Notes on the Black Bear, *Ursus americanus* Pallas, in Alaska, with particular Reference to Dentition and Growth

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I. Introduction

Incidental to other studies, I have been able to collect data and materials relating to the natural history and taxonomy of bears in Alaska since 1949. One purpose of this work has been to define criteria that would permit the determination of age in individual animals, or, at least, the delimitation of age classes. The black bear, *Ursus americanus* Pallas, is the subject of this initial study.

The annual cycle of the black bear is strongly influenced by climatic factors, with the period of denning (fasting) attaining its maximum duration in regions having comparatively long and severe winters. Even at lower latitudes, the Winterruhe of the black bear was regarded by Eisentraut (1956) as being remarkably long, but in south-central Alaska these animals typically remain in the dens for about half of each 12-month period. It will be shown in the present paper that little growth takes place during the time spent in the den, and the age classes defined herein have been related largely to the pattern of intermittent growth characteristic of the black bear at this latitude.

In addition to findings relating to dentition and growth, some data on other aspects of the natural history of the black bear in Alaska are presented in this report.

II. Materials and Methods

The animals utilized for this study originated within a relatively restricted area of Alaska (Fig. 1). Skulls, and sometimes other materials, were obtained from 219 animals; of these, 183 were wild individuals, and 36 were captives of known age. Entire bears were weighed and measured. Whenever possible, the skull, a femur and a humerus, the genital organs, and sometimes other materials, were collected from each animal. Bones were cleaned by means of dermestid beetles and bleached in hydrogen peroxide. After cleaning, the penile bones were dried thoroughly before being weighed and measured. The soft tissues were preserved in 10 per cent formalin. Sections of testes and ovaries were prepared by the paraffin method and stained in hematoxylin-eosin. Special techniques were applied in a few cases, as described below.

Routinely, the right upper canine was removed from the skulls and stored in fluid. The teeth from older animals were sawed longitudinally by passing the blade directly through the center of the pulp cavity, and the surfaces so exposed were polished to intensify detail. Thin sections were prepared in some cases. The canines from young animals were usually studied uncut.

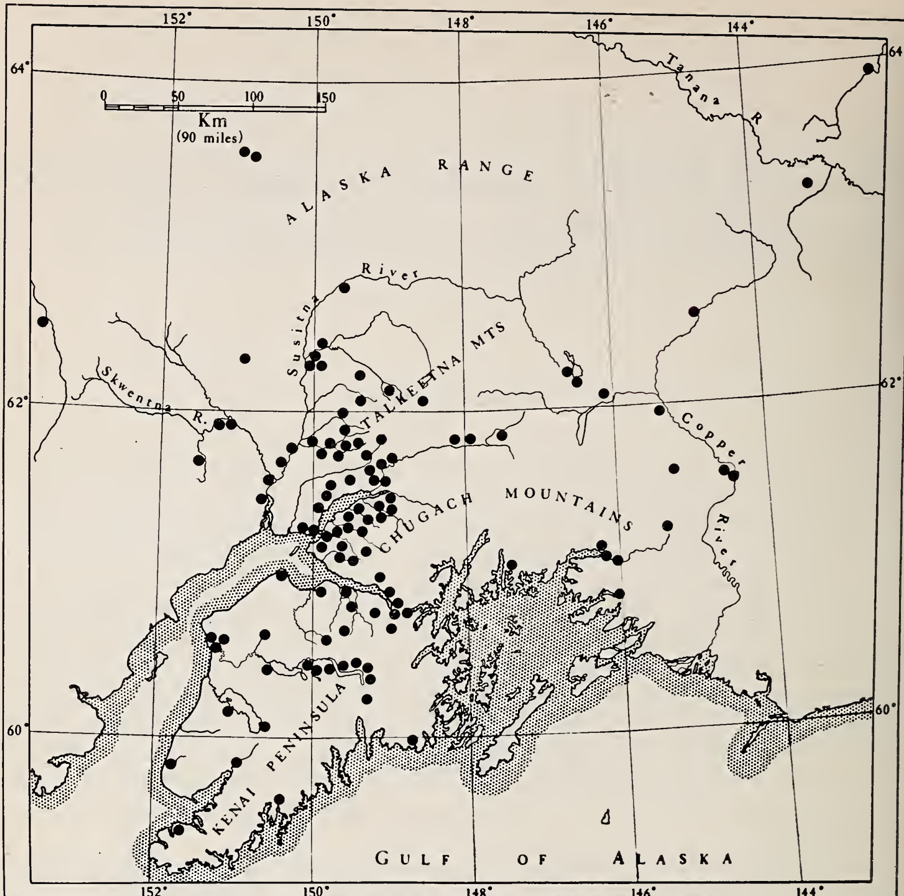


Figure 1. Map of south-central Alaska, showing locations from which black bears were obtained

In the following description of dentition, the deciduous and permanent teeth are represented by lower-case and capital letters, respectively. The deciduous post-canine teeth are designated premolars in this report. All data on the eruption of teeth are based on cleaned skulls. The stated ages of bears are approximate, based on an assumed birth date of February 1.

