declined to a lower level, which prevailed through the remainder of life. However, none of the differences in body weight among age classes from 5 to 13 years of age was significant. Mean body weights of 3-year-old and 4-year-old classes were not significantly different from each other. However, both individually and together they were significantly smaller than the mean of the group 5 to 13 years old.

Among females the graph suggests that body weight continued to increase to an age of 7 years and decreased with advancing age after 9 years. However, the difference between the mean body weight of the group 10 to 18 years old and that of the group 5 to 9 years old was not significant. The 4-year-old class was the youngest which was not significantly smaller in body weight than all older animals as a group. The mean body weights of the 2- and 3-year-old classes were not significantly different from each other. However, both individually and grouped together the body weights of those classes were significantly smaller ($P < 0.01$) than the mean of the group 4 to 18 years old.

Inspection of the mean body weights and confidence limits shows that for all age classes represented by four or more animals, males were significantly heavier than females. The mean body weight of all

males 5 years old and older was 333 kg as compared to a mean of 259 kg for females 4 years old and older.

The data indicate that in males an increase in hind foot length continued to at least 3 years of age and that an increase in chest girth and body weight continued to 5 years old. The graphs suggest that slight growth might have continued to 6 years in the case of hind foot length, 10 years in the case of chest girth, and 7 years in the case of body weight. If the chest girth really continued to increase beyond 7 years while body weight failed to do so, the explanation is not known.

For females, the data indicate that growth as shown by each measurement continued to at least 4 years of age. However, the graphs suggest that slight growth might have continued to 6 years of age in the case of hind foot length, and 7 years of age in the case of both chest girth and body weight.

The graphs suggest a decline in hind foot length, chest girth, and body weight of males after 7 years of age. Among females the data suggest a decline in chest girth after 10 years of age and perhaps in body weight after 9 years of age. However, the samples of old wapiti are small and variable. Only in the case of chest girth of females was the reduction statistically significant. Huxley (1931) reported that the body weight of red deer stags in an English park reached a maximum at about 10 years of age, after which it declined.

The early attainment of maximum hind foot length is consistent with the findings of Palsson and Verges (1952) with regard to lambs, that skeletal growth tended to occur earlier at the extremities and to progress toward the central region of the body, and that bone had priority in growth over muscle and fat.

The observation that female wapiti attained adult body weight at a younger age than males is similar to the findings of Wood, Cowan, and Nordan (1962) for various races of deer of the species *Odocoileus hemionus*. Similarly, a growth curve for European moose (*Alces alces*) published

by Skuncke (1949) and reproduced by Peterson (1955:77) indicated that on the average the maximum body weight in males was attained at about 12 years of age, whereas that of females with calves was reached at about 9 years. Skuncke's data showed a male superiority in body weight in moose similar to that observed in wapiti in the present study, although his data did not show a difference in the weight of the sexes before 18 months old. Johnson's (1951) data indicated a male superiority in average body weight of wapiti at birth, and the present data show that among wapiti about 6 months old, males were significantly larger than females in both hind foot length and body weight.

Data presented later show that female wapiti taken during the slaughters had fat deposits that were, on the average, at least equal to those of females taken at any other time of year. The fat reserves of males taken during the slaughters were, however, smaller than those of females taken in the same period, and data collected throughout the year suggested that they had declined from a peak in August. We might therefore expect that the difference in body weight between males and females in similar physical condition would be greater than that observed in the sample taken in the slaughters.

Reproductive characteristics of the male

Testicular changes with season and age

Testes were collected from all males slaughtered in 1961–62 in Banff and from those in the research series. The epididymides were removed and the testes weighed to the nearest gram.

The weights of testes of the males taken in the slaughter are summarized in relation to age in Figure 11. The values represent the sum of the weights of the right and left testes. The data indicate an increase in testis size each year from the calf class to at least 6 years of age and probably older. The mean weight of testes of the 5-year-old class was significantly smaller than that of the group 6 to 13 years old. Among specimens older than 5 years, weight of testes did not vary significantly in relation to age. However, data to follow indicate that testis size attains a peak in August and September from which it decreases markedly by November. It is quite possible that among animals older than 5 years, there are differences associated with age in the maximum testis size attained during the peak of the breeding season.

One testis from each male in the research series was sliced transversely through the middle and the exposed surface smeared across a microscope slide. A smear was also prepared from the tail of the epididymis in the same way. The smears were dried in sunlight or near a gasoline lantern and stored. Later, without staining, each smear was scanned under a binocular microscope at 150 \times and assigned to one of the following categories based on the absence or presence and abundance of spermatozoa: (0) no spermatozoa observed, (1) one to ten spermatozoa observed, (2) more than ten spermatozoa observed but not common, (3) spermatozoa abundant but not packed together, (4) field packed with spermatozoa. The testes weights and spermatozoa abundance values are presented by month according to age group in Figures 12 and 13.

A seasonal cycle in testis size is apparent. The peak of testis size was reached in September in both 2-year-olds and animals

Figure 11. Weight of testes of wapiti of each age slaughtered in winter in Banff National Park. Median horizontal lines represent means, vertical bars represent 95 per cent confidence limits, and vertical lines represent ranges.

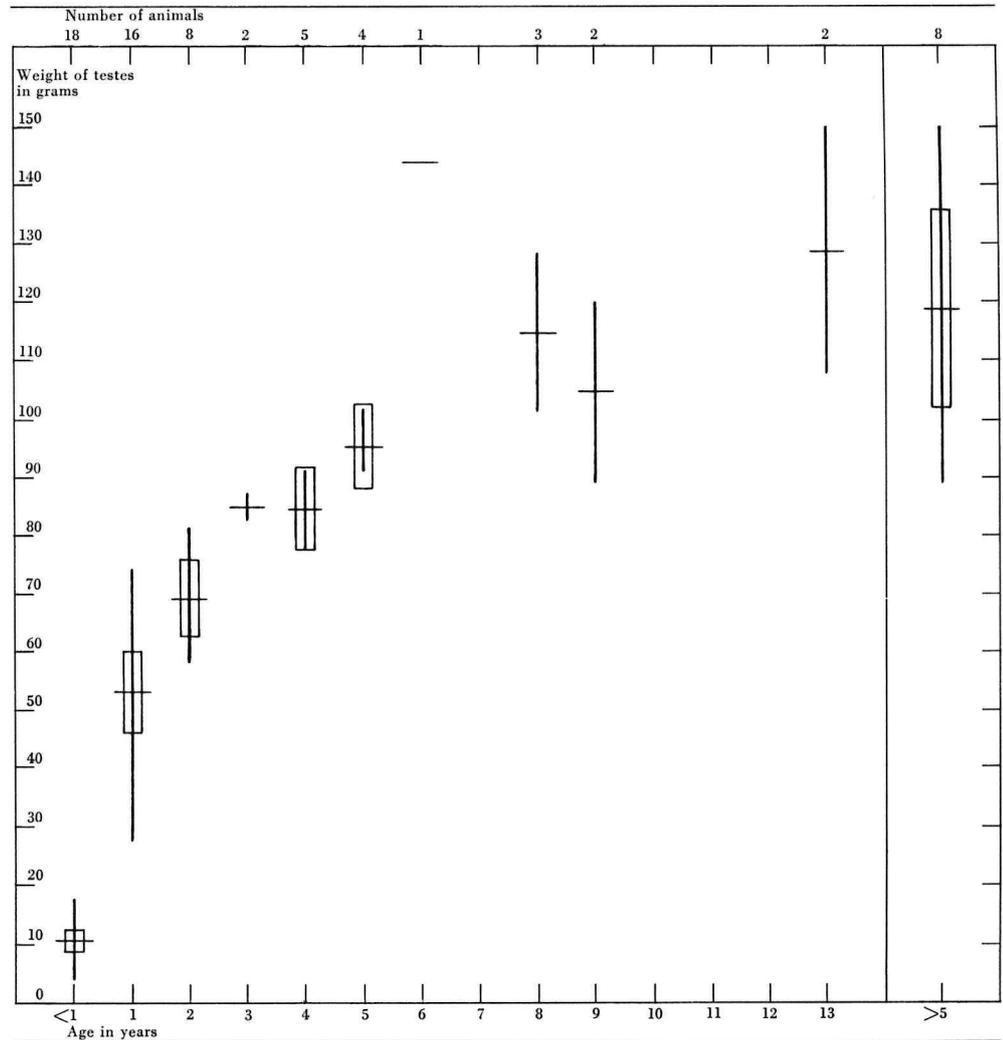


Table 9
Harem associations and weights of testes in relation to age of bulls collected in September, Banff National Park

Date	Age, years	Weight of testes, grams	Association
Sept. 8, 1965	7	455	Harem
Sept. 11, 1961	5	274	Solitary
Sept. 12, 1961	9	143	Solitary
Sept. 15, 1961	8	328	Harem
Sept. 27, 1965	12	357	Harem

Figure 12. Abundance of spermatozoa in smears of testis and epididymus, and weight of testes, of individual yearling and 2-year-old wapiti, according to month of collection, Banff and Kootenay National Parks and the Ya Ha Tinda Ranch. The numbers beside the plotted symbols represent number of specimens if more than one.

3 years old and older. The autumn increase in testis size was much less marked in yearlings, but data on that group also conform to an autumn peak.

The data on the abundance of spermatozoa in the smears of the testes and epididymides also show a seasonal cycle which coincides with the cycle in testis size. Spermatozoa were first found in testis smears of a few animals taken as late as February. However, no spermatozoa were found in testis smears from yearlings taken after October. In all age groups the period during which spermatozoa were abundant in smears was longer for the epididymides than the testes. May and June were the only months in which spermatozoa were not found in any epididymal smears. The above results agree with those of Conaway (1952), who found active spermatogenesis in the testes of several yearling and one adult wapiti shot in September in Montana. He found that although spermatozoa were abundant in the epididymides of most specimens from September through December (the latest month represented in his collection), the regression of the seminiferous tubules began in November. Struhsaker (1967) studied the behaviour of wapiti during the rut, in the Cascade Valley in Banff in 1965. He used the term heterosexual behaviour to include a number of clearly defined behavioural interactions between males and females, and observed that the peak of such behaviour was from September 8 to September 21.

Although Graf (1955) reported having observed a yearling male wapiti mount a cow and copulate, Struhsaker (1967) found that the participation of the young classes of males in rutting activities was slight. The five instances of completed copulatory mounting which Struhsaker observed were all performed by bulls older than 3-year-olds. He observed 348 heterosexual approaches by males older than 3-year-olds, only 6 such approaches by 2-year-olds, and 14 by yearlings.

Only five bulls older than 2 years old were collected in September. Their ages,

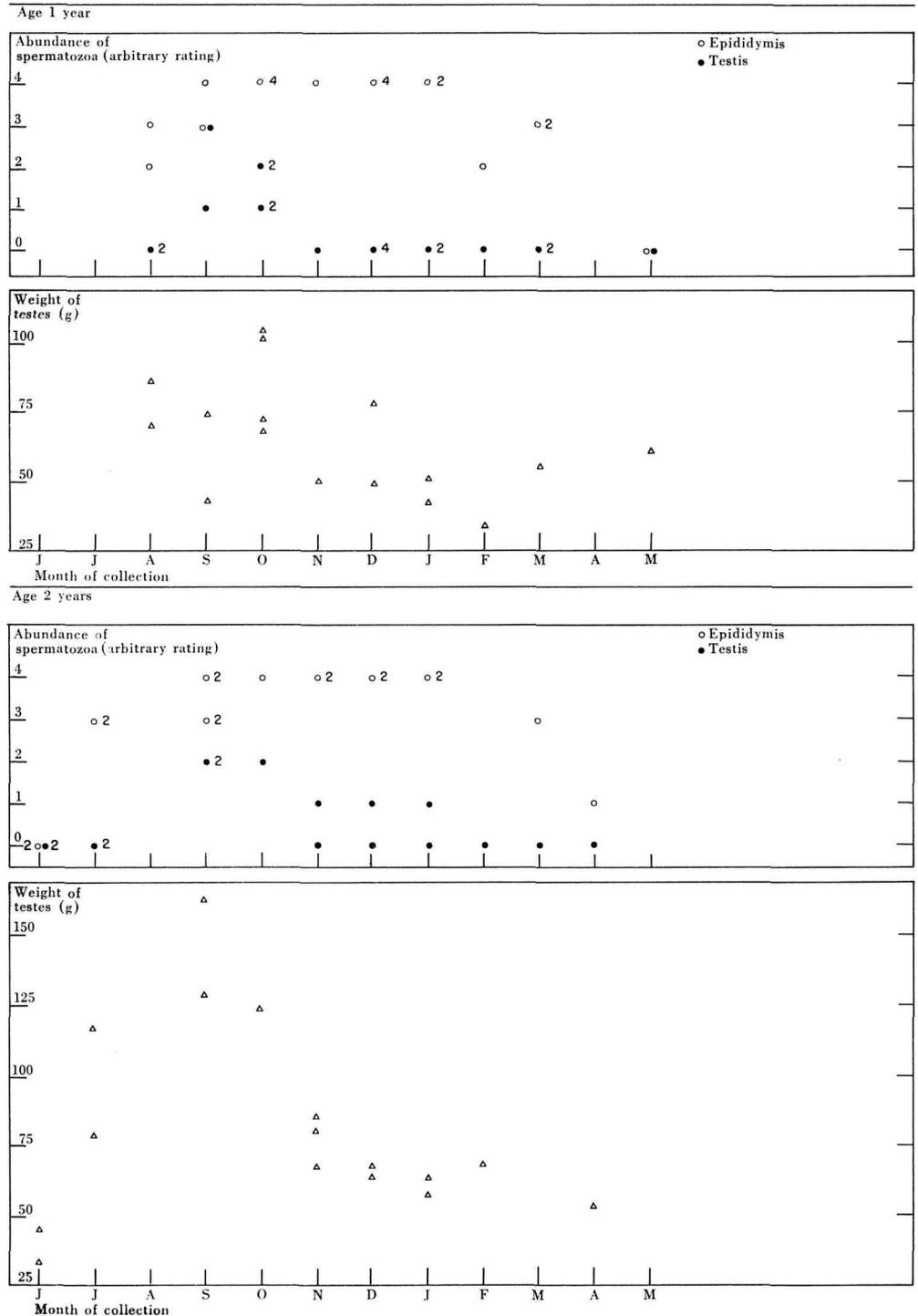
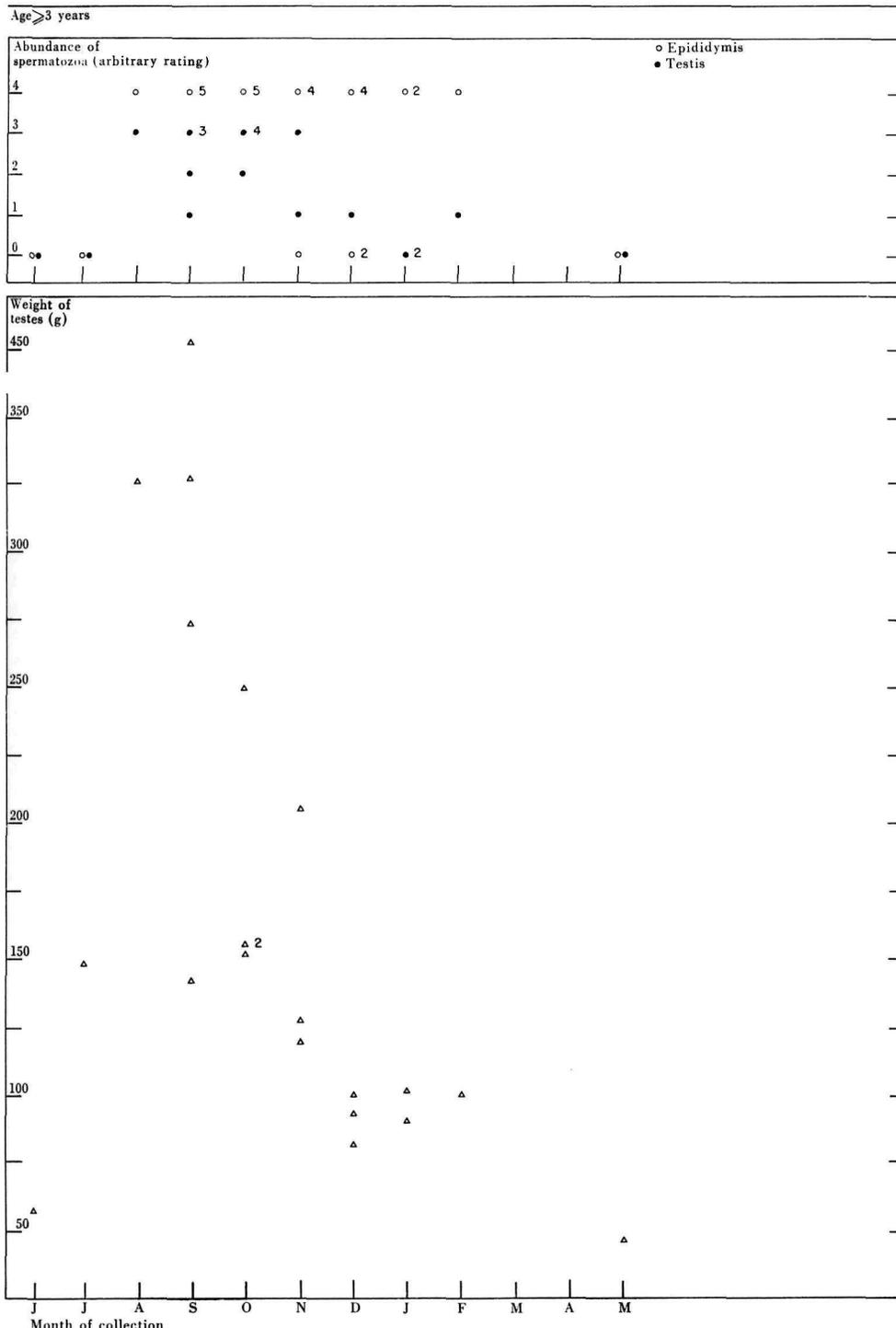


Figure 13. Abundance of spermatozoa in smears of testis and epididymus, and weight of testes of individual wapiti 3 years old and older, according to month of collection, Banff and Kootenay National Parks. The numbers beside the plotted symbols represent number of specimens if more than one.



dates of collection, weights of their testes, and information on whether they were with cows are given in Table 9. The data are meagre but they indicate that bulls between the ages of 7 and 12 years actively participate in the rut.

Replacement and size of antlers

Murie (1951) found that most antler shedding took place in March. In the present study, two males about 22 months old, collected March 28 and 30, still carried their first set of antlers, but another male of the same age collected March 28 and two 2-year-olds collected June 2 had shed their first antlers and produced new vascular knobs. A bull approaching 3 years of age collected April 2 carried its old antlers but an adult taken May 24 had vascular antlers.

In antlers, according to Goss (1963), the hardening of the bone, vascular constriction, and shedding of the velvet are controlled by secretion of testosterone. The close coincidence of those events with the enlargement of the testes was evident in this study.

The period of antler growth and shedding of the velvet was later in yearlings than in older wapiti. A 10-year-old animal collected August 19 was the earliest observed with polished antlers. Two other adults seen on the same day carried antlers still completely covered with velvet. All adult and 2-year-old bulls collected after September 8 had polished antlers. However, two yearlings taken September 14 and one taken October 15 had antlers that were still vascular and in velvet, and the earliest that a yearling with hardened antlers was collected was October 14. Although the antlers of all yearlings collected after October 15 were hardened, some retained all or part of their velvet covering until they were shed in the spring. Murie (1951) reported the same condition in some yearlings in Wyoming and Montana.

Data on the weights of antlers of wapiti taken in the slaughters in Banff in 1960-61, 1961-62, and 1962-63 are presented in

Figure 14. Weight of antlers of wapiti of each age slaughtered in winter in Banff National Park. Median horizontal lines represent means, vertical bars represent 95 per cent confidence limits, and vertical lines represent ranges.

Figure 14. Mean antler weight increased with each successive year of age from the yearling class to 7 years old. Although the mean antler weight of 6-year-olds was significantly smaller than that of 7-year-olds, it was not significantly smaller than that of all specimens 7 years and older. The mean antler weight of 5-year-olds was, however, significantly smaller than that of all older animals. The graph suggested a decline in antler weight following 7 years. However, statistical comparison of the group 8 to 13 years old with the 7-year-old class did not show a significant difference.

Statistical comparisons show that the youngest age class which was not significantly smaller in antler weight than all older animals was the 6-year-old class, while the youngest age class that belonged with the adult group homogeneous in body weight was the 5-year-old class. However, the configurations of the graphs in Figures 9 and 13 suggest that peaks of both body weight and antler weight may not be reached until 7 years of age. Huxley (1931) found that the weights of successive sets of antlers, as well as the body weights, of red deer stags in an English park increased in relation to age until both reached peaks at about 10 years and declined thereafter. The size of antlers produced annually, body weight, and reproductive activity might all be expected to decline in old age as part of the process of senescence.

Mortality from rutting combat

Struhsaker (1967) observed that in sparring during the rut, almost all contact was between the antlers of the combatants. Only once in 49 sparring encounters which he observed in detail during one season was a blow to the body noted, and in that instance the recipient did not appear to be injured. Struhsaker noted that sparring was more intense between bulls that were 3 years old or older than between younger males, and particularly when one of them possessed a harem. Apparently dominance is usually resolved without injury, particularly in the younger classes. However,

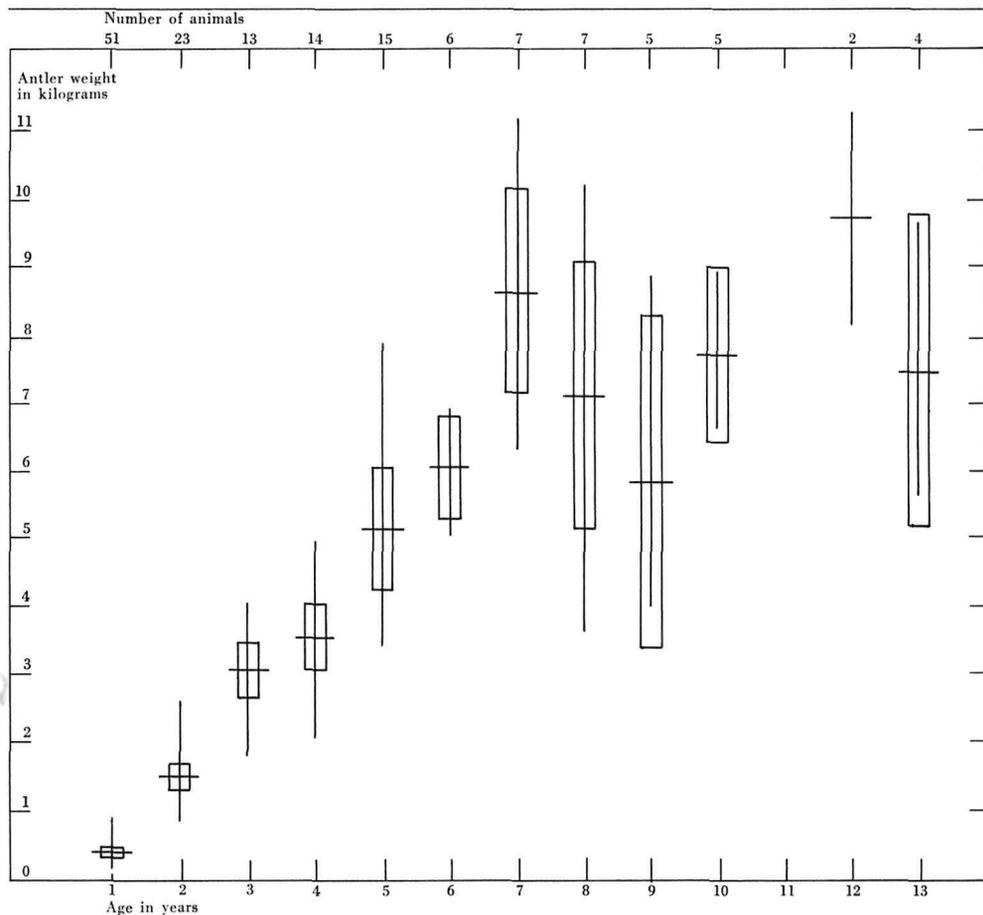


Table 10
Bull wapiti killed in rutting combat

Date	Locality	Remarks	Observer
Sept. 15, 1958	Banff	Adult, neck broken	G. A. Balding*
Sept. 1959	Lac La Biche, Alta.	Adult, abdomen torn	D. Kerik†
Sept. 3, 1960	Jasper	Large adult, lungs punctured	W. Measor*
Autumn 1965	Waterton Lakes	Adult, body punctured	E. B. Cunningham*
Sept. 7, 1966	Jasper	12-year-old, body punctured, testes torn out	F. Burstrom*
Sept. 19, 1966‡	Jasper	7-year-old, left eye knocked out, left side chest punctured	N. Young*

*National Parks Service.

†Alberta Fish and Wildlife Division.

‡Still living when found, shot.

Reproductive characteristics of the female

Harper *et al.* (1967) included rutting battles among causes of mortality in Roosevelt elk (*Cervus canadensis roosevelti*) in California.

During the present study reports of six instances of mortality caused by rutting combat were received (Table 10), one of which was outside the parks. Each wapiti killed was an adult bull. The two from which dentaries were obtained were 7 and 12 years of age. While the number found was small, neither were many found of which death could be attributed to any other specific cause except collisions with vehicles.

Evidence of an increase in mortality of males after about 7 years of age will be given later. Data on the relationship of age to size of testes and antlers and to association with harems suggest that bulls 7 years old and older may be the most reproductively active. It will be shown later that males older than 7 years enter the winter with lower fat reserves than other wapiti and are probably therefore more prone to winter mortality. The relationship of fat depletion to rutting activity will be discussed. Rutting combat, although it almost certainly removes fewer bulls than winter mortality, is evidently selective for the age of greatest sexual activity and should not be discounted as an influence on population structure.

In wapiti taken in slaughters beginning December 1957 in Jasper, December 1958 in Banff, December 1960 in Elk Island, and January 1963 in Waterton Lakes, uteri were inspected and if enlarged were opened to determine the number and sex of foetuses. During some slaughters, the mammae were incised and inspected for the presence of milk.

All foetuses from cows slaughtered in Banff in November and December 1966 and in Jasper in December 1966 and January 1967 were preserved in 10 per cent formalin. Foetal length was measured according to the method of Morrison, Trainer, and Wright (1959). As was suggested by Morrison *et al.*, their graph relating foetal length to age was enlarged. The age of each foetus was estimated from the graph, and the conception date extrapolated by back-dating from the date of collection.

Age-specific pregnancy rate

The percentages of cows pregnant in samples taken from different parks and in different years from December 1957 to January 1967 are shown in Table 11. Females older than yearlings are combined. No calves examined were pregnant. The pregnancy rate among yearlings varied greatly (0–78 per cent) even in samples taken in the same park in different years; it was high and fairly consistent among cows 2 years old and older. Evidently development of breeding condition is more subject to the effects of environmental conditions in yearling than in adult females. The same relationship has been reported among white-tailed deer fawns (Cheatum and Severinghaus, 1950; Ransom, 1967) and yearlings (Ransom, 1967), and mule deer yearlings (Julander, Robinette, and Jones, 1961).

Buechner and Swanson (1955) reported a pregnancy rate of 54 per cent in a sample of 35 yearling wapiti in the Blue Mountains of Oregon. They suggested that the high rate of natality could be attributed to

Table 11
Pregnancy rates according to park and year in cow wapiti slaughtered in Elk Island, Jasper, Banff, and Waterton Lakes National Parks, 1957–67

Park	Year	Age 1 year		Age \geq 2 years	
		Pregnant, %	Number examined	Pregnant, %	Number examined
Elk Island	1960	0	18	97	31
	1963	29	7	93	28
Jasper	1957–58	71	7	100	27
	1963–64	0	17	95	106
	1966–67	78	9	92	107
Banff	1958–59	29	7	94	36
	1959–60	23	13	91	140
	1960–61	16	19	97	101
	1961–62	8	12	92	100
	1962–63	13	15	96	92
	1963–64	50	4	92	41
	1964–65	29	7	82	88
	1965–66	0	1	88	24
	1966–67	50	4	81	32
Waterton Lakes	1963	50	12	100	59
Total		24	152	93	1012

Table 12
Pregnancy rates according to age in cow wapiti slaughtered in Elk Island, Jasper, Banff, and Waterton Lakes National Parks, 1961-67

Age, years	Pregnant, %	Number examined
1	27	88
2	93	115
3	97	98
4	92	76
5	92	64
6	90	71
7	94	49
8	94	36
9	94	50
10	97	29
11	100	17
12	100	12
13	87	15
14	77	13
15	73	11
16	75	8
17	60	5
18	20	5
19	100	2

a reduction in the density of the population by heavy hunting. Hancock (1955) reported that six yearlings of seven examined were pregnant in hunted populations in Utah. Before the above studies, observations of pregnant yearlings had been so uncommon as to be considered noteworthy. Mills (1936) reported one yearling pregnant among five examined in Yellowstone Park. Murie (1951:123) found no pregnancies in "a large number of so-called yearling cows" examined, presumably in Yellowstone Park and Jackson Hole. Kittams (1953) found one yearling cow pregnant among 39 examined in Yellowstone. Coffin and Remington (1953) reported one yearling pregnant among seven examined in Rocky Mountain National Park, Colorado, and Saunders (1955) reported a single observation of a pregnant yearling in Montana. Perhaps the scarcity of such observations before 1955 is not surprising inasmuch as the ranges where extensive data had been collected were

Table 13
Percentages of cows lactating, according to month, among wapiti 3 years old and older, Banff and Jasper National Parks

Park	Year	November		December		January	
		Lactating, % examined	Number	Lactating, % examined	Number	Lactating, % examined	Number
Jasper	1966-67	25	4	65	43	40	35
Banff	1958-59	—	—	69	29	60	5
	1959-60	—	—	60	53	42	60
	1960-61	—	—	57	49	36	39
	1961-62	64	31	67	36	36	14
	1962-63	—	—	67	52	43	23
	1963-64	—	—	71	24	57	7
	1964-65	61	33	62	16	57	28
	1965-66	58	19	17	6	—	—
	1966-67	68	25	75	4	—	—
Banff total		63	108	66	240	43	171

heavily stocked with wapiti and depleted of forage (for example, Jackson Hole, see Anderson, 1958 and Yellowstone, see Kittams, 1953).

Pregnancy rates in samples of cows older than yearlings, reported in the literature, are generally high. Murie (1951) reported that of 334 cows "of breeding age" from Jackson Hole and 156 from Yellowstone, 89.2 and 90.4 per cent, respectively, were pregnant. Kittams (1953) reported that pregnancy rates in samples of cows 2½ years old and older slaughtered in five different years in Yellowstone varied from 74 to 94 per cent with a mean of 85 per cent, in a total of 1,053 specimens.

Green (1950) examined wapiti taken in slaughters in Banff between 1944 and 1948 and reported no pregnancies among 47 yearlings, and 78 per cent pregnant among 632 females 2½ years old and older. However, by Green's method of age determination (Green, 1946; Banfield, 1949), all specimens with more than one pair of permanent incisors would have been included in the older class. Quimby and Gaab (1957) found that the second pair of incisors had been replaced in a substantial proportion of yearlings collected in winter. There may, therefore, have been yearlings among the pregnant animals reported by

Green (1950), and as there were almost certainly some non-pregnant yearlings among the animals which he assigned to the group 2½ years old and older, the pregnancy rate in the group actually 2½ years old and older was probably higher than reported.

When the pregnancy rate among yearling cows is compared with that among older cows in the total sample examined in this study (Table 11), using the χ^2 test (Simpson, Roe, and Lewontin, 1960:187), a significant difference ($P < 0.005$) is indicated.

In Table 12, data collected in slaughters in all parks from November 1961 to January 1967 are consolidated to show the percentages of cows pregnant at different ages. It is evident that from 2 to 13 years old the pregnancy rate was consistently high, followed by a slight decline at about 14 years. Among 632 cows examined in the group 2 to 13 years old, 592, or 94 per cent, were pregnant. In comparison, 30, or 68 per cent, of 44 cows aged 14 to 19 years were pregnant. The latter rate is significantly lower ($P < 0.005$).

Multiple pregnancies

Only two multiple pregnancies were found in 1,186 gravid uteri examined during this study, both from Jasper. Both were sets of female twins, one carried by a 2-year-old shot in December 1963, and the other, by an 8-year-old shot in December 1966. Kittams (1953), after consolidating published and unpublished data, reported, "All available quantitative records of the Rocky Mountain elk total 1,690 pregnancies with 5 twinnings." Reports from Waterton Lakes quoted by Cowan (1950) placed the percentage of twins among wapiti calves in that area at between 20 and 25 per cent. However, the uteri of 199 pregnant cows slaughtered in that park between 1949 and 1962 were opened by park personnel to identify the sexes of fetuses. As no twins were recorded in that sample, it seems likely that the information reported to Cowan was based, as Kittams (1953) suggested, on calf-at-heel observations, which can be misleading. It can be concluded that even under favourable environmental conditions, multiple pregnancies are very rare in wapiti.

Duration of lactation

Data on the condition of the udder were collected from cows slaughtered in Banff, December 1958 to December 1967, and in Jasper, December 1966 to January 1967. The incidence of lactation among cows 3 years old and older shot in each of the 3 months, November through January, was tabulated separately (Table 13). This gives an indication of when lactation was usually terminated. In the total sample from Banff, the proportion of cows shot in December that were lactating was similar to the proportion lactating among those shot in November. However, the proportion of cows lactating among January specimens was significantly lower ($P < 0.005$) than among those taken in November and December. With the exception of the samples taken in November 1966 in Jasper and December 1965 in Banff, both of which were very small, the samples from indi-

vidual slaughters conformed to the pattern shown by the total sample.

Kittams (1953) showed consistent, statistically significant decreases in the percentage of lactating specimens among cow wapiti 3½ years old and older slaughtered in Yellowstone in successive weekly periods in 1949–50, from 46 per cent in the week beginning December 19 to 31 per cent in the week beginning January 11. The decreases indicate that weaning was in progress at that time. In 1951 he noted incidences of lactation of 16, 18, and 14 per cent for the three successive one-week periods beginning January 3. Both higher calf survival and later weaning could have contributed to making the incidence of lactating cows higher at Banff and Jasper than at Yellowstone. As Kittams described widespread deterioration of the Yellowstone winter range, the differences may have been related to nutritional levels. The data from Banff and Jasper demonstrate that few cows terminated lactation in November or December but that a substantial proportion did so in January.

Age-specific incidence of lactation

Milk in the udder is evidence that a cow was suckling a calf at least until shortly before the time of examination. As few if any cows terminated lactation during November and December, the data on incidence of lactation in those months provide a measure of the proportion of cows that had calves living at that time of year.

As was anticipated in view of the absence of pregnant calves, none of the yearlings examined was lactating. Percentages of cows lactating at different ages older than yearlings are given in Table 14. The data used are from slaughters in Banff from November 1961 to December 1966, and in Jasper in November and December 1966. Samples from other slaughters were not used because the animals were shot after January 1, or because the data were incomplete. Among the 2-year-olds, 11 per cent were lactating. Percentages of cows

Table 14

Percentages of cows lactating according to age, in samples* slaughtered before weaning, Banff and Jasper National Parks

Age, years	Lactating, %	Number examined
2	11	53
3	64	36
4	55	31
5	72	36
6	65	34
7	67	33
8	70	20
9	75	24
10	71	17
11	50	10
12	64	11
13	43	7
14	67	9
15	0	4
16	67	6
17	60	5
18	25	4
19	0	1

*Banff, November, 1961, 1964, 1965, and 1966, December, 1961 to 1966, and Jasper, November and December, 1966.

lactating in individual age-classes from 3 to 14 years old do not indicate any change within that age range. Among the 268 cows 3 to 14 years old, 65 per cent were lactating. As was anticipated in view of the decline in pregnancy rate noted at 14 years of age, the data indicate a decline in the frequency of lactating cows at 15 years. Of the 20 cows 15 to 19 years old, only 8, or 40 per cent, were lactating, which is significantly lower than among younger cows.

By dividing the percentage of cows lactating by the pregnancy rate, the rate of survival of calves from about 3 months post-conception to about 6 months post-parturition can be estimated. Survival was estimated thus for calves in Banff, using data from the slaughters from November 1961 to December 1966, with January data on lactation excluded (Table 15). That determination does not take into account any losses of fetuses or calves that are associated with mortality of the dams. The

computed rate of survival of calves carried by cows of all ages was 69 per cent. In neither the 2-year-old group (yearlings at conception) nor the group 15 years old and older (≥ 14 years at conception) was the number of cows lactating significantly lower than the number expected on the basis of the observed pregnancy rate and a calf survival rate equal to that of dams 3 to 14 years old (2 to 13 years at conception).

It was shown previously that yearling cows and those 14 years old and older exhibited lower pregnancy rates than cows 2 to 13 years old. However, the above analysis suggests that both yearlings and cows 14 years old and older, which became pregnant and survived the following year, were as successful mothers as were cows in the intermediate age group.

Distribution of dates of breeding and calving

Morrison (1960) reported an average oestrous interval of 21 days for a group of captive wapiti. Two periods of oestrus in one season were the most specifically mentioned. However, the cows used in that study were enclosed with a fertile bull after their first oestrus, and most conceived in their second.