III. The Deciduous Dentition

The formula for the deciduous dentition of the black bear is $i^3/_3$ $c^1/_1$ $p^3/_3$. The first incisor, both above and below, is very small and weakly developed. The canines are well developed and persist longer than any of the other deciduous teeth. Both p^1 and p_1 are lacking; p^2 and p_2 resemble their permanent successors in form. Although it has only two roots, p^3 is rather similar to P^4 in the form of its crown; p^4 has three roots, and its crown somewhat resembles that of M^1. The p_3 is quite small, but possesses two roots and is rather similar to P_4 in the shape of its crown; p_4 likewise has two

Figure 2. Complete deciduous dentition in a 4-month-old black bear (female, killed May 25). The crown of P_1 is almost fully erupted, and the tip of P^1 is visible

roots, and in form it most closely resembles M_1. The fully erupted deciduous teeth are shown in Fig. 2.

The deciduous dentition is complete by the time, usually in the last part of April, the young bear leaves the den in which it was born. Because of the difficulty in locating dens containing female bears with young, I have been unable to determine the sequence of eruption of the deciduous teeth. The youngest animal available was a captive-born bear about 22 days old, a male, with a condylobasal length of 60 mm. The skull was removed and radiographed, after which it was stained with alizarine red S, dehydrated in ethanol, cleared in terpineol, and dissected.

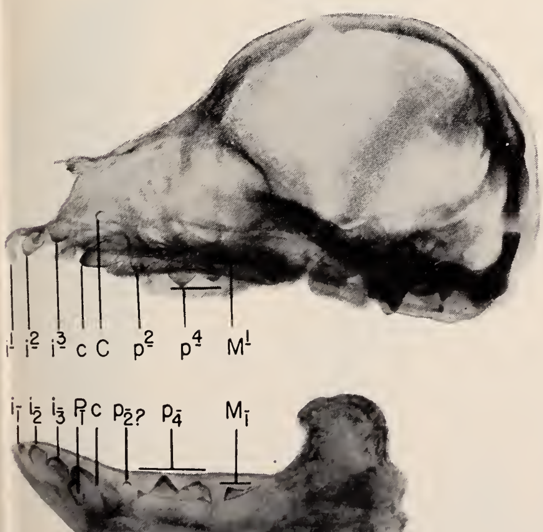


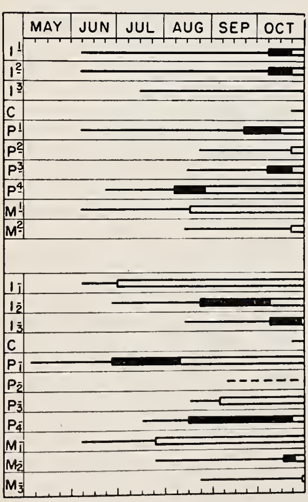
Figure 3. Retouched radiograph of the skull of a 3-week-old male bear, showing dentition

None of the deciduous teeth had erupted in this specimen, but the tip of i^1 barely protruded through the gingival tissue. The tip of i^2 lay just below the surface; i^3 was incompletely developed and still lay deep in the alveolus. The conical upper canines, 4 mm long, were likewise deeply situated. The permanent upper canines were represented by minute cones at the proximal end of their alveoli dorsal to the deciduous canines. The crown of the tooth tentatively identified as p^2 or p^3 was well developed but had not begun to erupt. The crown of p^4, easily recognized, had not emerged above the level of the alveolar margins. Two small cones of M^1 were present posterodorsal to p^4. The tips of both i_1 and i_2 were quite near the gingival surface; i_3 was comparatively undeveloped and deeply situated. In form, size, and position, the lower deciduous canines were much like the upper ones. The crown of P_1 was well formed and situated medial to the deciduous canine; no trace of the permanent lower canine was found. Neither p_2 nor p_3 could be located, but the crown of p_4 was well developed though still below the level of the alveolar margins. A single cone of M_1 was identified. The relationships of these teeth are shown in Fig. 3.

All other animals with deciduous dentition were obtained after they had emerged spontaneously from the dens. Assuming a birth date of February 1, the youngest of these, a male, was about 3 months old when killed on May 4; the complete deciduous dentition was present, and P_1 was erupting. The crowns of M_1 and M_2, as well as that of M_1, were visible through their open alveoli. The permanent canines at this stage measured about 11 mm long. A female killed on May 25, when about 4 months old, possessed a dentition similar to that of the male. Some of the deciduous teeth, particularly p^2 and p_2, may persist in adult animals when their permanent successors are lacking. In such cases, they usually remain buried in the gingival tissue. The deciduous canines often become worn before they are lost.

IV. The Permanent Dentition

The permanent dentition is represented by the formula $I^3/_3$ $C^1/_1$ $P^4/_4$ $M^2/_3$. The sequence of eruption of the permanent teeth is approximately the same in the black



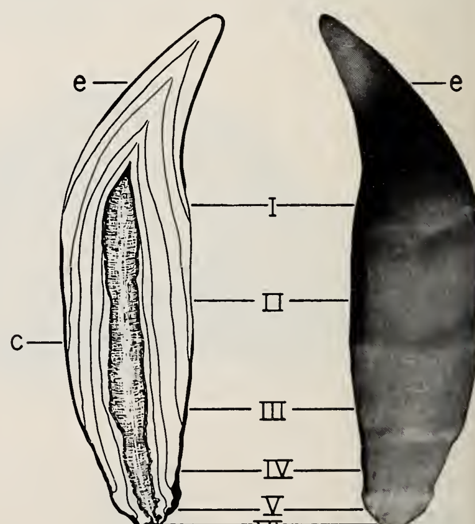


Figure 4. Eruption of the permanent teeth during the first summer of life. The heavy line indicates the period during which eruption is taking place; the solid bar indicates the period during which teeth may or may not be fully erupted; all are fully erupted thereafter, as indicated by open bar. (Based on 31 skulls.)