The distribution of conception dates of wapiti in Banff and Jasper in 1966 estimated from foetal lengths is presented in Figure 15. The conception dates of all specimens from Banff except one were within the period September 6–25, which coincides closely with Struhsaker's (1967) findings in that area in 1965. He showed a peak of heterosexual activity between September 8 and September 21. The mean estimated conception dates in 1966 were September 11 for the Banff sample and September 19 for the Jasper sample. Those are significantly different. The mean conception date for six yearlings from Jasper Park was September 28 as compared to September 18 for older cows, but the difference is not significant. The one November conception occurred in a 5-year-old cow.

Morrison *et al.* (1959) reported a gestation period of 247 days for one cow of

Table 15
Calf survival from approximately 3 months post-conception to 6 months post-parturition, estimated from pregnancy rate and frequency of lactation among cow wapiti* slaughtered, Banff National Park, November 1961 to December 1966

Age of dam at conception, years	Pregnancy rate, %	Frequency of lactation, %	Calf survival, %
1	21 (43)	13 (46)	62
2–13	92 (340)	67 (225)	73
≥ 14	71 (38)	40 (20)	56
≥ 1	83 (421)	57 (291)	69

*January data on lactation excluded.

Note: Values in parentheses are numbers of specimens examined.

which the breeding date of the dam and the birth date were known. Harper *et al.* (1967) reported gestation periods of 258 and 265 days for two Roosevelt elk. Lantz (1910, quoted by Murie, 1951) reported a gestation period in wapiti of from 249 to 262 days. Using the midpoint, 256 days, and the mean estimated conception dates of September 11 in Banff and September 19 in Jasper, the mean birth dates in 1967 would have been May 24 and June 1 respectively. Johnson (1951) reported that for 158 calves examined soon after birth in the West Gallatin River drainage of Montana, the peak period of birth was June 1, and the extremes were May 21 and June 12.

Foetal sex ratio

Usable data on the number of foetuses of each sex carried by wapiti slaughtered in all parks during the present study are given in Table 16. Data on sex of foetuses from Elk Island in December 1958 and in 1959 up to December 3 and from Waterton Lakes before 1963 are excluded because in those slaughters a substantial number of foetuses were not identified as to sex, and among small foetuses, males may be more readily identified than females. Similarly, data on foetuses from cows shot before December 3 in the Elk Island slaughter of November 1959 to January 1960 are excluded because

a large number of them were not identified.

In the total of 1,159 foetuses included in the sample (Table 16), the sex ratio was 113 : 100 (males : females), which differs significantly from an even ratio. The sex ratio of 462 foetuses from wapiti slaughtered in Banff in November, December, and January 1944–48 was 111 : 100 (Green, 1950). Bourlière (1964:296) pointed out that an early preponderance of males is common among species of ungulates and pinnipeds which are polygynous and which have a preponderance of females in the adult populations. Robinette *et al.* (1957) consolidated published and unpublished data on the sexes of 2,299 mule deer foetuses, and obtained a sex ratio of 111 : 100.

Chapman, Casida, and Cote (1938) showed that in a sample of 2,044 foetuses of domestic cattle, the proportion of males decreased in relation to advancing gestation. Robinette *et al.* (1957) presented data on mule deer which suggested that when adverse circumstances affect the dams, male foetuses may be more prone to mortality than females. In view of those findings, it seems likely that in wapiti the ratio of males to females would be equal to, or slightly higher than, 113 : 100 at conception and perhaps lower than that at birth. The following data on the sexes of wapiti captured within a few days after birth

conform to the latter expectation. Johnson (1951) reported a sex ratio of 96 : 100 among 155 calves captured in the Gallatin River drainage in Montana and Yellowstone. Picton (1961) reported that a sample of 472 calves captured in the Sun River drainage of Montana contained 50.4 per cent males, which is equivalent to a sex ratio of 102 : 100.

Kittams (1953) presented data on the numbers of males and females among 1,167 foetuses from wapiti shot in winter in Yellowstone and Jackson Hole. The sex ratio was 101 : 100 as compared to 113 : 100 in the present study. The pregnancy rate of cows 2 years of age and older in Kittams' sample was 86 per cent as compared to 93 per cent in the present study. That difference in pregnancy rate may have resulted largely from higher intra-uterine losses in the sample from Yellowstone and Jackson Hole, and male embryos may have predominated among those lost.

Miller (1932) mentioned the view of a number of Scottish deer stalkers that female red deer which had not given birth the year previous, and those which lost their young and therefore ceased lactating, being in better physical condition, usually gave birth to male calves in the subsequent season. Of 405 red deer foetuses collected from Scottish estates, Miller was able to identify the sex of 271. Males were in the majority among foetuses from both lactating and non-lactating hinds, 51 of 79 in the former and 111 of 192 in the latter. Because the sex of so many foetuses could not be identified, Miller considered his data inconclusive.

The present data provide an opportunity to examine the possibility that lactation by the dam during pregnancy reduces the survival of male foetuses relative to female foetuses. Data presented previously indicate that many cows ceased lactating in January due to weaning. Therefore only data on foetuses from wapiti shot before January 1 in slaughters held in Banff and Jasper were used in the comparison. The numbers of foetuses of each sex are presented in Table

Table 16
Numbers of foetuses of each sex from wapiti slaughtered in Jasper, Banff, Waterton Lakes, and Elk Island National Parks

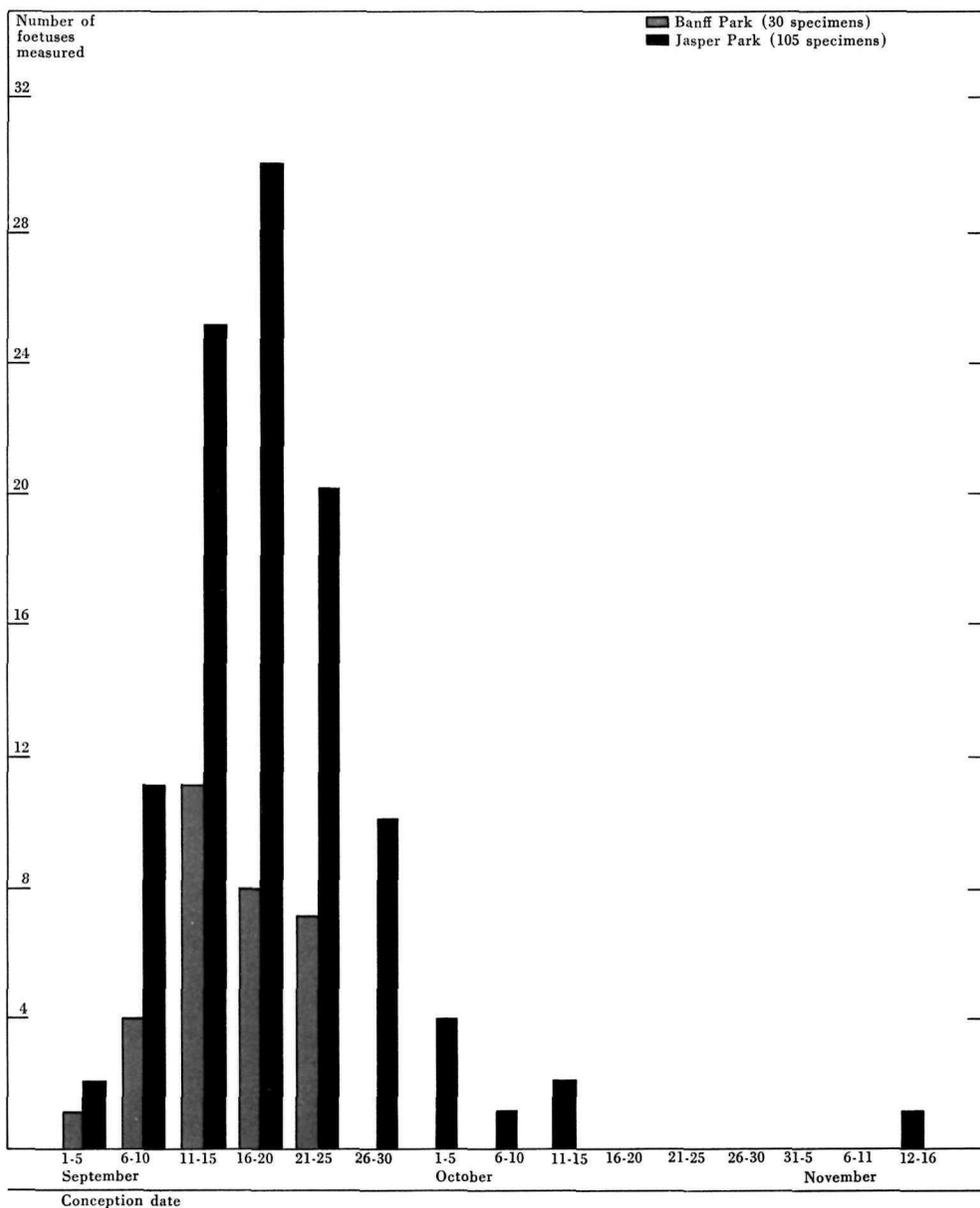
Park	Period of slaughter	Foetuses			Ratio ♂ : ♀
		No. of males	No. of females	No. too small to identify	
Jasper	Dec. '57	22	14	0	
	Dec. '63–Jan. '64	54	50	2	
	Nov. '66–Jan. '67	61	46	1	
	Total	137	110	3	124:100
Banff	Nov.–Dec. '57	11	12	0	
	Dec. '58–Jan. '59	24	15	1	
	Dec. '59–Jan. '60	67	70	0	
	Dec. '60–Jan. '61	54	49	0	
	Nov. '61–Jan. '62	58	39	0	
	Dec. '62	38	52	1	
	Dec. '63–Jan. '64	20	20	0	
	Nov. '64–Jan. '65	44	32	5	
	Nov. '65–Dec. '65	16	12	3	
	Nov. '66–Dec. '66	21	11	1	
	Total	353	312	11	113:100
Waterton Lakes	Jan.–Feb. '63	33	35	1	94:100
Elk Island	Dec. '59–Jan. '60	59	52	1	
	Dec. '60	16	14	4	
	Dec. '63	18	20	1	
Total	93	86	6	108:100	
All parks	Total	616	543	21	113:100

Table 17
Sex of foetuses according to age and udder condition of dam from wapiti shot in Banff and Jasper National Parks before January 1 in each slaughter November 1957 to December 1965

Age of dam, years	Presence (+) or absence (–) of milk	Foetuses		Ratio ♂ : ♀
		No. of males	No. of females	
1	—	8	7	114:100
2	+	9	6	150:100
2	—	29	26	112:100
≥3	+	117	106	110:100
≥3	—	74	70	106:100
≥2	+	126	112	112:100
≥2	—	103	96	107:100

Figure 15. Distribution of conception dates of wapiti, Banff and Jasper National Parks, 1966, estimated from lengths of fetuses and dates of slaughter of dams.

17 according to the age of the dam and whether it was lactating. In each group the number of males exceeded that of females. There were no significant differences between the sex ratios of fetuses of cows of different ages, or between those of lactating and non-lactating cows. Thus, no influence of lactation on losses of male fetuses relative to female fetuses was indicated. However, cows slaughtered in Banff and Jasper were generally in good physical condition regardless of age and whether or not they were lactating, and the high pregnancy rates showed that if any intra-uterine losses occurred before the time of slaughter, the numbers of embryos lost were very small.



Fat reserves

Figure 16. Kidney fat indices of individual wapiti older than calves, according to sex, age, and month of collection, Banff and Kootenay National Parks and the Ya Ha Tinda Ranch.

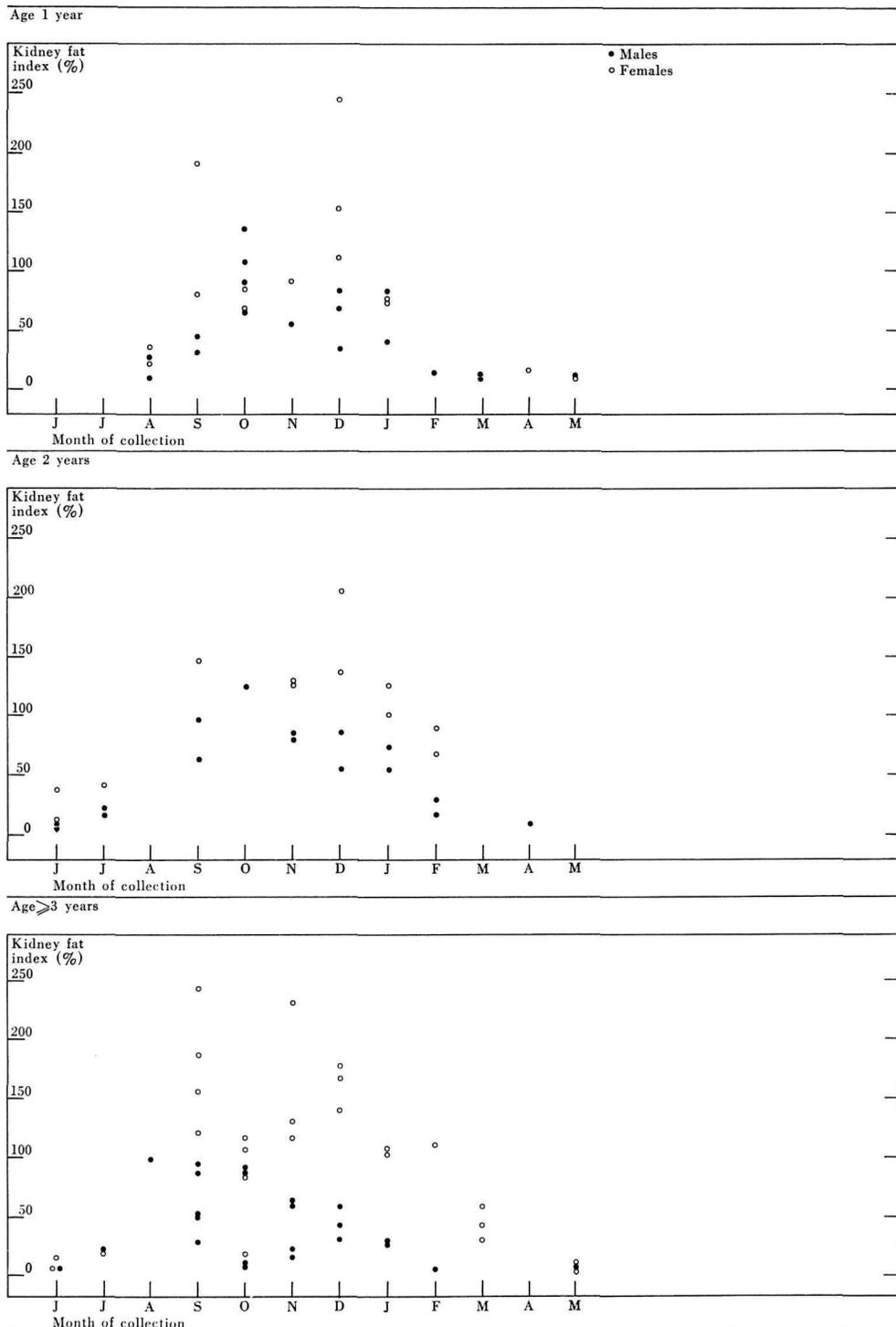
On the basis of studies of large samples of red deer in New Zealand, Riney (1955) reported, "Examination of all the red deer used in this investigation showed that the first fat depot to respond to a favourable metabolic change was bone marrow, followed by the fat around the kidney, intestines, and stomach in that order, and finally, by the subcutaneous fat on the back. Mobilization of the fat depots observed was in reverse order to that of deposition."

Riney (1955) evaluated various techniques of determining the physical condition of red deer and concluded, "The kidney index (weight of kidney fat/weight of kidney) was the most satisfactory. This index showed how the fat-depot reserves in deer of both sexes and various ages changed during the seasons. It also showed that deer living in different environments had different quantities of fat reserves."

Seasonal changes in fat reserves

For each animal in the research series, a kidney fat index was determined in a manner similar to that described by Riney (1955). Each kidney with its surrounding fat was removed from the carcass, and the fat was trimmed by two cuts passing against the anterior and posterior ends of the kidney at right angles to its longitudinal axis. The weight of the two kidneys and surrounding fat was measured to the nearest gram. The perinephric fat (*capsula adiposa*) along with the capsule of connective tissue (*tunica fibrosa*) beneath it were then peeled off the kidneys and the latter were weighed alone. The weight of the fat plus connective tissue was calculated by difference and expressed as a percentage of the weight of the stripped kidneys. The percentage was referred to as the kidney fat index.

By including the weight of the capsule of connective tissue with the weight of perinephric fat, the indices were elevated slightly over what they would have been otherwise. An index of 5 or slightly higher indicated an absence of perinephric fat. The kidney fat indices are presented in Figure 16.



Because the number of animals studied was small, data from those of various ages older than 2 years and from those collected in different years were combined. That contributed to individual variation in kidney fat indices. In spite of that high variation, the data demonstrate a seasonal cycle in fat reserves.

In all groups, the index dropped to a low in the spring from which it first showed substantial recovery in August and September. The indices in females were generally high from September through December. The one exception was specimen 103, a cow collected October 14, 1962, with a kidney fat index of 21. That specimen was 18 years old and had a large abdominal abscess.

In adult males, high indices were observed in August, September, and October, but minimum values also occurred in the latter two months. A series of five bulls 7 to 12 years old, collected between August 19 and November 19, 1965, showed a consistent decline in kidney fat indices from the one collected August 19, to one collected October 19, with a partial recovery in the specimen taken November 19. In view of that pattern, it is suspected that in Figure 16 variation associated with different ages and years obscured a decline in the fat reserves of adult males during the rut in September and early October.

Indices in yearling and 2-year-old males were highest in October and declined in November. Perhaps there is a delay in the decline in fat reserves in those two classes, as compared with adult males, that is related to a delay in their rutting activity. The data on testis size and spermatozoa abundance (Figs. 12 and 13) do not provide clear evidence of such a delay. However, Struhsaker's (1967) data indicate a tendency for yearling and 2-year-old males to join groups of cows in October, apparently concurrent with a decrease in the sexual arousal and aggressiveness of older bulls.

A general decline in kidney fat indices from early or mid-winter until spring is evident in all groups. In November, males

had consistently lower indices than females. Similarly, the perinephric fat was exhausted in some males examined in February, whereas the females examined in March still had substantial deposits.

Kidney fat indices of adult bulls tended to be lower than those of yearlings and 2-year-olds in each month from October to February. That probably results from the more intensive rutting activity of the adults (Struhsaker, 1967).

The seasonal fluctuation in fat reserves in wapiti shown by the above data are similar to those reported by Riney (1955) for red deer in New Zealand. He showed that fat deposits of adult males increased rapidly through the summer to reach a peak in late summer. They declined from autumn until early spring. In female red deer the summer deposition of fat was slower than in males, but it continued until mid-winter. The fat reserves of females declined from mid-winter until late spring, but the spring low occurred later and was less acute than that of males.

Magruder *et al.* (1957) found that captive male white-tailed deer fed *ad libitum* on a high-level ration underwent a decrease in body weight during the middle and late rut in November and December. From December to January there was little change, but a second decline occurred during February and March. The animals also showed a pronounced voluntary reduction in food consumption in autumn and winter. The data of Magruder *et al.* suggest a lag of about one month in the response of body weight to either an increase or a decrease in food consumption.

Wood *et al.* (1962) reported that captive male deer of various races of *Odocoileus hemionus* raised to 4 years of age on *ad libitum* feeding exhibited a seasonal cycle in growth as measured by body weight. Body weight increased during late spring and summer, then declined from an early autumn peak to a spring low. The seasonal pattern of growth of female deer was similar to that of males. However, the magnitude of the fluctuations was less marked,

and in the first 2 years of life the does did not lose weight in winter, but rather gained at a slower rate than in summer. Wood *et al.* found by dissection that an "appreciable part" of the spring and summer weight gain, and most of the winter weight loss, consisted of adipose tissue. They reported individual differences in the exact date at which seasonal changes in the growth curve began. Differences similar to the above may have contributed to the variation in kidney fat indices observed among wapiti of the same sex and age group collected in the same month in the present study.

The observation here that kidney fat indices of adult male wapiti tended to decline to lower levels during the rut than those of other sex-age classes, is entirely consistent with Struhsaker's (1967) behavioural observations. He showed that during the rut, bulls older than 3½ years spent much less time feeding than any other sex-age class. In comparison to other sex-age classes, adult bulls with harems spent less than one-half as much time feeding, less time lying down, and more time standing, walking, herding cows, thrashing woody vegetation with their antlers, digging with their antlers, and whistling. All these activities, with the possible exception of whistling, require considerable energy output.

Fat metabolism of bulls during the rut

It was noted that the livers of adult bulls collected during September and October, 1961 and 1962, were distinctly light in colour and granular in appearance. Livers of males collected at other times of the year, and those of females collected at all times of the year, were consistently dark red. Livers of yearling males collected in September and October were only slightly lighter in colour than normal.

The possible physiological significance of changes in the liver during the rut was recognized later. Fresh liver samples were taken from five male and three female wapiti collected in Banff between August and November 1965. Large bulls with large

antlers were selected, to reduce variation associated with age. In addition, samples were taken from one adult male and one adult female collected in Riding Mountain National Park, Manitoba, in February 1966.

The fresh samples were sealed in polyethylene bags and frozen on dry ice. They were analysed for moisture, ether-extractable lipids, crude protein, and iron. Also, cubes of liver, 5 mm on a side, were preserved in 10 per cent formalin. Frozen sections 30 microns thick were stained with Sudan IV, mounted, and examined microscopically for fat droplets at 40 \times and 100 \times . Sections which showed more than traces of fat droplets were sampled by a line intercept method at 40 \times using 20 randomly located transects, each 3.3 mm long and divided by means of an ocular disc micrometer into 100 lineal sampling units.

In addition, among the eight wapiti collected in Banff, the thickness of the subcutaneous fat was measured at a point approximately 20 cm anterior to the base of

the tail and 5 cm to the right of the mid-dorsal line.

The results of the studies of the liver samples are presented with corresponding data on kidney fat indices and rump fat thicknesses in Table 18. The rump fat measurements and kidney fat indices of the four bulls taken from August 19 to October 19 showed a marked decline in both fat depots with each successive specimen. The kidney fat index of the specimen taken November 19 showed considerable recovery of depot fat, whereas in the specimen taken February 10 it was lower, following the winter trend shown in Figure 16. The relationship of the rump fat measurements to the kidney fat indices conformed to Riney's (1955) conclusion that the subcutaneous fat depots on the back followed the visceral depots in receiving fat under conditions of favourable metabolic change, and preceded them in being depleted under conditions of fat mobilization.

The fresh livers of the males collected September 8, September 27, and October 19, 1965, were distinctly light in colour

and granular in appearance, similar to those from males taken during the rut in 1961 and 1962. On close inspection of the surface of the liver or dissected interfaces, the granular effect was seen to be caused by dark areas on a light background. When slices of frozen liver from each of those three specimens were examined under a dissecting microscope after thawing, it was seen that the dark-coloured areas were the central areas of the hepatic lobules. The lobules refer here to the polygonal prisms in the centre of each of which is an originating tributary of the hepatic vein referred to as a central vein (Bloom and Fawcett, 1962). The light-coloured areas were distributed around the outside of the lobules. When the tissue was covered with a film of water and the surface probed with a dissecting needle, droplets of clear fluid immiscible with water were released to the surface from the light-coloured areas.

The fat content of the liver of males, as shown by ether extraction, increased markedly with each successive specimen from August 19 to reach a peak in the specimen

Table 18
Carcass fatness indices, and results of chemical analyses and histological examinations of livers, of individual wapiti taken autumn and winter, 1965-66

Date	Spec. no.	Age, years	Rump fat thickness, mm	Kidney fat index, %	Liver			Fat droplet abundance, %*	
					Moisture, %	Percentage of dry matter Protein	Iron		Fat
Males									
Aug. 19	106	10	70	100	69.5	70.7	0.08	8.2	Tr
Sept. 8	107	7	25	94	69.0	57.9	.13	24.8	18
Sept. 27	108	12	0	30	62.0	38.6	.05	49.8	38
Oct. 19	110	12	0	7	63.3	56.0	.24	31.5	26
Nov. 19	113	7	3	64	68.8	71.6	.16	14.3	4
Feb. 10	RM1	4	—	37	66.5	71.2	.10	11.6	Tr
Females									
Sept. 29	109	4	38	244	69.7	71.6	.16	7.8	Tr
Oct. 21	111	<1	10	146	66.7	65.6	.21	20.6	0
Nov. 18	112	8	13	232	67.5	71.0	.11	13.2	0
Feb. 9	RM2	4	—	131	75.5	71.5	.12	13.2	0

*Percentage of area of histological section showing stained fat.

Figure 17. Photomicrographs of sections of liver of wapiti from Banff National Park, 1965, stained with Sudan IV, showing sequence of physiological fatty infiltration in bulls during the rut. All photomicrographs have same scale as F.
 A, specimen 106, male, 10 years old, August 19;

B, specimen 107, male, 7 years old, September 8;
 C, specimen 108, male, 12 years old, September 27;
 D, specimen 110, male, 12 years old, October 19;
 E, specimen 113, male, 7 years old, November 19;
 F, specimen 109, female, 4 years old, September 29.

taken September 27, which is late in the rut. Following that, the fat content decreased with each successive specimen to reach a level in the November 19 specimen that approximated that of the females. The liver samples from females did not exhibit a pronounced build-up in fat content during the rut. Specimen 111, a calf, had a liver fat content higher than that of other females. That may be a juvenile characteristic.

The percentage of protein in the liver tended to follow an inverse relationship to that of fat, but variations in the iron content did not appear to follow a consistent pattern.

Differences in the fat content of the liver as demonstrated by ether extractions were accompanied at high fat levels by corresponding trends in the abundance of stained fat droplets visible in histological sections (Table 18, and Fig. 17). In all cases the fat was distributed around the portal canals. In most samples of liver which had only a relatively low fat content, the histological preparations either failed to show stained lipid droplets or else showed only traces of them. In this regard Maximow and Bloom (1957:411) noted that there is a masking of much of the fat in liver cells which is an obstacle to using staining methods for estimating the amount of fat present. Similarly Wachstein (1963) stated, "histochemical methods reveal only a small fraction of the total lipids in liver cells".

Thornton (1949:126) used the term "physiological fatty infiltration" to apply to the condition of accumulation of fat in the liver within limits in which the process is reversible. He reserved the term "pathological fatty infiltration" for the condition reached when fat accumulation is accompanied by damage to the hepatic cells. The condition observed in specimens 107, 108, and 110, which were bulls collected during the rut, can clearly be termed physiological fatty infiltration.

Barrett, Best, and Ridout (1938) showed by deuterium marking that fat depots are the major if not the only source of excess fat which accumulates in the liver during

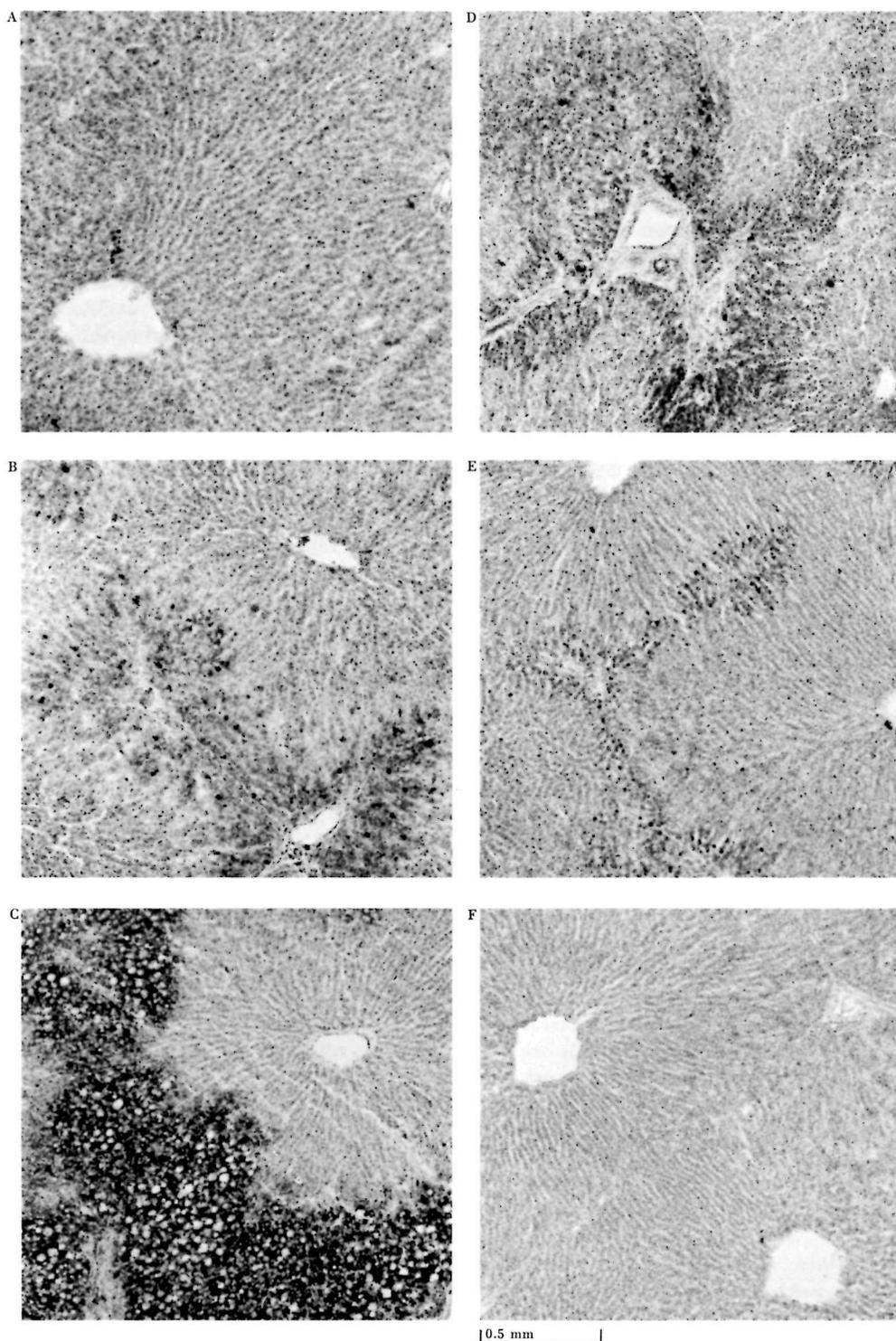


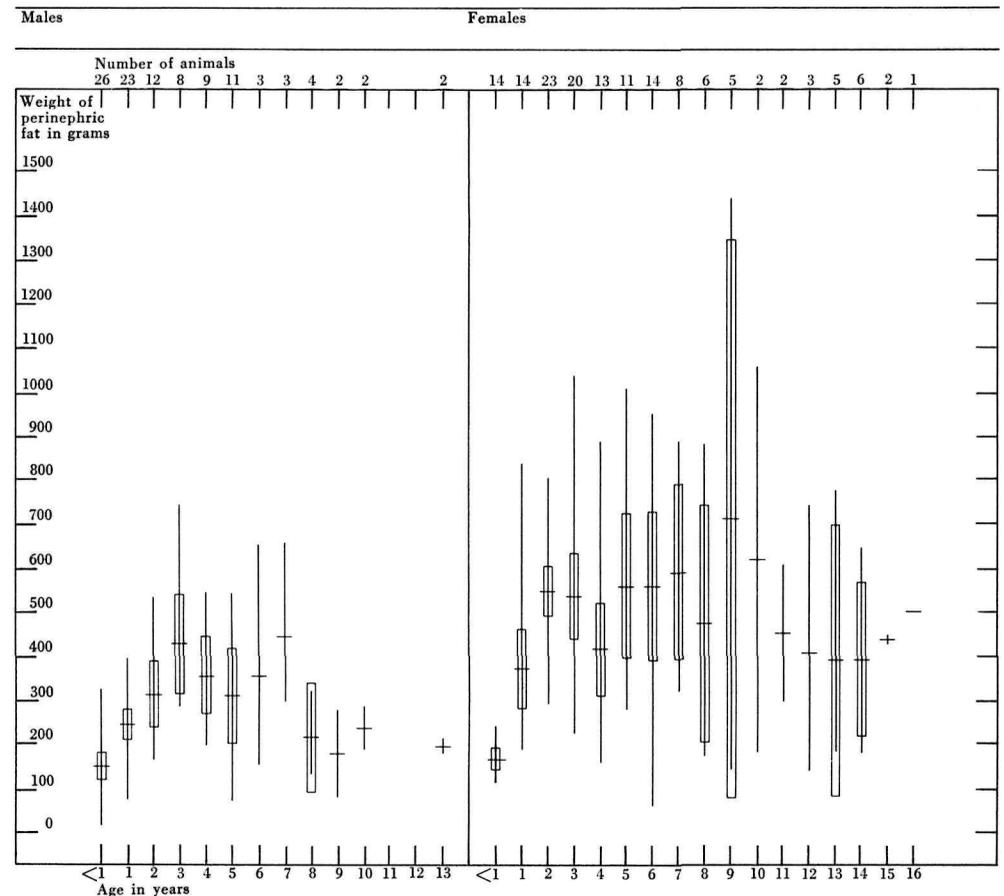
Figure 18. Weight of perinephric fat of wapiti of each sex and age slaughtered in winter in Banff National Park. Median horizontal lines represent means, vertical bars represent 95 per cent confidence limits, and vertical lines represent ranges.

fasting. Dible and Popjak (1941) found that in the absence of depot fat, no fat will accumulate in the liver of a fasting animal. Steinberg (1963) reviewed the subject of regulation of fatty acid mobilization. The information contained in the following two paragraphs, which was extracted from his discussion, is basic to interpreting the fluctuations in liver fat observed in wapiti in this study.

Depot fat consists of triglycerides which are in a dynamic state constantly being converted to free fatty acids that are released into the blood stream and, at the same time, being replaced by the conversion of free fatty acids to triglycerides. A decline in the concentration of glucose in the blood below a certain threshold, such as can occur in fasting, retards the conversion of free fatty acids to triglycerides, thus causing an increase in the concentration of free fatty acids in the blood, and therefore an increase in the rate of delivery of free fatty acids to the liver. Stimulation of the nerves supplying the fat depots has also been shown to increase the rate of mobilization of depot fat. In addition, a number of hormones, including those secreted by both the medulla and cortex of the adrenal, are known to stimulate the release of fatty acids.

In the liver, free fatty acids are converted to triglycerides that are either secreted into the plasma as lipoproteins or oxidized. An increase in the rate of delivery of free fatty acids to the liver results in an increase in the rate of secretion of lipoproteins. However, even though the liver is functioning normally, the delivery of excessive amounts of free fatty acids to it can exceed its capacity to dispose of them by oxidation or resecretion as lipoproteins, in which case an accumulation of triglycerides in the hepatic tissue results. The liver, when it accumulates a large amount of fat, such as occurs in starvation or diabetes, may secrete ketone bodies into the blood.

As an explanation for the mechanism of ketosis, Krebs (1965) suggested that under certain conditions that demand a high rate of gluconeogenesis, much of the oxalo-



acetate made available in the liver is used in that process. The resulting fall in the level of oxaloacetate reduces the rate of completion of the carboxylic acid cycle for which it is also required. That leads to the production of ketone bodies, a process regarded by Krebs as an alternative type of respiration that in mild form is a normal physiological adaptation to a fall in blood sugar. Whether or not ketone bodies were being produced in any of the wapiti studied is not known.

It was evident that the high level of fat in the liver in adult bulls disappeared shortly after the rut without leaving any apparent liver damage. In view of Steinberg's (1963) discussion, it seems fairly certain that the factors leading to the development of fatty

liver among the adult males are the fat condition attained by them before the rut and their partial fast and high level of activity during the rut, as documented by Struhsaker (1967). Also, it might be expected that the high frequency and intensity of agonistic and heterosexual interactions in which the bulls participate during the rut would be associated with increased nervous and hormonal activity that would tend to stimulate mobilization of depot fat.

In the context of the welfare of the wapiti population, physiological fatty infiltration of the liver can be regarded as an annual event in the lives of the adult males, and a manifestation of the marked and rapid depletion of energy reserves which they undergo during the rut.

Differences in fat reserves associated with sex and age

The kidneys and fat surrounding them were removed from the wapiti taken in slaughters in Banff in 1961–62 and 1962–63. The fat was trimmed in the same manner as described previously, and the kidneys and fat were sealed in polyethylene bags and frozen. Later they were thawed and the perinephric fat with the capsule of connective tissue beneath it was removed and weighed. By weighing a few specimens before freezing and after thawing it was found that weight loss was negligible.

The data on weight of perinephric fat of slaughtered animals are summarized in Figure 18. These data represent the weights of the fat from the left and right kidneys together. To provide substantial samples of each specific age, data from November 1961 through January 1962, and December 1962 through January 1963, were consolidated. Inspection of the graph for males showed smaller mean values among animals 8 to 13 years old than in each age class from 1 to 7 years old. The mean perinephric fat weight of animals 8 to 13 years old was significantly smaller than the means of the groups 4 to 7, 3 to 7, or 2 to 7 years old. Within the group younger than 8 years old, the 2-year-olds were the youngest class in which the mean perinephric fat weight was not significantly smaller than that of older classes consolidated.

Among females the mean kidney fat weight of yearlings was significantly smaller than the mean of all older specimens. Adult kidney fat weight was first attained by the 2-year-old class. The graph of perinephric fat weights of females suggested a decline after 10 years of age. The mean kidney fat weight of the group 11 to 16 years old was significantly smaller than that of the group 2 to 10 years old. The mean kidney fat weight of the 4-year-old class was significantly smaller than that of the group 2 and 3 years old and of the groups 2 and 3, and 5 to 10 years old combined. No explanation of the apparent depressed condition of the 4-year-old females is known.