Figure 5. Externally visible growth zones and the pattern of dentin layers in the canine of a black bear of age class VI; cementum is indicated by „c," and enamel by „e."

bear as has been described by Pohle (1923) for the brown bear, *U. arctos* Linnaeus, and the polar bear, *U. maritimus* Phipps.

The eruption of the permanent teeth begins late in the third month of life, when the crown of P_1 first appears, and usually all but I^3, the canines, and sometimes M_3 are in place by the end of the 9th month (October); by this time the animals have already entered the dens. The sequence of eruption of the permanent teeth during the first summer is shown in Fig. 4. Both I^3 and M_3 may be in place by the time the animals emerge the following spring, although no observations were made prior to the first of June (17th month).

The roots are usually closed in P^4, M^1, I_2, and sometimes in P_4, at the end of the 9th month (October). All of the permanent teeth but I^3 and the canines have closed roots when the animals emerge from the dens in the third spring (ca. 28th month). The apex of the root of I^3 is still open in the fall of the third summer of life, but is closed in the 4th spring.

The crowns of the upper and lower canines are fully formed within the alveoli by the end of the 9th month, but the growth of their roots proceeds slowly and it is not until the 4th summer that their dentino-enamel junctions emerge beyond the alveolar margins. Complete eruption of the canines is attained in the 5th summer, and the apices of their roots usually close in the 6th summer.

An unusual combination of characteristics was observed in one specimen, a wild male killed on June 4. In dimensions (condylobasal length, 150 mm; zygomatic width, 89 mm) and conformation, the skull was typical of those from bears killed in their first spring, at an age of about 4 months. The dentition, however, was indistinguishable from that of animals a year older, at an age of about 16 months. There was no evident explanation for this anomalous development.

The pattern of intermittent growth characteristic of the black bear in south-central Alaska is reflected in the dentition. The teeth that develop slowly (i. e., I^3 and the canines) show annulations resembling those described by Scheffer (1950) in the canines of the fur seal, *Callorhinus ursinus* (Linnaeus). In the teeth of the bears, these annulations demarcate

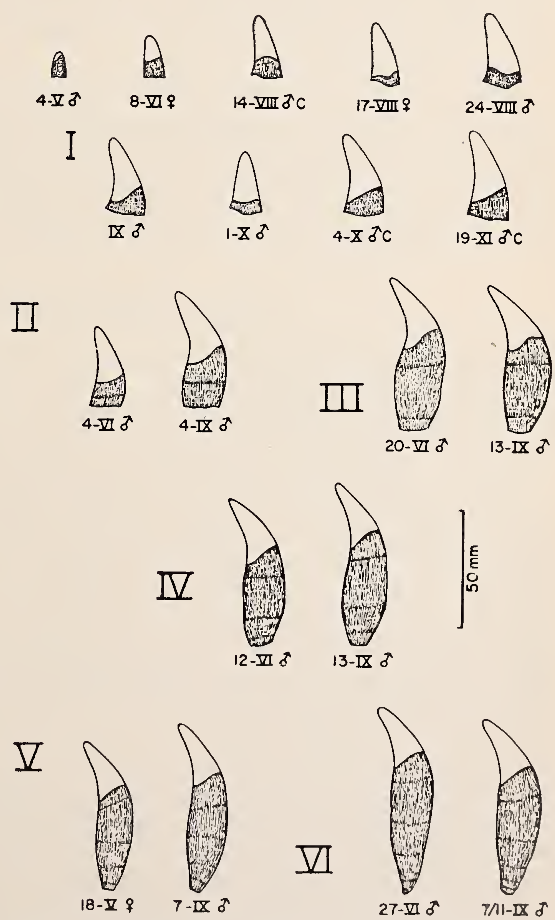


Figure 6. Development of the right upper canine of the black bear, correlated with age classes I–VI

comparatively broad zones of dentin that represent successive seasons of growth. Since I^3 attains complete development prior to the beginning of the 4th summer, it exhibits only three growth zones. The canines grow through at least 6 summers and usually exhibit 6 externally visible growth zones (Fig. 5). The sequential pattern of the layers of dentin is best seen in longitudinal sections (Fig. 5). These annulations provide the simplest means by which the younger bears can be segregated into age classes (Fig. 6). Of the 10 classes distinguished, as mentioned earlier, numbers I through VI correspond respectively to the first 6 summers of life. The changes in canines are described below.

The rate at which dentin is deposited changes inversely with age. At the end of the first summer, the crown of the canine is complete and a layer of dentin is present. The bulk of the root is produced during the second and third summers, after which the annual increment decreases progressively until the apex of the root closes. The following values, in terms of percentage of the greatest length of the complete upper canine, are representative of the relative proportions of the annual increments: first summer (including the crown), 41%; second summer, 20%; third summer, 17%; fourth summer, 13%; fifth summer, 6%; sixth summer, 3%. In general, the age of bears killed at any time during the first 6 years of life can be determined from the characteristics of the canines, but it is sometimes difficult to differentiate the last one or two growth zones.

After the 6th or 7th year, the wall of the root gradually thickens, particularly at the apex, as cementum accumulates externally and dentin is deposited in the pulp cavity. The cementum appears as alternating dark and light layers which may be correlated with age. These layers are often very difficult to count, and no attempt was made to utilize them in the present work. The maximum diameter of the pulp canal is not less than 2–3 mm in the oldest animals.