A comparison of the mean kidney fat weight and confidence limits of male calves with those of female calves did not show any significant difference. However, the mean value of males was significantly smaller than that of females in the yearling class, in the group 2 to 7 years old ($P < 0.01$), and in the group 8 to 13 years old ($P < 0.01$).

The foregoing data indicate that, on the average, animals of both sexes attained their adult early-winter kidney fat weight at 2 years of age. After 7 years of age males underwent a decline in early-winter kidney fat weight, and females underwent a similar decline after 10 years of age. The data also corroborate the observation made in the research series, that in all age classes older than calves, males entered the winter with smaller perinephric fat deposits than females.

Adrenal glands

Selye (1950) has pointed out that a wide variety of agents that upset the homeostasis of a mammal stimulate similar physiological responses of the body. He termed such agents "stressor agents", and the responses of the body "the general adaptation syndrome". He demonstrated that increased secretion of ACTH (adrenocorticotrophic hormone) by the anterior pituitary and the resulting increased secretion of steroid hormones by the adrenal cortex are important features of the response of the body to the effects of stressor agents.

Selye (1950) divided the general adaptation syndrome into three stages: alarm reaction, resistance, and exhaustion. He defined the alarm reaction as the sum of all non-specific, systemic phenomena elicited by the sudden exposure to stimuli that affect large portions of the body, and to which the organism is quantitatively or qualitatively not adapted. Some of those phenomena consist of damage to the organism. Others, which include increased secretion of corticoids and hypertrophy of the cells of the adrenal cortex, are manifestations of active defence against damage and they become apparent very soon after the application of the stress. During the latter part of this stage resistance to stresses in general usually is increased.

The stage of resistance is the sum of all non-specific, systemic reactions elicited by prolonged exposure to stimuli to which the organism has acquired adaptation. It is characterized by an increased resistance to the particular stressor to which the body has been exposed, often accompanied by a marked decrease in resistance to other types of stress. This stage is characterized by both hypertrophy and hyperplasia of the adrenal cortex.

The stage of exhaustion represents the sum of all non-specific, systemic reactions that ultimately develop as the result of very prolonged exposure to stimuli to which adaptation has been developed but could no longer be maintained. In this stage abnormal function of the anterior pituitary - adrenal cortex relationship causes an

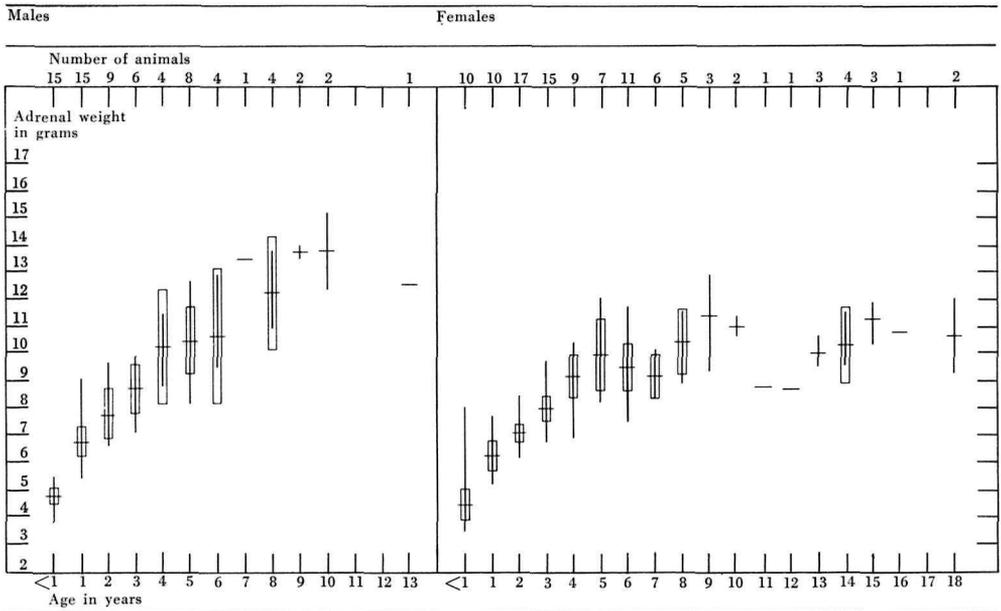


Figure 19. Weight of adrenals of wapiti of each sex and age slaughtered in winter in Banff National Park. Median horizontal lines represent means, vertical bars represent 95 per cent confidence limits, and vertical lines represent ranges.

upset in general metabolism.

In a number of eutherian species in which the relative weights of the adrenal medulla and cortex have been measured, the cortex makes up most of the total weight. The size of the medulla in contrast to that of the cortex is relatively stable (Jones, 1957:11; Selye, 1950:300). Therefore, the weight of the adrenal glands provides a suitable indicator of changes in the size of the cortex. Stress stimulates secretion of ACTH. That usually causes adrenal enlargement, a widening of the zona fasciculata, and a narrowing of the zona glomerulosa (Jones, 1957:28,237).

Difference in adrenal size associated with sex and age

To provide material for comparing the sizes of adrenal glands according to sex and age, adrenals were collected from wapiti slaughtered in Banff in 1961-62 and 1962-63. They were preserved in neutralized saline formaldehyde solution. Later the glands were trimmed of remaining fat, blotted lightly, and weighed to the nearest 0.01 gram.

The 7-year-old males and the 5-year-old females were the youngest classes in which the mean adrenal weights were not significantly smaller than the means of all older animals of their respective sexes (Fig. 19). Thus, the adrenals apparently continued to grow for 2 years in males and 1 year in females, on the average, after full body weight was attained. The graph suggested that adrenal weight might have continued to increase to 10 years old in males and 8 years old in females, 3 years and 1 year older, respectively, than the corresponding ages for body weight. Preliminary data published by Taber, White, and Smith (1959) suggested a tendency for the adrenal weight of mule deer to continue to increase in advanced age.

In each age class in which males were represented, their mean adrenal weight was higher than that of females. The difference was not significant in yearlings but it was significant in calves, 2-year-olds, 3-year-olds, and the groups 4 to 6 years of age, and 7 to 13 years of age.

In an attempt to put the adrenal weights of animals of different body size on a com-

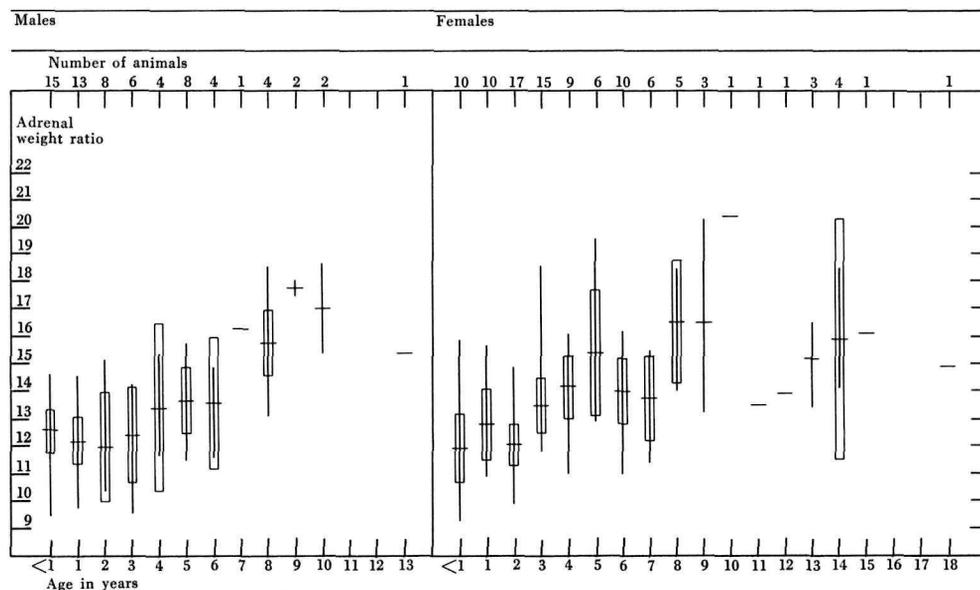
Figure 20. Adrenal weight ratios of wapiti of each sex and age slaughtered in winter in Banff National Park. Median horizontal lines represent means, vertical bars represent 95 per cent confidence limits, and vertical lines represent ranges.

mon basis for comparison, an adrenal weight ratio was derived. Adrenal weight tends to relate more closely to surface area of the body than to body weight (Jones, 1957:6). A general formula given by Spector (1956:175) for estimating the surface area of mammals from body weight is $K = A/W^{2/3}$ where K = a constant for the particular species, A = surface area in square centimetres, and W = body weight in grams.

Kleiber (1965) pointed out the obstacles to measuring surface area and interpreting its relationship to metabolic rate. He reported that, for a large group of homoiothermic species, the basal metabolic rate was, on the average, proportional to the body weight raised to approximately the three-quarter power. He acknowledged that for individual species the most appropriate exponent varied somewhat from three-quarters. The European Association for Animal Production accepted Kleiber's proposal that they adopt the term "metabolic body size", and that it be equivalent to body weight in kilograms raised to the three-quarter power.

In the absence of data specifically applicable to wapiti on either basal metabolic rate or the relationship of body weight to surface area, metabolic body sizes of wapiti slaughtered in Banff in 1961-62 and 1962-63 were estimated as body weight in kilograms raised to the three-quarter power. For each animal an adrenal weight ratio was calculated by dividing the weight of the paired adrenals in grams by the estimate of metabolic body size, and multiplying the quotient by 100 to make the ratio a whole number.

The above treatment of the adrenal weight data reduced some of the variation associated with age (Fig. 20). In the males there were no significant differences among the adrenal ratios of calves, yearlings, 2-year-olds, and 3-year-olds. Similarly in the females there were no significant differences among calves, yearlings, and 2-year-olds. However, in adults of each sex, the adrenal weight ratio tended to increase



in a step pattern in relation to age. In males there were significant differences between the mean ratios of the calf to 3-year-old group and the 4- to 6-year-old group, and between those of the 4- to 6-year-old group and the 7- to 13-year-old group ($P < 0.01$). In females there were significant differences between the mean ratios of the calf to 2-year-old group and the 3- to 7-year-old group ($P < 0.01$), and between those of groups 3 to 7 years old and 8 to 18 years old. The increase in adrenal weight ratio with age, as well as the previously described increase in absolute adrenal weight, both suggest an increase in the demands for corticoid hormones in relation to age, in addition to the increase related to body size.

The spread of confidence limits (Figs. 19 and 20) relative to their respective means suggests that within each sex-age class the variability of the adrenal weight ratio was similar to that of the adrenal weight.

Most or all of the variation in adrenal weight associated with sex was compensated for by dividing it by metabolic body size. There were no significant differences between the mean adrenal weight ratios of males and females in each of the age

groups: calves to 3-year-olds, 4- to 6-year-olds, and 7 years and older. That similarity suggests that the demands of males and females for corticoid hormones are very similar in relation to body size.

Histology of the adrenal cortex

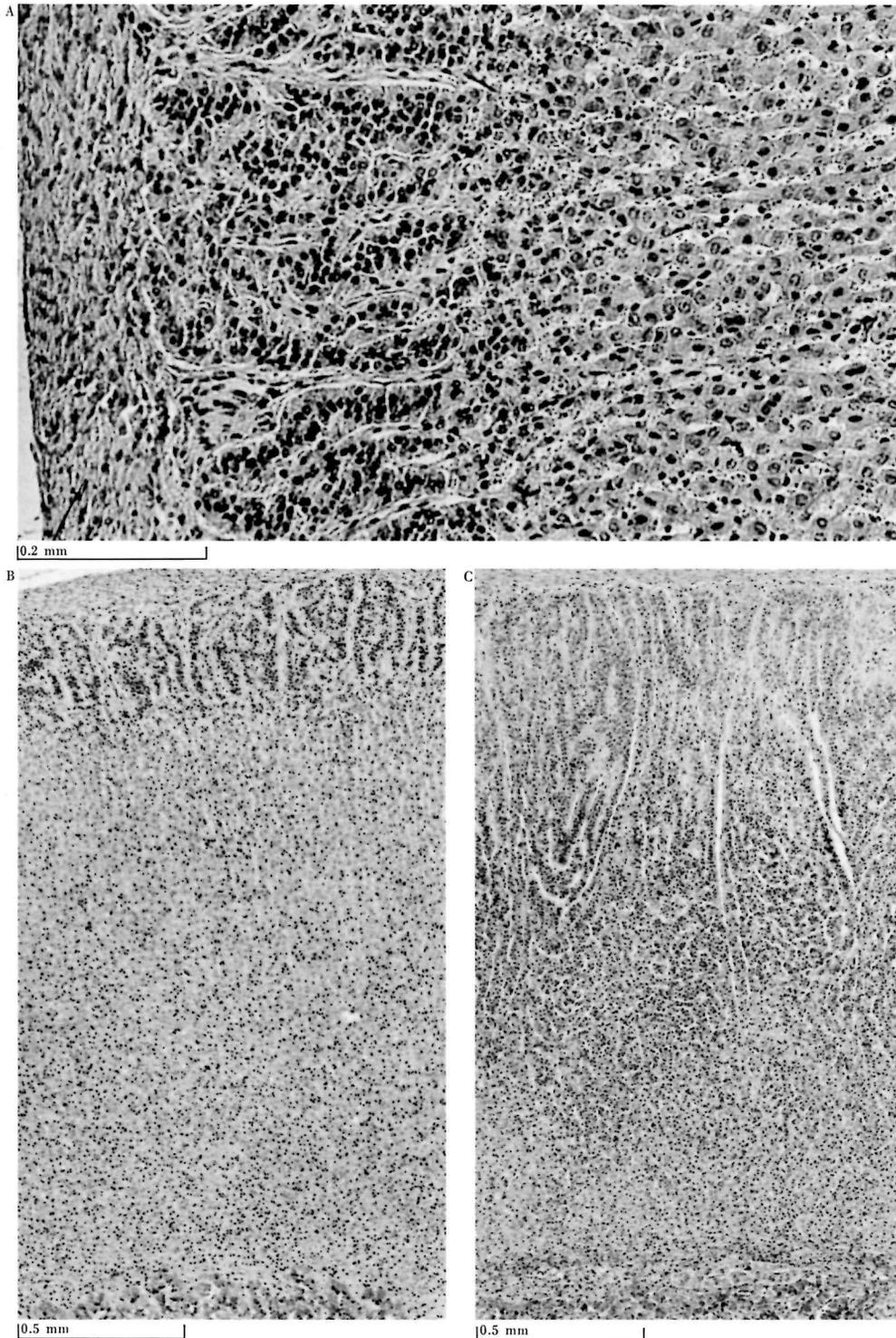
The gross histology of the adrenal cortex was studied in specimens in the research series, as well as those which had been exposed to various stressors to be discussed later. The glands were fixed in neutralized saline formaldehyde solution. After weighing, sections were prepared and stained with hematoxylin and eosin. They were examined under a compound microscope at $40\times$ and $100\times$ to distinguish the zones.

Hucin (1957) described the histology of the adrenal cortex of red deer. Apart from the proportionately greater width of the zones of the gland in wapiti, his description is applicable to the latter species as well. He used the term "zona arcuata" for the zona glomerulosa, as a number of authors have done in describing the adrenals of ungulates (Bourne, 1949).

In the present study the boundary between the capsule and the zona glomerulosa

Figure 21. Photomicrographs of adrenals of wapiti. H and E stain. A, specimen 76, female, 9 years old, March 30, 1962, Ya Ha Tinda Ranch. Left to right: capsule, zona glomerulosa, zona fasciculata; B, specimen 76. Top to bottom: capsule, zona

glomerulosa, zonae fasciculata/reticularis, medulla; C, specimen 86, male, 6 years old, June 1, 1962, Banff National Park. Note wider zona glomerulosa, narrower zonae fasciculata/reticularis, and wider transition between them.



was found to be quite distinct (Fig. 21A). The zona glomerulosa was distinguishable from the zona fasciculata by both the configuration and arrangement of cells. The cell nuclei of the zona glomerulosa were more darkly stained and the cells more tightly crowded together than those of the inner zones of the cortex. The cells of the zona glomerulosa were arranged in loops, arches, and columns usually a few cells wide, separated by radial trabeculae of connective tissue. The cells of the zona fasciculata were arranged in crooked radial strings usually one cell wide. In specimens in which the zona glomerulosa was of small or moderate width, the boundary between it and the zona fasciculata tended to be fairly distinct (Fig. 21B). However in specimens with wide glomerular zones the staining characteristics and arrangement of the cells graded less abruptly into the zona fasciculata (Fig. 21C). In specimens of the latter type the boundary was considered to be the line where characteristics were approximately intermediate between those typical of the two zones. Toward the medulla, the cell columns typical of the zona fasciculata became disorganized in the zona reticularis. Between the zone of clearly fascicular arrangement of cells and that of reticular arrangement there was a zone of gradation which within a gland varied considerably in width and in proximity to the zona glomerulosa and to the medulla. Hucin (1957) noted that in red deer the transition from the zona fasciculata to the zona reticularis often is not very distinct. Hoffman and Robinson (1966) stated that in white-tailed deer normally only two major zones can be easily distinguished, the zona glomerulosa and the "zonae fasciculata/reticularis", and they did not attempt to divide the latter further.

Only the width of the zona glomerulosa was measured in the present study. Measurements were made using an ocular disc micrometer at a magnification of 100 \times . The magnitude of variation in width of the zona glomerulosa measured in the right and left adrenal of the same wapiti,

and at different locations in the same gland, was tested using the adrenals of specimen 30, a 2-year-old female collected November 27, 1961. Four transverse sections were taken at equal intervals along the length of the left gland, and three sections were taken from the right. In this wapiti and in most the right gland was shorter than the left. In each section, the width of the zona glomerulosa was measured at eight points, four distributed at about equal intervals on each of the two flattened sides of the gland. The width of the zona glomerulosa, represented by the mean of the eight measurements, was determined for each section (Table 19). Since the measurements were very uniform, one transverse section from the centre of each adrenal was used for measuring the zona glomerulosa and eight measurements were taken from it in the manner described above. Zona glomerulosa widths presented here-

after represent, in most cases, the mean of 16 measurements, 8 from each adrenal gland. In the few instances in which only one usable gland was available, the mean represents eight measurements from that gland.

Effects of stressors on the adrenals

To help interpret data on the adrenal measurements of wapiti, the adrenals of animals which were known to have been subjected to certain stressor agents, i.e., accelerated loss of body heat, bacterial and parasite infections, and malnutrition, were studied. These were all mentioned by Selye (1950:27-51) as agents which can elicit the general adaptation syndrome.

To study the effects of accelerated loss of body heat on the adrenals, six wapiti were captured from Banff and Yoho in November 1961 by immobilization with succinylcholine chloride (Flook *et al.*, 1962) and released in a large, partly wooded enclosure which contained good stands of native forage. Unfortunately, four escaped from the enclosure and only one was recovered. Thus, experimental data were available from only two animals: a 2-year-old male captured in Yoho Park on November 25, and a male calf in Banff on November 21. Immediately after capture and before release in the enclosure, the hair was shorn from a rectangular area from immediately behind the shoulder to the base of the tail, and extending on each side of the mid-dorsal line a distance equal to one-sixth the

chest girth. Another 2-year-old male was captured in Banff on November 24 and released in the enclosure without treatment, as a control animal. The calf was among those which escaped from the enclosure, but it was shot December 5, 13 days after shearing. The two bulls were shot December 19, which was 24 and 25 days after their release in the enclosure.

During the 24-day interval between shearing and slaughter of the 2-year-old bull the mean daily minimum, mean daily mean, and mean daily maximum temperatures were 1, 9, and 19°F, respectively. Corresponding values for the 13-day interval between clipping and slaughter of the calf were 4, 15, and 28°F. For both periods the extreme low was -29°F.

On butchering, it was found that the control animal had contracted a *Staphylococcus** infection in the hip puncture inflicted by the projectile syringe used to administer the immobilizing drug. Therefore, that animal was subjected to stress, and the results were interpreted accordingly. The shorn 2-year-old carried five giant liver flukes (*Fascioloides magna*). No other endoparasites were observed in any of the animals.

The body weight losses and kidney fat indices of the three animals are presented in Table 20. All three lost a high proportion of body weight during the experiment. At the end of the experiment all three had relatively low kidney fat indices but none had exhausted the fat deposits surrounding the kidneys. The animal with the *Staphylococcus* infection lost the highest proportion of its body weight and had the lowest kidney fat index.

As specimen 102, a 21-year-old cow collected October 14, 1962, in the Cascade River Valley, carried an extremely heavy pulmonary infection of hydatid cysts (*Echinococcus granulosus*), it too will be included in the present analysis.

Table 19

Width of zona glomerulosa in cross sections from different locations in the adrenals of specimen 30, a 2-year-old female

	Section	Mean* width of zona glomerulosa, mm
Left adrenal	1	0.51
	2	.54
	3	.53
	4	.51
Right adrenal	1	.51
	2	.50
	3	.52

*Mean of eight measurements.

Table 20

Body weight losses and kidney fat indices of three male wapiti stressed experimentally in November and December

Age, years	Treatment	Body weight		Kidney fat index, %
		Initial, kg	Loss, %	
2	<i>Staphylococcus</i> abscess	281	15.6	28
2	Shearing	272	11.7	37
<1	Shearing	176	9.5	47

*Identified by Canada Department of Agriculture, Veterinary Research Laboratory, Lethbridge, Alberta.

Table 21
Adrenal measurements of stressed wapiti
compared to those of normal wapiti

Stressor	Individual stressed specimen				Standard for comparison							
	Month of death	Sex	Age, years	Adrenal measurement	Month of death	Sex	Age, years	Mean	Range	Standard error	No.	
Heat loss	Dec.	♂	<1	zg* width (10 ⁻¹ mm)	4.0	—	—	—	—	—	—	—
Heat loss	Dec.	♂	2	adrenal wt (g)	9.8	Nov.—Jan.	♂	2	7.8	6.6–9.7	0.37	9
				zg width (10 ⁻¹ mm)	4.6	Dec.—April	♂	2	4.4	3.4–5.2	0.31	6
Abscess	Dec.	♂	2	adrenal wt (g)	7.7	Nov.—Jan.	♂	2	7.8	6.6–9.7	0.37	9
				zg width (10 ⁻¹ mm)	4.0	Dec.—April	♂	2	4.4	3.4–5.2	0.31	6
Hydatid cysts	Oct.	♀	21	adrenal wt (g)	12.9	Nov.—Jan.	♀	≥5	10.1	8.4–12.9	0.56	52
				zg width (10 ⁻¹ mm)	6.4	May—Nov.	♀	≥3	5.6	3.7–7.6	0.30	15
Malnutrition	March	♂	1	adrenal wt (g)	6.2	Nov.—Jan.	♂	1	6.8	5.4–9.1	0.25	15
				zg width (10 ⁻¹ mm)	3.4	Dec.—April	♂	1	5.0	4.3–7.1	0.33	8
		♀	10	adrenal wt (g)	10.6	Nov.—Jan.	♀	≥5	10.1	8.4–12.9	0.56	52
				zg width (10 ⁻¹ mm)	3.2	Dec.—April	♀	≥3	4.4	3.0–5.6	0.31	8

*zg - zona glomerulosa.

Note: None of differences between measurements of stressed specimens and normal samples were significant at 0.05 level of probability by *t* test.

A. L. Lovaas of the Montana State Game Department supplied data and adrenals from nine wapiti that died in extremely emaciated conditions between March 4 and April 4, 1962, in the Gallatin Canyon, Montana. The forage stands of that area were badly depleted as a result of many years of overstocking with wapiti in winter (Peek, Lovaas, and Rouse, 1967). Lovaas (pers. comm.) reported that the femur marrow was of gelatinous consistency. In eight specimens it was red, and in one calf it was grey. According to Riney's (1955) findings on the relationship of the consistency and colour of femur marrow to its fat content, those specimens would have had very little marrow fat. It seems reasonable to assume that malnutrition was the primary cause of death of the Gallatin specimens, and data on their adrenals will be interpreted accordingly.

The adrenal weights and zona glomerulosa widths of all wapiti known to have been exposed to stressor agents were compared with the mean values of untreated animals of the same sex and age group collected at the most comparable time of year. Table 21 includes all the comparisons

except that for a group of six female calves from the Gallatin. Statistics for that group are given in Table 22.

Animals exposed to stressor agents (Tables 21 and 22) did not exhibit a consistent response in either adrenal enlargement or reduction in zona glomerulosa width. Using Student's *t* test (Simpson *et al.*, 1960:176, 182), none of the adrenal measurements of animals exposed to stress was found significantly different from those of normal animals. The adrenal weight of the cold-exposed 2-year-old male and the aged cow with the heavy hydatid infection were each approximately equal to the highest extreme in the most appropriate control group (Table 21). The adrenal weight of each of the other specimens exposed to stressor agents was well within the range of extremes of its control group. It seems particularly noteworthy that the mean adrenal weight of the four calves which died of malnutrition was about equal to the mean adrenal weight of their control group, and the adrenal weight of each of the two older specimens which died of malnutrition was well within the range of extremes of its control group.

The zona glomerulosa widths of all the specimens which died of malnutrition tended to be small. However, no data on the zona glomerulosa width of normal wapiti calves in March and April were available for comparison. Zona glomerulosa width of none of the other specimens exposed to stressors differed appreciably from the mean of its corresponding control group.

Light infections of five parasites were commonly noted in this study: winter ticks (*Dermacentor albipictus*), giant liver flukes, hydatid cysts, fringed tapeworms (*Thysanosoma actinoides*), and thread lung-worms (*Dictyocaulus viviparus*). To determine if these infections were associated with increased adrenal size or decreased width of the zona glomerulosa, the individual and mean values of adrenal weight and thickness of zona glomerulosa of wapiti infected with each parasite were compared with those of specimens of the same sex and age category not infected with that particular species.

In cases where inspection of the data suggested the possibility of a real difference, Student's *t* test was applied. None of

the individual or mean zona glomerulosa widths of parasitized animals was significantly smaller than that of the non-parasitized group of the same age and sex. Similarly, none of the individual or mean adrenal weights of parasitized specimens was significantly larger than that of the non-parasitized group of the same sex and age. When the adrenal measurements of specimens carrying two or more species of parasites were inspected and compared with mean and individual measurements of others in their sex-age groups, no consistent differences from the norm were noted. The number of animals infected with each parasite was small and the parasite loads generally light. Perhaps larger samples of animals as heavily parasitized as specimen 102 might be found to exhibit detectable differences in either adrenal size or zone widths when compared to non-parasitized samples.

The literature contains the results of a number of experiments conducted to study the effects of stress on the adrenal glands in various mammals. Munday (1961) showed that laboratory rats exposed to 0 to 2°C for 48 hours exhibited increased sodium retention and potassium excretion, mediated by the adrenal, and he concluded that increased secretion of mineralocorticoids was involved. Rats exposed to that temperature range for 28 days had a significantly greater adrenal weight than control animals, and rats exposed to cold for several weeks showed hypertrophy of the cortex and an increase in width of the zona fasciculata. In contrast, Griffiths, Calaby, and McIntosh (1960) found no detectable effects of cold on wild rabbits exposed to 0°C. Rabbits of reasonably uniform body size collected from the field showed marked variation in adrenal weight, both absolute and relative to body weight. Rabbits exposed to -12 to -15°C for 6 to 7 hours daily for 20 days and then held at that temperature for 3 days without food or water showed a mean relative adrenal weight only slightly higher than that of control animals, and the difference was not

Table 22

Adrenal measurements of female wapiti calves which died of malnutrition in Gallatin Valley, Montana, in March and

April, compared to those of female calves slaughtered, Banff National Park, November to January

Cause of death	Adrenal weight, grams				Zona glomerulosa width, 10 ⁻¹ mm			
	Mean	Range	Standard error	No.	Mean	Range	Standard error	No.
Malnutrition	4.50	3.6-5.1	0.349	4	2.97	2.8-3.5	0.341	6
Slaughtered	4.46	3.5-8.1	0.736	10	—	—	—	—

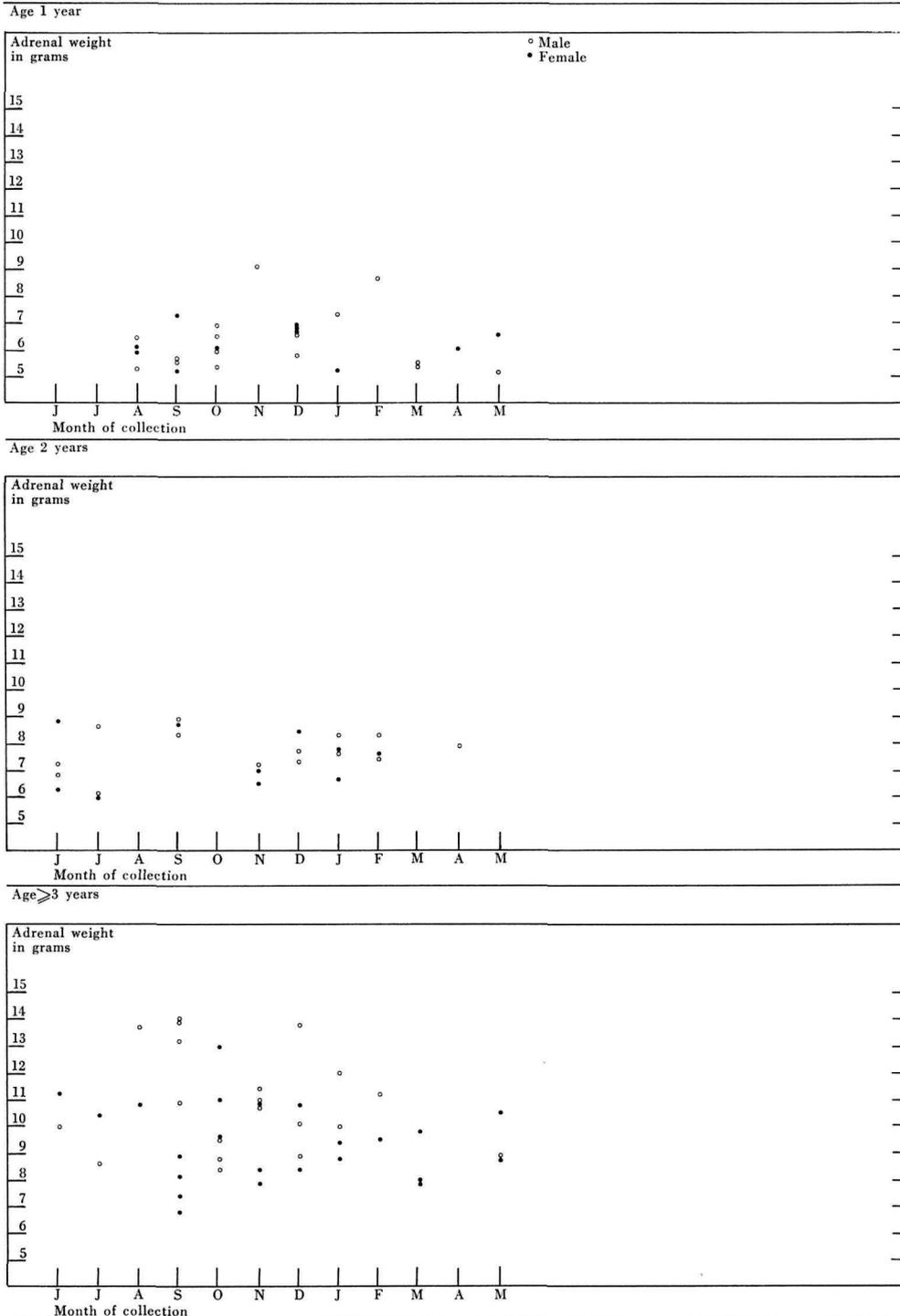
significant. Rabbits injected with dilute formaldehyde over a 7-day period, and killed 18 days later after 15-18 hours of cold exposure, exhibited marked adrenal hypertrophy. Noise-adapted rabbits exhibited increased resistance to cold stress, but rabbits which previously had been injected with formaldehyde and apparently resisted it, were unable to resist cold stress. Griffiths *et al.* concluded that in wild rabbits both histological change and hypertrophy of the adrenal cortex are exhibited only under much more severe stress than that required to induce such effects in laboratory mammals.

The literature contains evidence that adverse circumstances can cause adrenal enlargement in cervids. Hughes and Mall (1958) found a significant negative correlation between adrenal weight and kidney fat deposits in adult female Columbian black-tailed deer. Bubenik and Bubenik (1967) compared the adrenal weight relative to dressed carcass weight of roe-deer (*Capreolus capreolus*) from a population living at low densities in favourable habitat with comparable data from a population living at high densities in less favourable habitat. They divided the samples from each population according to sex, age, and physical condition, the latter rated by size of body and antlers, fat deposits, disease, parasites, and injuries. Relative adrenal weight tended to be greater in samples from the dense population and in animals in poorest condition. When absolute adrenal weights are calculated from the data of Bubenik and Bubenik, the trends

are in the same direction, but less pronounced and less consistent.

Christian, Flyger, and Davis (1960) reported that adrenal enlargement was associated with a late winter die-off in a dense, insular population of sika deer (*Cervus nippon*) and concluded that the die-off was caused by physiological disturbances induced by socio-psychological pressures related to crowding. Their adrenal data were based on 4 specimens collected during the die-off and 13 specimens collected 3 and 1 year before, and 1 and 2 years after, the die-off. They used relative adrenal weights (adrenal weight/body weight) in their comparisons. However, body weights of the four specimens collected during the die-off were the lowest for their sex-age classes. When absolute adrenal weights of the four deer collected during the die-off are calculated from their data, they differ less markedly from those of the pre- and post-die-off specimens than is the case in the relative adrenal weights. The range of variation in adrenal weight noted in the present study (Fig. 19) suggests that, if sika deer are similar to wapiti in this respect, variation in adrenal weight of the magnitude noted by Christian *et al.* between specimens taken during the die-off, as compared to those taken before and after it, could be encountered under normal circumstances.

Figure 22. Weights of adrenals of individual wapiti older than calves, according to sex, age, and month of collection, Banff and Kootenay National Parks and the Ya Ha Tinda Ranch.



Seasonal changes in the adrenals

Weights of the adrenals of wapiti in the research series are presented in Figure 22, with the animals distinguished as to age group and sex. As was noted for wapiti taken in the slaughters, the adrenal weights showed great individual variation. The data suggest a peak in adrenal weight in adult males in August and September. However, since the single high August value, the three high September values, and the single high December value all represent specimens 7 years old or older, and 11 of the 14 lower values represent specimens younger than 7 years old, the suggested peak is apparently a function of differences in age. Similarly, the low level of the adrenal weights of the four adult females taken in August is attributable to their ages, which are all less than 6 years. Apart from the features of the data mentioned above, the distribution of adrenal weights of each sex-age group suggests no seasonal trend.