Variation in the numbers of teeth

The first three permanent premolars, above and below, are small in size and probably have little functional value. On the basis of data published by Hall (1928), Erdbrink (1953, p. 306) concluded that there is a tendency for the elimination of P^2 and P_2 in the black bear. This hypothesis is supported by the findings in the Alaskan material; in addition, the same tendency is exhibited to a lesser degree in P_3.

The permanent premolars were counted in 159 skulls, excluding others which had been damaged, cubs with incomplete permanent dentition, and aged animals in which secondary loss of teeth had occurred. Excepting P^4 and P_4, the permanent premolars are quite variable in size and position, and poorly developed teeth can be confused with persistent deciduous premolars. The latter and anomalous teeth of questionable identity were not included in the counts. Disregarding sex and differences between right and left sides, 29 different combinations of premolars were recorded (Table 1). The most frequent combination (28% of the specimens) was $\frac{1-3-4}{1-4}$; only 3 (2%) had all of the premolars present.

In reference to the long-muzzled species of bears, Colyer (1936, p. 367) stated that certain of the permanent premolars "... seldom persist through the whole life of the animal, the second tooth in the upper and the second and third in the lower being usually lost at an early stage of life." In the Alaskan material, no differences were noted in the frequency of missing premolars between first-year and older animals when aged individuals were excluded. My observations do not substantiate Colyer's opinion that the permanent premolars are lost more frequently than any of the other teeth.

Apart from the premolars, the incisors and M_3 were the only teeth found to vary in number in the specimens studied. The left I_3 was lacking in one animal, in which the left I_2 and the adjacent canine were in apposition. The rigth M_3 was absent in a female about 8 months old. Supernumerary third incisors were observed in two specimens. One, killed in August of the second summer, possessed an extra right I^3. The tip of the partially erupted right mandibular canine occluded with the latter, which had rotated outward through about 90^0. The long axis of this incisor had assumed a nearly horizontal position. Although only partially erupted, the supernumerary incisor was normal in size and form, while both the crown and root of the adjacent I^3 were malformed. The second animal, killed in September of its third year, had a supernumerary left I^3. In this case, the left mandibular canine occluded with both the normal and the supernumerary incisors; as a result, the tooth in normal position had rotated inward through about 45^0, and the eruption of the supernumerary tooth was retarded. Again, the tooth regarded as supernumerary had developed normally, but both the crown and the root of the I^3 in normal position were somewhat malformed. In both cases, however, the malformed teeth were clearly typical of third

Table 1

Combinations of permanent premolars and their frequencies in 159 skulls. The line separates upper and lower teeth. Whether left or right side is not considered

Combination	Number	%	Combination	Number	%
1 — 3 — 4 / 1 — 4	44	28	2 — 3 — 4 / 1 — 2 — 3 — 4 1 — 3 — 4	3	2
1 — 2 — 3 — 4 / 1 — 3 — 4	21	13	1 — 2 — 3 — 4 / 1 — 2 — 3 — 4	3	2
1 — 2 — 3 — 4 / 1 — 4	17	11	1 — 3 — 4 / 1 — 2 — 3 — 4 1 — 3 — 4	3	2
1 — 3 — 4 / 1 — 3 — 4	13	8	1 — 2 — 3 — 4 / 1 — 2 — 4	2	1.3
1 — 3 — 4 / 1 — 3 — 4 1 — 4	11	7	1 — 3 — 4 3 — 4 / 1 — 4	2	1.3
1 — 2 — 3 — 4 1 — 3 — 4 / 1 — 4	8	5	1 — 3 — 4 / 1 — 2 — 4 1 — 4	2	1.3
1 — 2 — 3 — 4 1 — 3 — 4 / 1 — 3 — 4	7	4	1 — 2 — 3 — 4 1 — 3 — 4 / 1 — 3 — 4 1 — 4	2	1.3
1 — 2 — 3 — 4 / 1 — 3 — 4 1 — 4	5	3	1 — 2 — 3 — 4 / 1 — 2 — 3 — 4 1 — 2 — 4	1	0.6
1 — 3 — 4 / 1 — 2 — 4	2	1.3	1 — 3 — 4 / 3 — 4	1	0.6
1 — 2 — 3 — 4 1 — 3 — 4 / 4	2	1.3	1 — 3 — 4 / 1	1	0.6
1 — 2 — 3 — 4 / 3 — 4	1	0.6	1 — 4 3 — 4 / 1 — 4	1	0.6
1 — 3 — 4 / 1 — 3 — 4 1 — 2 — 4	1	0.6	1 — 3 — 4 / 2 — 3 — 4 1 — 4	1	0.6
1 — 2 — 3 — 4 1 — 4 / 1 — 4	1	0.6	1 — 3 — 4 / 1 — 4 1	1	0.6
1 — 2 — 3 — 4 / 1 — 2 — 4 1 — 4	1	0.6	1 — 3 — 4 / 1 — 2 — 3 — 4 1 — 4	1	0.6
1 — 2 — 3 — 4 / 1 — 3 — 4 3 — 4	1	0.6			

incisors in size and form. The malocclusion resulting from the presence of such supernumerary teeth probably would later give rise to periodontal disease.

COLYER pointed out (1936, p. 368) that the mandibular incisors of bears are subject to some variation in position. This was rather striking in the black bears considered here, but there was no evidence that such variation had any functional significance. Almost no variation was noted in the position of the upper incisors or of the molars.