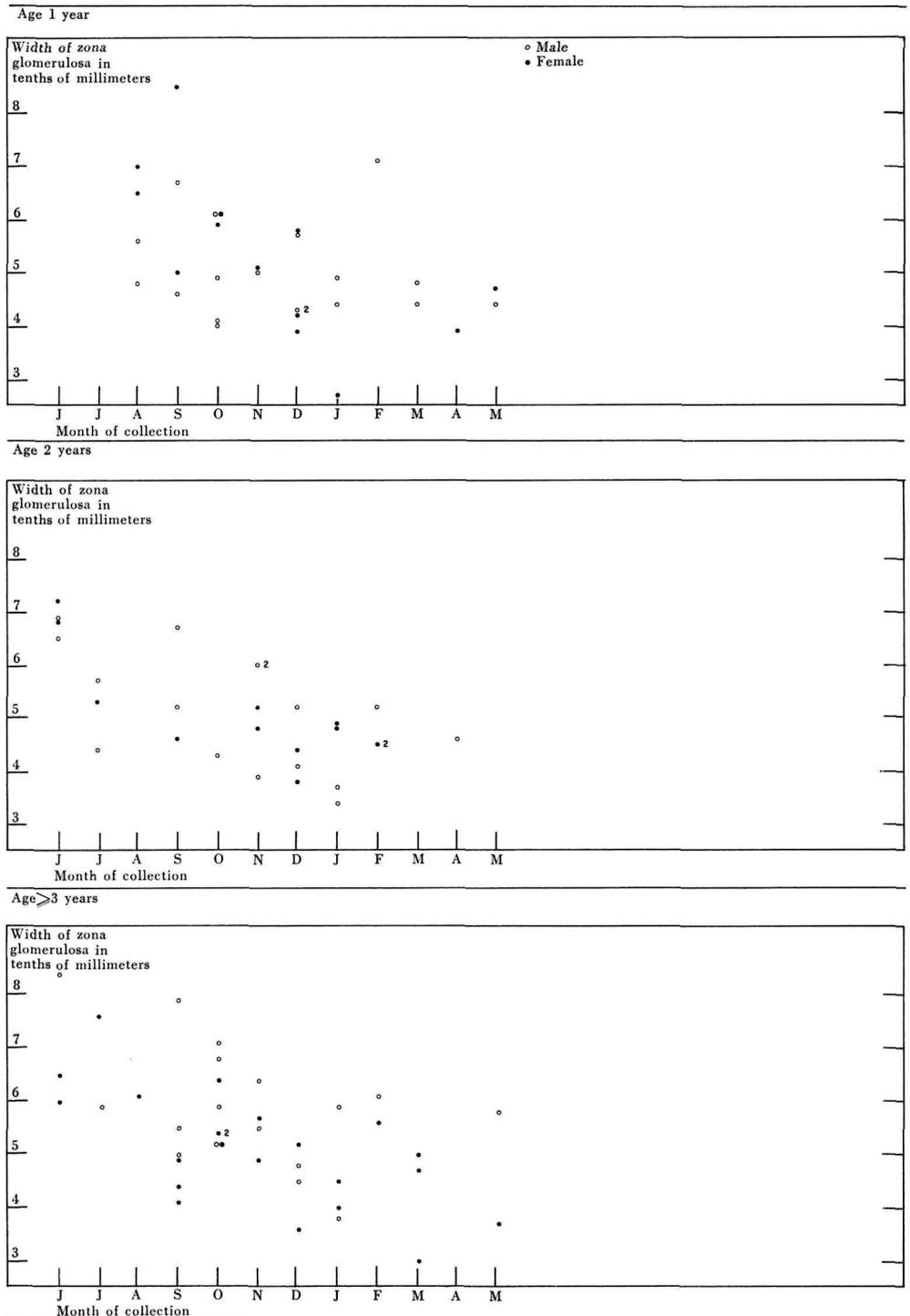
A ratio of adrenal weight to body weight, or to an exponential function of body weight, is commonly used for comparison (Jones, 1957:6). An adrenal weight ratio was used in the present study to compare adrenal size in specimens of different sex and age taken from November to early January. Some workers have used such an index to compare adrenal weights of deer collected at different seasons, and with markedly different amounts of depot fat (e.g. Taber *et al.*, 1959, mule deer; Hoffman and Robinson, 1966, white-tailed deer), or collected under other differing circumstances which would be expected to influence fat reserves (Christian *et al.*, 1960, sika deer; Bubenik and Bubenik, 1967, roe-deer). However, as white fat is a relatively inactive tissue metabolically (Hayward, 1964:55-58), it is not to be expected that a decrease in body weight which represents utilization of depot fat will be accompanied by a proportionate decrease in adrenal size. It has been shown in Columbian black-tailed deer (Hughes

Figure 23. Zona glomerulosa widths of individual wapiti older than calves, according to sex, age, and month of collection, Banff and Kootenay National Parks and the Ya Ha Tinda Ranch.

and Mall, 1958) and roe-deer (Bubenik and Bubenik, 1967) that lower fat reserves and correspondingly lower body weight are sometimes accompanied by larger adrenal weight in animals of the same sex and age group, presumably a manifestation of the general adaptation syndrome. In the present study, while fat reserves (Fig. 16) and body weight declined from early winter to spring, adrenal weight apparently remained stable (Fig. 22). However, samples of deer with low fat reserves and correspondingly low body weights, even though their adrenals are not enlarged, have a higher ratio of adrenal weight to body weight than do fat deer, simply because the index is a function of body weight. Indices based on the relationship of adrenal weight to body weight are therefore useful only in comparing samples in which the fat deposits relative to body size are reasonably similar.

Hoffman and Robinson (1966), who studied white-tailed deer in a crowded population in Maryland, reported two seasonal peaks in adrenal weight relative to body weight, one in November and December, and one in March and April. When bimonthly mean absolute adrenal weights are calculated from their data, they show only a single annual peak in November and December. This contrasts with the apparent seasonal stability in adrenal weight indicated here for wapiti.

Zona glomerulosa widths for the research series are presented in Figure 23, with the specimens distinguished as to age group and sex. The widths exhibit great variation even between animals of the same age and sex and collected in the same month. However, they suggest a seasonal trend, widest from June until September and narrowest from December to April. Figure 21, B and C illustrate the adrenal cortices of specimens with one of the smallest and the largest zona glomerulosa widths observed, respectively. Within each of the six sex-age groups studied, the zona glomerulosa widths of specimens collected from May through November was com-



pared with those collected from December through April (Table 23). The differences were significant in each group except yearling males. No yearlings were collected in June and July, the months when the older animals showed their greatest zona glomerulosa widths. Had the yearling males been represented in collections made in those months they too might have shown a significant difference between summer and winter. As the total size of the adrenal gland appears not to have changed in relation to season, the reduction in zona glomerulosa widths in winter indicates an increase in the size of the zonae fasciculata/reticularis.

The seasonal trend in zona glomerulosa width of wapiti conforms in part to the findings of Hoffman and Robinson (1966), whose data showed that in white-tailed deer the smallest bimonthly mean zona glomerulosa width for the year occurred in January and February. However, in wapiti, there was no evidence of a second decrease in July and August such as was suggested by the data of Hoffman and Robinson.

The few specimens in the present study which were known to have been exposed to accelerated heat loss, infection, or malnutrition did not respond consistently in either adrenal enlargement or reduction of the zona glomerulosa. The adrenals of two specimens, one cold-stressed and one infected with hydatid cysts, were relatively large, but the zona glomerulosa widths were normal. On the other hand, the zona glomerulosa widths of the specimens which died of malnutrition were relatively small but the adrenal weights were normal. Jones (1957:237) reported that stimulation by ACTH caused the zona glomerulosa to decrease in width in rats and dogs, and when ACTH stimulation caused a 50 per cent increase in the adrenal weight of rats, the zona glomerulosa disappeared. Controlled experiments with cervids are needed to explain the significance of the seasonal difference in zona glomerulosa width indicated by the present study.

Table 23
Comparison of zona glomerulosa widths of wapiti collected May through November with those of wapiti collected December through April

Age, years	Sex	Zona glomerulosa width, 10^{-3} mm					
		May–November			December–April		
		Mean	Standard error	No. specimens	Mean	Standard error	No. specimens
1	Male	5.02	0.275	10	4.98	0.334	8
	Female	6.10	.442	8	4.10	.497	5
2	Male	5.56	.334	10	4.36	.310	6
	Female	5.65	.442	6	4.48	.158	6
≥3	Male	6.28	.309	12	5.02	.433	5
	Female	5.59	.296	15	4.45	.307	8

A tentative interpretation is that it can be attributed to the stressful effects of low temperatures, snow accumulation, and less abundant food supplies in winter. While the level of ACTH secretion was evidently high enough in winter to cause the zona glomerulosa to be partly replaced by zonae fasciculata/reticularis, the adrenal weight data (Fig. 22) show that it did not cause an increase in the total size of the gland.

It is noteworthy that while the zona glomerulosa width decreased simultaneously with a winter decline in fat reserves (Fig. 16), it increased earlier in the spring.

Neither the data on adrenal weights nor zona glomerulosa widths provide evidence that male wapiti were subjected to more severe stress than females. However, because wapiti subjected to cold, heavy parasitism, bacterial infection, or starvation to the point of death showed no differences in adrenal measurements from untreated animals, the absence of either general adrenal enlargement or reduction in the zona glomerulosa cannot be regarded as evidence that wapiti have not been severely stressed.

Discussion

Although recognized biases in the population data prevented the determination of age-specific mortality rates of males and females, certain conclusions can be reached regarding differences in mortality rates between the sexes and their probable causes.

In Elk Island, apparently more males than females were lost to non-harvest mortality over a 19-year period, but the difference was relatively small. The sex ratio in the net production from Elk Island during that period was 85:100.

The sex ratios of wapiti older than calves in classified counts in Banff, in summer and autumn, and among wapiti killed by trains and highway vehicles in Banff and Jasper at all seasons were between 36:100 and 37:100. The sex ratio of wapiti older than yearlings in a total sample shot without deliberate selection in all the mountain parks in winter (Table 4) was 36:100. However, the apparent disappearance of a large number of males in the mountain parks from the ranges where they were reared, between their second and third winters of life, suggests a dispersal. Bulls outnumbered cows in winter at the high elevations and are thought to do so at other seasons as well. One might suspect, because bulls are more solitary, that in addition to using the alplands more than cows they also use small grassy or shrubby openings in the forest more. Thus, the distribution of cows in the mountain parks coincided more closely with accessible areas and perhaps with areas of good visibility than did that of bulls. Therefore, population data from the mountain parks obtained by counts and analyses of slaughtered samples are believed to be biased in favour of cows.

The apparent dispersal of young males in the mountain parks to new areas may take some of them into unsuitable habitats and thus contribute to mortality of males. Also, the wintering of some bulls at higher elevations, where the snow is often deeper and the temperatures colder than on the lower ranges, may make them more

vulnerable to winter mortality. Males in Elk Island are not exposed to these hazards because the park is fairly uniform in climate and dispersal from it is prevented by a fence. Greater exploitation by man may also have reduced the effects of natural mortality selective for males in Elk Island as compared to the mountain parks. These environmental differences between the mountain parks and Elk Island could lead one to hypothesize that the differences in life expectancy between males and females should have been greater in the mountain parks than in Elk Island. However, it is not possible to confirm that relationship with the information available because of the bias in the data on sex ratios from the mountains.

The sex ratio of foetuses collected in winter from all parks was 113:100 and differed significantly from equality. Perhaps, as Cowan (1951) suggested, the sex ratio begins at conception to shift from one in which males predominate toward one in which females predominate and continues to do so throughout life. If there were slight changes in the sex ratio during the first 1½ years of life, they could not be detected because of biases in the slaughtered samples. The samples from all parks indicated that no substantial changes took place before 1½ years of age. The suggested dispersal of many males in the mountain parks, from the ranges where they were reared to areas not accessible to slaughter, between their second and third winters of life, made it impossible to determine the age when non-harvest mortality of males first appreciably exceeded that of females. However, a marked loss of males was indicated, beginning after 7 years of age and continuing until 14 years, the age of the oldest males represented. In contrast, the numbers of females declined gradually in successive age classes from 2 to 19 years of age, the maximum age represented in the slaughtered sample.

The data showed that in Banff, Waterton Lakes, and Elk Island males abraded

their molariform teeth more rapidly than females, by differences of approximately 9, 26, and 40 per cent respectively in the three parks. While the effect of tooth abrasion on health is probably a gradual rather than a threshold one, it seems likely that it would not have great effect until the more advanced stages. Because tooth wear is accompanied by general senescence in both sexes, and probably by changes in the participation in breeding by males, its effects cannot be isolated with the data available. It is evident that any effects that tooth wear has on the welfare of wapiti in the three parks mentioned would confer an advantage on females. In the absence of exploitation, when more animals would be given the opportunity to reach older ages, tooth wear could be expected to be more significant in limiting longevity and thus in affecting the sex ratio in those parks. In Jasper, tooth wear, being more rapid than in the other parks, would adversely affect wapiti of both sexes at a younger age. However, it would affect males and females equally at equal ages.

The major features of the life histories of males and females will be briefly summarized and compared. In females, body growth continued to about 4 years of age. Some conceived as yearlings, and most did so each year thereafter. The pregnancy rate declined significantly after 13 years of age. However, both the 19-year-olds examined in winter were pregnant. The kidney fat deposits of females measured in early winter were at their maximum level in animals from 2 to 10 years of age, declined significantly at 11 years, and remained at a low level until 16 years, the age of the oldest animal so measured. That decline is presumably caused by a lowering in metabolic efficiency related to general senescence, including tooth deterioration.

From conception, males grew more rapidly, in terms of absolute rate, than females. They also continued to grow later in life, to an age of at least 5 years. The presence of spermatozoa in the testes and epididymides suggested that yearling males



were physiologically capable of breeding. However under the circumstances which prevailed in the parks males do not usually have the opportunity to breed until at least 4 years of age (Struhsaker, 1967). The size of testes measured in post-rut condition increased with age until at least 6 years, and remained high until 13 years, the age of the oldest bull examined. The oldest male examined during the rut, aged 12 years, was in breeding condition and possessed a harem. The data suggest that few if any bulls lived to an age of reproductive incapacity. Antlers were produced annually, beginning at 1 year of age. The size of successive sets, on the average, increased to reach a maximum at 6 or 7 years of age. Kidney fat deposits of males, as measured in early winter, increased in relation to age to 2 years, remained fairly stable until 7 years, then decreased significantly between 7 and 8 and, until 13 years, the age of the oldest specimen measured, remained at a uniform level lower than in any class except calves. Perhaps the accumulated effects of "wear and tear" on the organism, including tooth deterioration, cause a decline in metabolic efficiency to become evident between 7 and 8 years of age. However, the following items of evidence suggest that there may be an increase in breeding activity at about that age which could cause older bulls to deplete their energy reserves. The three bulls shot during September (when most breeding occurred) that were with cows were 7, 8, and 12 years old. There was no decline in the post-rut weight of testes between 6 years of age, when maximum size was first reached, and 13 years, the age of the oldest specimen measured. Similarly, there was no significant decline in antler weight from 7 until 13 years of age.

Since males attain greater body size than females, their food requirements for growth and maintenance (Brody, 1945) can be expected to be greater. Data are not available to compare directly the nutritional requirements of antler production and breeding activity in males with those of foetal growth and lactation in females. However, the re-

sults of the comparisons of rates of tooth wear, if the interpretation is correct, indicate that from the time complete permanent dentition is obtained, at about 2 years of age, females have a lower food intake than males. This suggests females have a lower food requirement, which would give them an advantage in survival.

Probably differences between males and females in their seasonal timing of storage and depletion of energy are more important than total food requirements in placing males at a disadvantage in survival. The slow recovery of fat reserves in all wapiti, through the summer from a spring low, coincides with an abundance of food on the one hand and, on the other, muscular and skeletal growth in the younger animals, antler growth in the bulls, and lactation in the cows. In the rut, the deposition of fat is at least slowed in yearling and 2-year-old males, and in adult males high physical activity and partial fasting are accompanied by a heavy and rapid drain on fat reserves. The fat reserves of females remain high through that period.

A period of negative energy balance in both sexes occurs from about December until April or May. Perhaps, as the experiments of Magruder *et al.* (1957) have shown for white-tailed deer, and Wood *et al.* (1962) have shown for black-tailed and mule deer, wapiti fed *ad libitum* on a high quality diet in winter would exhibit a negative energy balance with a voluntary reduction in food intake. However, in the areas where the present study was conducted, the low temperatures coupled with snow cover and seasonally inferior food supply would probably impose a more stringent limitation on the energy balance than the potential for the species in winter. In any case, males older than calves, having entered the winter with lower fat reserves than females, tend to reach potentially critical levels before females. They are thus more vulnerable to death at that time caused basically by an inadequacy of energy.

It was previously mentioned that, perhaps as a result of an increase in breeding

activity, males 8 years of age and older entered the winter with lower fat reserves than younger males. It is suggested therefore that the marked increase in non-harvest mortality of males after 7 years of age, as indicated by the composition of the slaughtered samples, was a result of that condition, i.e. that older bulls are particularly prone to death in late winter in which the primary cause is an inadequacy of energy.

Few dead wapiti for which the season and cause of death could be determined have been found in any of the parks in recent years. However, R. Jones, chief park warden, and A. Roberts, retired park warden, mentioned (pers. comm.) that in earlier years when Elk Island was heavily stocked, dead or dying wapiti were found commonly in severe winters. They were usually found late in winter, and large bulls and calves predominated. Anderson (1958) mentioned a higher rate of winter deaths of bulls than cows on the National Elk Refuge in Jackson Hole. Darling (1939:115) wrote of red deer, "the season of April and early May is the time when many deer of both sexes die, but there is an undoubtedly higher mortality among stags than among hinds. It is the common experience to find the population of deer in a given area composed of females to males in the proportion of two to one, though among the calf crop the ratio is almost equal, or if anything in favour of the males."

Several of the parasites found among the wapiti studied were sufficiently common to suggest a potential for affecting a large proportion of the population: giant liver fluke, fringed tapeworm, hydatid cyst, thread lungworm, biting louse, and winter tick (Flook and Stenton, in press). Their effects, while probably slight in most instances, would tend to lower the tolerance of the host to other adverse circumstances. In winter, male wapiti have lower fat reserves than females. Those parasites which infected the sexes in equal incidence and equal loads could help to make that sex difference operate to cause a proportionately higher winter-kill in males than in females.

Two of the parasites studied appeared to infect one sex more frequently than the other. The incidence of infections with giant liver fluke was significantly higher in females than in males in Waterton Lakes. Thus, any contribution which it makes to mortality in that park can be expected to affect proportionately more females than males. However, the giant liver fluke was absent or rare in Jasper, and in Banff apparently occurred only in immigrants from Kootenay.

In the research series, males had a significantly higher incidence of infections with winter tick than females. As the weakening effect of that parasite on its host is greatest in late winter and spring, it would add to the effect of the sex difference in fat reserves, to make males more vulnerable to winter-kill than females. The winter tick has been recorded in all the parks studied except Waterton Lakes (Cowan, 1951; Love, 1955; Gregson, 1956) and is probably present there as well. If a sex difference in incidence is universal, it may contribute to a sex difference in life expectancy of wapiti in all those areas.

It was initially hypothesized that the intense social interactions of the rut might stress males more than females to an extent that, through exhaustion of the adrenal cortex, the males would be less able to adapt to the effects of other stressor agents. The data obtained on adrenal weights and zona glomerulosa widths did not reveal any evidence of such a relationship. However, it was shown that those measurements varied considerably among specimens of the same sex and age collected at the same time of year. It was also shown that the adrenal measurements of animals of which the homeostasis had been severely insulted, were not recognizably different from those of untreated specimens. For those reasons the results are not conclusive.

A seasonal trend in width of the zona glomerulosa was noted in wapiti of both sexes, the width being greatest from June until September and least from December to April. It is suggested that the reduction

in width was caused by an increase in secretion of ACTH, which in turn was related to the stressful effects of low temperature, accumulation of snow, and the seasonally inferior food supply of winter.

Cowan (1950) suggested that disproportionate sex ratios in various ungulates might be related to overstocking and range depletion. Taber and Dasmann (1954), Robinette *et al.* (1957), and Klein and Olson (1960) discussed evidence for such a relationship in deer of the genus *Odocoileus*. Peek *et al.* (1967) attributed a disparity between the sexes in wapiti in the Gallatin drainage in Montana to range depletion.

Adverse nutritional conditions such as would occur with overstocking and range depletion would probably increase the sex difference in mortality in wapiti. In the present study the fat reserves of males in early winter were significantly smaller than those of females, in broad age groups older than calves. We might therefore expect that in each of those age groups males would have a lower tolerance to food shortage. However, in the present study, which was conducted under reasonably favourable circumstances of stocking and forage supply, the mortality of males did not greatly exceed that of females before 1½ years of age. The age at which the mortality rate of males began appreciably to exceed that of females is not known, but there were indications that the difference became marked after 7 years of age. It is evident that beyond whatever age the mortality rate of males begins to exceed that of females, the sex ratio will become more unbalanced with increasing age until in the oldest classes only females remain. The absence of substantial exploitation being a major factor predisposing overstocking in cervids, and reduced reproduction and survival of young of both sexes being characteristic of such a situation, it follows that populations affected by overstocking tend to have a higher proportion of old animals than populations on understocked ranges. Therefore, even if malnutrition were not to increase

the sex difference in mortality at any given age (reasons have been shown to expect that it would), a population of wapiti suffering the effects of overstocking could be expected to have a greater disparity of the sexes than one on an understocked range, simply as a function of greater age. Conversely, exploitation, by reducing the proportion of old animals and increasing the proportion of young, would bring the sex ratio nearer to 1 : 1.

Differences in the age distribution of populations and in the intensity of range use have probably contributed to the variation in sex ratios observed in this and previous studies. However, in view of the smaller difference between non-harvest losses of males and females in Elk Island, and indications of bias favouring observation of females in the mountain parks, the data available from classified counts in mountainous areas should be interpreted with caution.

In considering the evolutionary significance of the differences in distribution and mortality between male and female wapiti, Rand's (1952) comments are pertinent. He pointed out that in some birds, different distributions of the sexes at times other than the breeding season helps limit intraspecific competition for food. Similarly in wapiti the dispersal of many males from the range where they were reared to vacant or less densely inhabited areas, often to winter ranges with deeper snow, limits intraspecific competition. The tendency for an earlier death in males, by leaving fewer of them in the population, also leaves more food and space for females and young, and thus contributes to sustaining a high reproductive success. The extent to which this phenomenon occurs in other ungulates warrants further attention, in view of its significance to the capacity of a species to increase its abundance and distribution.

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Appendices

Appendix 1

Approximate mean* annual total precipitation, and mean* daily temperature for January, April, July, and October, for parks studied

Park	Precipitation, inches	Mean daily temperature, °F			
		Jan.	April	July	Oct.
Elk Island	16–18	5–10	35–40	60–65	40–45
Jasper	18–20	10–15	35–40	55–60	40–45
Banff	20–22	10–15	35–40	55–60	35–40
Kootenay	20–22	10–15	35–40	60–65	35–40
Waterton Lakes	22±	15–20	35–40	55–60	40–45

*Mean of 1921–50 incl. from Atlas of Canada (Canada Dept. Mines and Tech. Surveys, 1957).

Appendix 2

Cervid population estimates* and numbers slaughtered, Elk Island, north enclosure, 1959–66

Date	Wapiti		Moose		Mule deer and white-tailed deer		Source of data
	Pop.†	No. slaughtered	Pop.	No. slaughtered	Pop.	No. slaughtered	
Oct. 1959	640		220		10		Computed
Dec. 1959		410		141		0	
Feb. 1960	230		80		10		Flook (1960)
Nov. 1960	270		120		70		Computed
Dec. 1960		106		24		0	
Feb. 1961	160		100		70		Lovaas (1961)
Dec. 1961	230		150		100		Blood (1962)
Nov. 1963	330		260		70		Computed
Dec. 1963		87		87		0	
Jan. 1964	240		170		70		Blood (1964)
Jan. 1966	280		330		40		Blood (1966)

*Computed population estimates determined by adding the number removed in subsequent slaughter and post-slaughter count.

†Population estimates rounded to nearest 10.

Appendix 3

Park wardens' counts of wapiti in Jasper, 1959–66

Year	Number of wapiti by drainage		
	Athabasca	Brazeau	Total
1959 (Nov.)	1040	?	?
1960 (Dec.)	770	130	900
1965 (Oct.–Nov.)	1600	190	1790
1966 (Oct.–Nov.)	1630	100	1730

Appendix 4
Park wardens' counts* of wapiti in Banff,
1962-66

Year	Number of wapiti by valley			Total
	Bow	Cascade, Panther, and Red Deer	Other valleys	
1962	410	940	250	1600
1963	610	1120	400	2130
1964	360	1010	240	1610
1965	250	1000	190	1440
1966	260	590	280	1130

*Counts conducted in one-week period in late
September and early October.

Appendix 5
Park wardens' late-winter counts of wapiti
in Waterton Lakes, 1953-67

Year	No. of wapiti
1953-54	830
1954-55	1030
1955-56	1200
1956-57	1000
1960-61	650
1961-62	930
1964-65	680
1965-66	550
1966-67	690

Appendix 6
Numbers of wapiti of each sex removed
from Elk Island, March 1947 to January
1958, and method of removal

Sex	Method of removal	Year of removal*										Total
		1948-49	1949-50	1950-51	1951-52	1952-53	1953-54	1954-55	1955-56	1956-57	1957-58	
Male	Slaughter	155	12	1	37	36	—	127	76	130	143	717
	Capture	14	22	3	5	—	18	—	26	—	—	88
	Total	169	34	4	42	36	18	127	102	130	143	805
Female	Slaughter	97	1	2	6	75	—	74	—	168	141	564
	Capture	43	26	28	15	—	101	—	84	—	—	297
	Total	140	27	30	21	75	101	74	84	168	141	861
Not specified	Slaughter	—	—	—	—	—	—	4	—	6	3	13
	Capture	—	—	—	—	—	—	—	—	3	—	3
	Total	—	—	—	—	—	—	4	—	9	3	16
Both sexes	Total	309	61	34	63	111	119	205	186	307	287	1682

*Year measured from June 1 to May 31.

Appendix 7

Numbers of wapiti removed* from Jasper from 1942† to February 1957

Period	Number	Period	Number
1942-43	127	1948-49	103
1944-45	250	1952-53	78
1945-46	197	1953-54	60
1946-47	375	1954-55	137
1947-48	219	1956-57	152

*Shot in winter.

†First removal for population control.

Appendix 8

Numbers of wapiti of each age group and sex removed* from Banff from 1944† to February 1957

Year	Valleys hunted	<1 year		≥1 year		Total
		Male	Female	Male	Female	
1944-45	Bow	4	20	41	135	200
1945-46	Bow	30	25	80	217	352
1946-47	Bow	36	23	74	176	309
1947-48	Bow	22	18	33	181	254
1948-49	Bow and Cascade	5	12	8	78	103
1949-50	Bow and Cascade	16	22	41	191	270
1950-51	Bow and Cascade	10	6	46	81	143
1951-52	Bow and Cascade	8	5	20	69	102
1953-54	Bow	5	2	13	33	53
1954-55	Bow	—	—	—	7	7
1955-56	Bow	—	—	5	5	10
Total		136	133	361	1173	1803

*Shot in winter. In all years except 1954-55 and 1955-56 animals were shot without deliberate selection.

†First removal for population control.

Appendix 9

Numbers of wapiti of each age group and sex removed* from Waterton Lakes up to February 1957

Year	<1 year		≥1 year		Total
	Male	Female	Male	Female	
1947-48‡	14	11	17	44	87†
1948-49	4	1	13	15	33
1957-58	?	?	?	?	97

*Shot in winter without deliberate selection.

†Includes one specimen of unidentified sex.

‡First removal for population control.

Appendix 10

Wapiti of each year class and sex removed*
from Elk Island, 1958-63

Year class	Period of removal									
	Dec. 1958		Nov. 1959- Jan. 1960		Dec. 1960		Dec. 1963		Total	
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
1963							10	6	10	6
1962							8	8	8	8
1961							7	7	7	7
1960					4	13	4	8	8	21
1959			33	36	18	18	1	2	52	56
1958	2	15	44	30	3	7	4	5	53	57
1957	7	13	32	38	6	9	2	1	47	61
1956	19	11	20	50				2		
1955	10	11					1	1		
1954							1	4		
1953								2		
1952								1		
1951								1		
1950										
1949								1		
Older†	14	43	7	98	2	20				
?‡	15	12	11	11	1	5			27	28
Total	67	105	147	263	34	72	38	49	286	489

*Shot without deliberate selection.

†Age ≥ 4 years when slaughtered, but not determined to year.

‡Age not known, but carcass weight indicated age ≥ 1 year.

Appendix 11

Numbers of wapiti of each year class and sex removed* from Jasper, December 1957 to January 1967

Year class	Period of removal							
	Dec. 1957– Jan. 1958		Dec. 1963– Jan. 1964		Nov. 1966– Jan. 1967		Total	
	Male	Female	Male	Female	Male	Female	Male	Female
1966					10	14	10	14
1965					22	10	22	10
1964					7	11	7	11
1963			9	19	7	18	16	37
1962			15	16	3	20	18	36
1961			5	21	5	12	10	33
1960			9	22	3	11	12	33
1959			2	12	2	4	4	16
1958			4	10		10	4	20
1957	2	7	3	15		8	5	30
1956	11	7	3	9		3	14	19
1955	4	9	1	5		2	5	16
1954	3	3	2	9	1	4	6	16
1953			1	3		1		
1952				1		2		
1951						1		
1950			1					
1949				1				
1948				1				
1947								
1946				1				
Older†	9	22						
Total	29	48	55	145	60	131	144	324

*Shot without deliberate selection.

†Age ≥ 4 years when slaughtered, but not determined to year.

Appendix 12

Numbers of wapiti of each year class and sex removed from Cascade and Red Deer drainages, * Banff, 1960-66

Year class	Period of removal																												Total	
	Dec. '60- Jan. '61†		July '61- May '62‡		Nov. '61- Jan. '62†		June- Oct. '62‡		Dec. '62- Jan. '63†		Dec. '62§		Dec. '63- Jan. '64†		Dec. '63§		Dec. '64- Jan. '65†		Dec. '64§		Aug.- Oct. '65‡		Nov.- Dec. '65†		Nov.- Dec. '66†					
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀		
1966																										7	1	7	1	
65																					1		1	1	2	1		2	4	
64																	6	4	4	5			1	1			3	11	13	
63													1		1	1	2	3	6	5						1	5	11	14	
62												13	16			1	1	3	9					1	3	1	21	28		
61				1		1	2	2	2		9	10		1		1	3	11			1	1	1			1	17	29		
60	2	2	7	5			7	2		1		6			1	1	1	3					3	1		2	1	21	24	
59	2	1	4	3	2		1			1					3	1	6						2	2			4	13	20	
58		5	1	1	1					1		4	1	1			2	4			1			5			1	7	20	
57		5		3		2	1			1	2		4		1			6						3			1	2	27	
56		1	3	1	1		1	1			1	7	1	1			1	5						4			2	8	22	
55		2	1	1	1	1						7					1	6			1			2			1	4	20	
54		1		1		2						1	1	1				2									1	1	9	
53	1			1						1		6		1			2	2			2			2			1	3	16	
52		4	1	1				1				3					2	3							1			1	15	
51	2	4	1									3															1	3	8	
50		↑		1								1																		
49						1				1				1			1								1					
48		8				1																			2					
47						1						2																		
46												3				1									1					
45		↓										1				1														
44		↑						1				2																0	34	
43				1																										
42		1¶																												
41								1																						
40																														
39		↓																												
?**	1	1		1		1												8						3	10	1	9		5	30
Total	8	35	18	21	5	10	12	8	5	5	23	76	4	7	3	13	20	65	10	18	4	2	5	40	8	11	12	23	137	334

*Includes Panther Valley and Ya Ha Tinda Ranch.

†Shot without deliberate selection.

‡Shot selectively for research collection.

§Trapped without deliberate selection.

||Born between 1945 and 1950.

¶Born between 1939 and 1944.

**Age not known, body size indicated age ≥ 1 year.

Appendix 13

Numbers of wapiti of each year class and sex removed* from Bow Valley, Banff, 1957-66

Year class	Period of removal																				Total		
	Nov.-Dec. '57		Dec. '58-Jan. '59		Dec. '59-Jan. '60		Dec. '60-Jan. '61		Oct. '61		Nov. '61-Jan. '62		Dec. '62-Jan. '63		Dec. '63-Jan. '64		Dec. '64-Jan. '65		Nov. '65-Dec. '66		♂	♀	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	
1966																				3	1	3	1
65																				5	4	5	4
64																6	9			2	4	8	13
63														4	9	10	4				2	14	15
62												10	7	7	3	1	6			2	2	20	18
61											19	10	8	9	8	6	1	4			2	36	31
60							10	8	2		16	12	5	8	6	2	3			1	39	34	
59					27	17	13	18			6	21	4	9	3	2	1	1		1	54	69	
58			7	9	12	13	7	9			2	18	4	4	1	1	6				33	60	
57	4	5	6	9	9	31	4	16			5	12	7	1	2	1	2			1	37	78	
56	12	7	4	9	13	18	4	13			3	9	2	2	3	1	2			1	41	62	
55	4	7	0	4	18	25	3	16			2	10	3	1	2	2	4				32	69	
54	3	6			11	18	2	3			2	10		2	2		1			1			
53					4	15	1	1				5	1	1		2	1						
52					3	9	4	3			4	4	2			2							
51					6	10	1	3			1	4		1	1		1						
50					5	10	↑	↑				2		1		1	1						
49					↑	↑						1	1	1			3						
48							3	5				1		2		1	1						
47					1§	8§						2	4			1							
46													3		1								
45							↓	↓					1										
44					↓	↓		↑					1										
43					↑	↑							1										
42								2					1										
41					1¶	3¶																	
40								↓															
39																							
38					↓	↓																	
Older†	10	21	20	31																			
?‡	4	8			10	3	1	1				2	3	1	2							18	17
Total	37	54	37	62	120	180	53	98	2		64	133	48	52	39	34	18	49	1	12	20	431	682

*Shot. Animals collected October 15, 1961, and November 19, 1965, were selected as to sex and age. In slaughters of December 1964 to January 1965, and November to December 1966, shooting of bulls was avoided. In all other slaughters there was no deliberate selection.

†Age ≥4 years when slaughtered, but not determined to year.
‡Age not known, but carcass weight indicated age ≥1 year.
§Born between 1945 and 1950.
¶Born between 1939 and 1944.

Appendix 14

Numbers of wapiti of each year class and sex removed* from Waterton Lakes, November 1958 to February 1963

Year class	Period of removal						Total	
	Nov. 1958– March 1959		Nov. 1959– Jan. 1960		Dec. 1962– Feb. 1963			
	Male	Female	Male	Female	Male	Female	Male	Female
1962					11	12	11	12
1961					10	15	10	15
1960					1	13	1	13
1959			14	23	2	8	16	31
1958	7	14	19	13	1	6	27	33
1957	35	7	3	13	2	9	40	29
1956	19	10	5	13		11	24	34
1955	5	22				3		
1954						3		
1953					1	2		
1952						4		
1951						2		
1950							46	130
1949						2		
1948								
1947						1		
Older†	29	40	11	51				
?‡	6	1	1	1		3	7	5
Total	101	94	53	114	28	94	182	302

*Taken without deliberate selection, by shooting and trapping.

†Age ≥ 4 years when slaughtered, but not determined to year.

‡Age not known but carcass measurements indicated age ≥ 1 year.

Cette étude a été entreprise pour déterminer les causes du déséquilibre relevé chez les wapitis (*Cervus canadensis*) des parcs nationaux de l'Ouest canadien et qui a été signalé ailleurs, en ce qui a trait au rapport des sexes, rapport qui favoriserait les femelles.

Dans les parcs des montagnes, le rapport des sexes chez les wapitis adultes dénombrés en octobre et en novembre, exception faite des veaux, était de 37 mâles pour 100 femelles. Cependant, comme la répartition des femelles coïncidait plus étroitement avec les régions peu élevées, plus facilement accessibles aux observateurs que celles des mâles, les données recueillies dans ces régions au sujet du rapport des sexes sembleraient favoriser les femelles. Des données plus sûres ont été obtenues dans un enclos de 50 milles carrés au sol uniformément peu élevé, situé dans le parc national d'Elk Island, où les wapitis ont été abattus à un taux moyen d'environ 21 p. 100 au cours d'une période de 19 ans. Durant cette période, le rapport des sexes chez les bêtes abattues, calculé à partir de la somme du nombre total des bêtes abattues et des fluctuations nettes du nombre de bêtes du troupeau, était de 85 mâles pour 100 femelles.

D'après un relevé hivernal des nouveaux-nés de tous les parcs, le rapport des sexes est de 113 mâles pour 100 femelles, et jusqu'à l'âge de un an et demi les mâles ne semblent pas beaucoup plus touchés par la mortalité que les femelles. Le dénombrement des bêtes abattues par les gardiens de parcs, qui avaient été chargés de les tuer sans faire de distinction entre les sexes, a révélé une diminution sensible du nombre de mâles âgés de un an et demi à deux ans et demi aux niveaux peu élevés des parcs de montagne. Il semblerait que cette diminution soit due à une dispersion vers d'autres régions. D'autre part, il est fort probable que cette dispersion, en conduisant certains mâles dans des milieux qui leur sont défavorables, contribue à élever leur taux de mortalité. On attribue aussi à une mortalité plus élevée la baisse sensible du nombre de mâles âgés de plus de 7 ans, baisse qui se

poursuit jusqu'à 14 ans, âge des plus vieux mâles abattus. Au contraire, le nombre de femelles dans les groupes d'âge successifs diminue moins rapidement, la plus vieille bête examinée étant âgée de 21 ans.

On a constaté que la croissance des mâles est plus rapide en valeur absolue et se poursuit durant environ un an de plus que pour les femelles. Dans trois des quatre parcs, l'usure des dents était plus rapide chez les mâles; il est donc possible que ceux-ci souffrent d'un désavantage durant leur jeune âge. Ces constatations supposent que les mâles, tout en jouissant d'une capacité supérieure d'absorption, ont besoin d'un surplus d'alimentation.

La comparaison pondérale des glandes surrénales et l'examen quantitatif des glomérules des deux sexes n'indiquent nullement que, en période du rut, les mâles sont sujets à une plus grande tension que les femelles. Cependant, l'infiltration de graisse dans le foie et la résorption des dépôts adipeux autour des reins indiquent que, durant le rut, les mâles adultes, contrairement aux femelles, perdent rapidement leur réserve de graisse. Le fait est encore plus évident chez les mâles de plus de 7 ans, groupe d'âge où se manifeste apparemment la plus grande activité reproductrice. Les mâles adultes, surtout ceux qui ont plus de 7 ans, doivent affronter l'hiver, saison durant laquelle l'équilibre d'énergie est parfois menacé, avec une réserve de graisse plus faible que celle des femelles et, par conséquent, épuisent cette réserve plus vite que les femelles. C'est pourquoi les mâles, surtout les plus âgés, sont plus vulnérables que les femelles et risquent de mourir vers la fin de l'hiver et au printemps, le plus souvent d'une insuffisance d'énergie.

Deux facteurs contribuent au déséquilibre du rapport des sexes que l'on observe chez les wapitis des parcs: premièrement, une différence de répartition des sexes, chose attribuable à la dispersion des mâles; deuxièmement, une mortalité naturelle à un âge moins avancé chez les mâles que chez les femelles, ce dont témoignent les données recueillies au parc national d'Elk Island.

La suppression des mâles dans les centres de peuplement par ces deux agents naturels a pour effet de laisser davantage de nourriture aux femelles et aux jeunes. C'est là, croit-on, une des raisons pour lesquelles les wapitis peuvent maintenir un taux élevé de peuplement. L'importance que pourrait prendre ce phénomène lorsqu'il s'agit d'autres espèces d'ongulés mérite qu'on lui accorde plus d'attention, car il contribue à la capacité d'une espèce de se propager et d'élargir son aire de répartition.