Wear of teeth

The amount of wear exhibited by the teeth of bears increases with age, but there is considerable individual variation within any given age group. In the Alaskan material, signs of attrition were first noted in the teeth of animals killed during the third summer of life. Although there was no evidence of wear in most animals, the tips of I^1, or of I^1 and I^2, were slightly worn in a few. Most of the bears killed during the 4th summer also had unworn teeth, but in some the amount of wear exceeded that observed in any of the third-year animals. There was considerable variation as to which incisors were involved; thus, only I^1 was worn in some, both I^1 and I^2 in others, and I^1, I_1, and I_2 in a few. In one case, small attrition facets were present on the paracone and metacone of M^1, and in another on the cusps of M_1.

In the 5th summer, about half the animals still had unworn teeth. Wear in others was still limited to the incisors, but in such cases the crowns of I^1 or of I^1 and I^2 were sometimes worn quite flat. Attrition of the incisors was unequal, with the superior teeth always showing more severe wear than their inferior counterparts. Attrition facets were bilaterally present on the paracone and metacone of M^1 in two animals, and on the metaconid of M_1 in another. A rather deep cavity was found in the right M_2 in one instance. By the 6th summer, attrition facets were more regularly present on the cusps of M^1 and M_1, and in one case M_2 was slightly worn. In some individuals, however, the teeth were still unworn, and slight wear was evident only on I^1 and I^2 in others.

Since I was unable to determine the absolute age of black bears after the 6th summer, the remaining specimens were segregated into four classes (VII–X) according to relative age. These age classes are considered here in connection with tooth wear, but will be characterized later in this report. In class VII, I^1 and I^2 always showed some wear, although it was slight in some individuals. In one case, the tip of I^3 was worn. The lower incisors were either unworn or only slightly worn at the tips. Attrition facets were often present on the major cusps of M_1 and M^1, but the wear was superficial. In class VIII, I_1 and I_2 were usually worn, often only slightly. The tips of I^3 and I_3 showed attrition facets in several cases. The major cusps of M^1 and M_1 were usually worn, but in most examples the attrition facets were small. Wear was evident also on M^2 and M_2, and in one instance on M_3. Both the protocone and tetracone of P^4 had attrition facets in one animal.

Class IX consisted of older animals, all of which showed considerable tooth wear. Severely worn incisors were common, and it was not unusual for I^1 and I^2 to be worn down to the gingival tissue at their posterior edges. The tips of I^3 were usually worn, sometimes down to the level of I^1 and I^2. The lower incisors were less severely worn in most cases. In most of the specimens, attrition facets were present on the paracone and metacone of M^1, and on the protoconid and hypoconid of M_1; a longitudinal groove, more or less obliterating the protocone and hypocone, was often present along the crown of M^1. The amount of wear on M^2 and M_2, and on M_3 varied considerably, but generally was slight. The cusps of P^4 had attrition facets in a few cases. Broken teeth were occasionally noted in this age class.

The animals comprising class X regularly possessed badly worn and broken teeth, often with signs of periodontal disease. Incisors were commonly lacking or had been broken and worn down to the level of the gingiva. Premolars, including P_4, had been broken in several cases, although their roots, or fragments thereof, usually remained. Broken canines, usually worn quite smooth, were not uncommon; some barely protruded above the gingiva. The molars exhibited a variety of conditions, with a wide range in the degree of wear. Many possessed extensive cavities, sometimes extending into the pulp cavities of the roots, and often only the smoothly worn roots remained. Occlusal drift was evident, particularly in the canines.

It is apparent that tooth wear is variable within a given age class. Since the rate of wear must depend largely upon the amount of abrasive material that is chewed, it might be expected to differ from region to region. It is possible that such wear would vary less within a given age class among animals subject to uniform conditions. The order in which the teeth become worn in the black bear is approximately the same as that described by KURTÉN (1958) for the cave bear, *U. spelaeus* Rosenmüller and Heinroth.

Sexual dimorphism

In the series studied, the skulls of adult males averaged larger than those of adult females, and a corresponding sexual dimorphism was observed in the dentition. The mean values obtained for the crown lengths of the molars differed significantly, but the amount of overlap was so great as to preclude the use of these measurements to determine the sex of individuals. Greatest length and transverse diameter were determined for the upper canines, one of which was removed from each skull. The transverse diameter was taken just proximal to, and parallel with, the dentino-enamel junction. Only fully formed, unworn canines from animals belonging to classes VII through IX were used; consequently, the available sample was small, consisting of only 42 teeth equally divided as to sex. In order to avoid excessive mutilation of the skulls, the lower canines were not removed. The measurements of the canines are summarized in Table 2.

It may be seen from the table that the observed ranges of the two dimensions from the upper canines show no overlap between the sexes. Assuming a normal distribution, the limits of variation expected in a sample of 1000 individuals can be determined by calculating the standard range.[1] Accordingly, the range of canine length is 63.2 to 82.8 mm for males, and 50.7 to 70.6 mm for females; the overlap between the sexes is thus about 7.5 mm. The standard range for the transverse diameter is 10 to 14 mm for males, and 8.3 to 11.3 mm for females, with an overlap of only 1.3 mm. However, extreme variants would be rare at best, and the majority of animals could be expected to have canines with near-average dimensions. The reliability of the two measurements in determining the sex of individual black bears can better be appraised by calculating the coefficient of difference[2], from which the percentage of joint overlap can be determined. For canine length, the coefficient of difference is 2.3, and the joint overlap is 1 %; thus, canine length would serve to distinguish 99 % of the males and 99 % of the females. In the case of the transverse diameter, the

[1] $SR = \bar{M} \pm 3.24\,\sigma$ (Simpson, 1941).

[2] $CD = \frac{\bar{M}\,♂ - \bar{M}\,♀}{\sigma\,♂ + \sigma\,♀}$ (Mayr et al., 1953)

Table 2

Measurements of right upper canines (in mm)

	Sex	N	Observed Range	$\overline{M}$	σ	SR
Length	♂	21	68.2—78.2	73.0	3.0	9.8
	♀	21	57.4—65.3	60.7	2.3	9.9
Transverse diameter	♂	21	10.8—13.3	12.0	0.6	2.0
	♀	21	8.9—10.4	9.8	0.5	1.5

coefficient of difference is 2.0, and the percentage of joint overlap is about 3, indicating slightly less value for this dimension in distinguishing sex.

Sexual dimorphism in the dentition of bears, particularly in the canines, has previously been recognized. Koby (1949) found that the mean transverse diameter of the canines differed significantly between the sexes in samples of cave bears and of brown bears. More recently, Kurtén (1955) studied the aforementioned species as well as the polar bear, and he found comparatively little joint overlap in the lower canines (9 % in Fennoscandian brown bears; about 2 % in polar bears from Greenland; less than 1 % in three series of cave bears). The upper canines in all showed a higher degree of joint overlap and therefore had less value in determining sex.

V. Growth

Growth in wild bears has been studied mainly from the skull, although supplementary data were collected from the available long bones (humeri and femora) and from penile bones. Skull size could be correlated with age through the 6th summer, but thereafter, in the absence of recognized criteria that would permit grouping by year, the skulls were segregated according to relative age. Age classes VII through X are characterized as follows:

Class VII. The roots of the canines are closed at the apex, but little cementum has been deposited. The skulls of the males appear immature, and the sagittal crest is little developed. According to the numbers of dentin layers, these animals had been killed during the 7th or 8th summers of life.

Class VIII. The canines have a thicker layer of cementum around the apex of the root. The basioccipital-basisphenoid suture is tightly closed but readily perceptible. The suture between the zygomatic processes is open, and the skull is still growing in both length and width. These animals probably had been killed during the 9th to 11th summers.

Class IX. The basioccipital-basisphenoid suture has been obliterated and the maximum length of the skull probably has been attained. The suture between the zygomatic processes is open or partially closed; the width of the skull is still increasing. The molars exhibit moderate wear in most cases. It is estimated that animals in this class had been killed from the 12th to perhaps the 20th summers.

Class X. These are aged animals approaching the time of death. The teeth are badly worn and broken, and periodontal disease is commonly evident. The cranial sutures are tightly closed, and, in the oldest individuals, many of the sutures may no longer be visible. Growth has ceased. Although the maximum age attained by wild black bears is unknown, the available information on longevity in captives suggests a life span of about 30 years.

Two dimensions, condylobasal length and zygomatic width, were used to indicate skull size. These measurements are summarized by age class in Table 3.

Sexual differences

Adult male black bears average larger than females, although here is considerable overlap in skull size (Table 3). The number of female skulls available was too small to permit a satisfactory comparison, but a significant difference in skull size (condylobasal length) was not evident prior to the 5th summer (age class V). Using mean length of male skulls in class IX as 100, females in classes V through IX averaged 8 to 11 % smaller than the males in corresponding groups. A significant, but slight, difference may exist between males and females in the ratio of condylobasal length to zygomatic width ($P = 0.06$).

Growth in the skull of male black bears is portrayed in Fig. 7. The annual increments in condylobasal length are comparatively large for each of the first three summers of life, but thereafter the rate of increase gradually decreases until final size is attained. (This trend is well confirmed when the data are plotted semi-logarithmically.) If the mean skull length for age class IX is taken as 100, it is found that the skull has attained about 90 % of its final length by the end of the 4th summer. The annual percentage increase in zygomatic width remains more or less uniform after the 5th summer; the skull continues to increase in width after the final length has been attained. The pattern of growth in the skull of the female is similar to that of the male; there is a comparable increase in zygomatic width in the older animals, although it is not as strongly defined as in the male. Length and width of the comparatively small sample of female skulls are plotted in Fig. 8.

Table 3

Skull measurements (in mm) of black bears summarized by age class

Age Class	Sex	N	Range Length	$\bar{M}$	σ	v	Range Width	$\bar{M}$	σ	v
I	♂	8	151—176	157	8.0	5.1	90—103	95	4.8	5.0
	♀	4	118—168	145	—	—	75—104	88	—	—
II	♂	5	150—205	188	—	—	89—121	109	—	—
	♀	2	194—203	198	—	—	114—121	117	—	—
III	♂	11	215—240	225	7.6	3.3	120—131	124	4.0	3.2
	♀	3	206—215	211	—	—	121—124	122	—	—
IV	♂	5	228—246	234	—	—	124—137	131	—	—
	♀	3	222—238	228	—	—	121—139	129	—	—
V	♂	10	225—273	247	4.8	1.9	124—172	141	4.0	2.9
	♀	9	216—240	225	8.9	3.9	118—148	128	8.4	6.5
VI	♂	8	239—262	253	8.3	3.2	135—156	144	5.0	3.5
	♀	2	223—227	225	—	—	126—130	128	—	—
VII	♂	6	254—274	259	6.8	2.6	144—160	152	5.6	3.6
	♀	8	222—249	238	8.0	3.3	127—142	136	5.0	3.6
VIII	♂	11	249—275	265	8.5	3.1	153—170	161	4.8	3.0
	♀	5	222—243	236	—	—	127—144	140	—	—
IX	♂	36	233—297	269	12.6	4.6	141—181	169	10.2	6.0
	♀	16	223—256	241	8.4	3.4	140—153	148	4.6	3.1
X	♂	10	253—283	269	9.4	3.5	165—184	177	5.6	3.1
	♀	3	237—252	245	—	—	150—156	153	—	—

Growth in long bones

Femora and humeri were obtained from only 12 wild bears, but enough age classes were represented to provide limited information on growth changes.

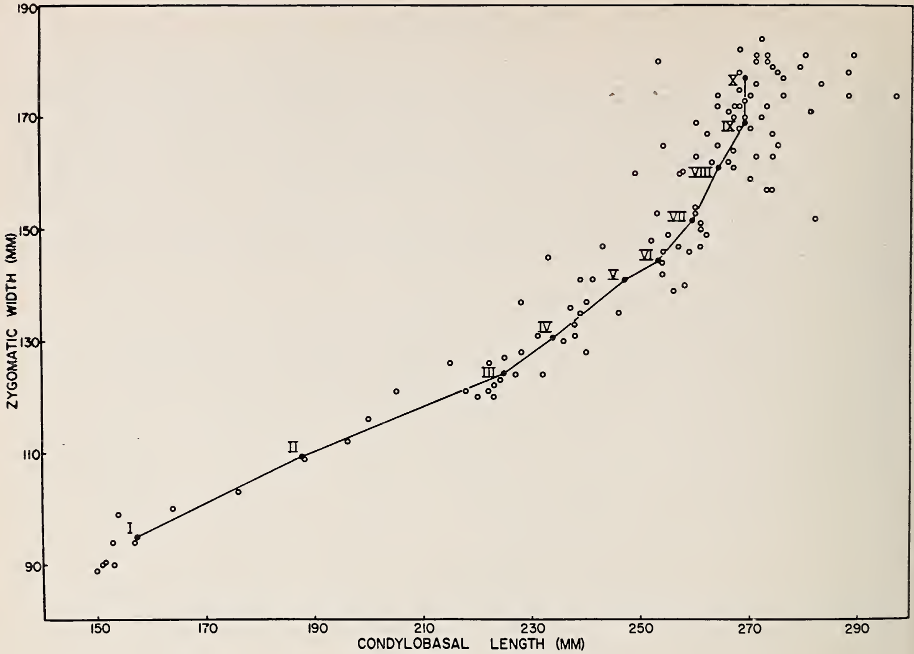


Figure 7. Skull growth in the male black bear (110 wild individuals). The line connects the mean values of the age classes

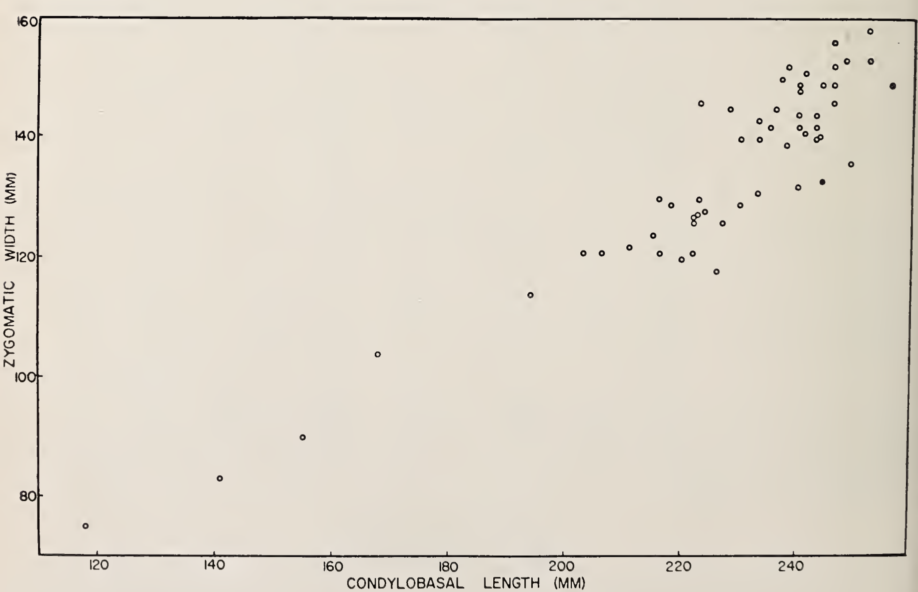


Figure 8. Skull growth in the female black bear (55 wild individuals)

The proximal end of the femur ossifies from two centers, of which one is for the caput femoris and the other for the trochanter major. The trochanter minor and the distal end of the femur each ossify from a single center.

Femora were obtained from three female bears killed during the first summer (age class I). In the youngest, killed on June 6, the caput consisted of an easily separable, round disc. The trochanter major was less advanced in development and consisted of a nodule of bone measuring only 10 mm in greatest diameter. The distal end was more fully developed but widely separated from the shaft. The femur was longer and more massive in an animal killed on August 17; the trochanter major had advanced in development, although the trochanteric fossa was still perforate. The caput was larger, but still widely separated from the shaft. The femur of the third animal, killed on October 31, was intermediate in size and development between the aforementioned. This animal probably had lost its mother and had been undernourished; this could account also for its not having denned.

In the femur of a male killed on August 28 of the second summer (age class II), the elements of the proximal end were more fully developed, the shaft was longer and heavier, the trochanteric fossa was perforate, and the distal end was separated from the shaft by a space of about 2 mm. Class III was not represented. The femur of a male of class IV, killed on May 2, was available. The main body of the caput was fully formed but still widely separated from the shaft. The trochanter major was almost fully formed; the shaft had increased in length and diameter, and the space separating the distal end was narrower than that in the class II specimen. Class V also was not represented. Femora were available from two males of class VI. In the first, from an animal killed on March 3, the caput appeared to be fully developed, although its margins were separated from the shaft by a well defined space. The trochanter major had largely fused with the shaft, particularly on the anterior face. The distal end was easily separable from the shaft, and the intervening space was well defined. The trochanter minor was still discrete. The second specimen, from an animal killed later in the summer, was longer but otherwise was essentially the same.

Material for class VII was lacking. Class VIII was represented by a single femur from a female bear killed in August. It differed little from those described for class VI in state of development, except that the spaces between the ends and the shaft had narrowed. The trochanter minor had not yet fused. This bone was relatively short and light, reflecting the smaller size of the females. Five femora were available for class IX; of these, two from females represented the younger component of this group. In one, the proximal end appeared to be completely fused with the shaft, but a narrow space persisted at the distal end. When the bone was sawed longitudinally, it was found that the trochanter major had fused completely, with growth continuing both in the caput and in the distal end; fusion had occurred between the trochanter minor and the shaft. The second animal was somewhat older, and growth was continuing in the caput. In the remaining femora, from males, both ends had fused completely.

The proximal end of the humerus ossifies from a single center. At the distal end is a center each for the median condyle, the median epicondyle, the lateral condyle, and the lateral epicondyle. By the 4th summer, the centers of ossification of the condyles become confluent and are no longer distinguishable, while those forming the epicondyles retain their identity for a longer time. In specimens representing class VI, the caput humeri had attained approximate adult size but was so poorly attached as to be easily removable from the shaft. The distal end was more advanced in development and, with the exception of the median epicondyle, the components had largely fused. The female specimen representing class VIII was similar, but the space around the margins of the caput had narrowed considerably. With the exception of the median epicondyle, the distal end had fused with the shaft to such an extent that no seam was visible. In the younger female specimens in class IX, a space of about 1 mm in width persisted at the margins of the caput, and it was evident that growth was continuing. The distal ends were completely fused, however. Both ends had fused with the shaft in the case of the males in class IX.

The age at which growth ceases in the long bones could not be accurately determined, but this presumably does not occur prior to about the 12th year. Growth may continue somewhat longer in the humerus than in the femur.

VI. Growth in Captive Bears

Thirty-six bears, most of which had been captured during the 4th and 5th months of life, were maintained in outdoor enclosures for periods of time ranging from a few months to about 10 years. Of three of these animals that denned regularly, two seemed comparable in this respect to wild bears. One other denned intermittently, but the majority remained active throughout the year. The latter exhibited a pattern of growth strikingly different from that of wild bears.

In south-central Alaska, wild bears usually enter the dens before the middle of October. In fact, of the specimens included in the present study, the only representatives of the younger age classes killed after September 30 were first-year animals that probably had lost their mothers and were incapable of denning alone. It appears that denning usually begins not later than the period between the middle of September and the first of October. The physiological changes that take place in the black bear during this time have been little investigated. Kalabukhov (1956) indicated that body temperature does not drop, and Eisentraut (1956) mentioned only that denning is regulated by intrinsic factors and does not result from a lack of food. Hock

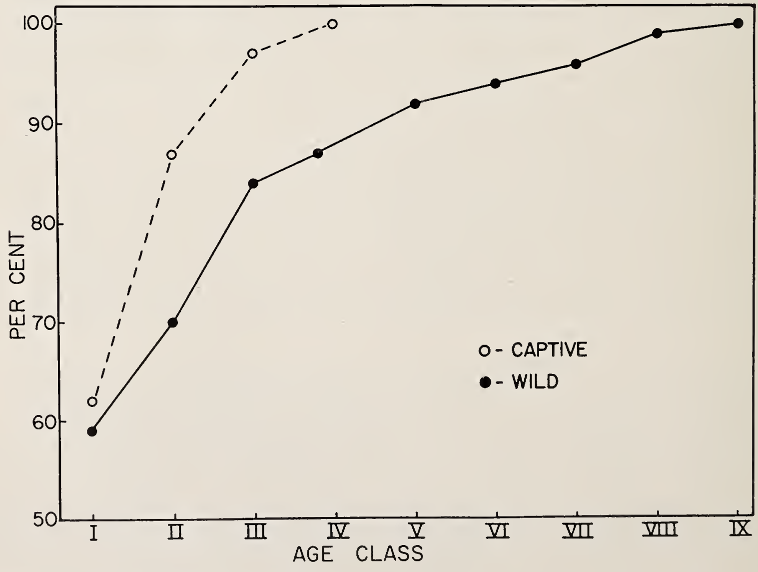


Figure 9. A comparison of mean skull size in captive and wild black bears, by age class

Table 4

Comparative growth of captive bears. Two animals indicated (*) denned regularly

Age Class	Number	Age[1]	State of development compared with wild bears	Equivalent age class of wild bears
I	6 males, 8 females	4 to 9 months	Skull averages somewhat larger than in wild specimens of class I.	I
II	3 males, 3 females	15 to 20 months	Mean condylobasal length of males falls between class III and class IV; root of upper canine equal in development to class III; development of femur approaches class IV.	III
III	2 males[2], 1 female	27 to 33 months	Canines fully erupted; root of upper canine equal in development to class V or VI; basioccipital-basisphenoid suture closed; development of femur like that of class VI.	VI
IV	3 males	40 to 43 months	Mean condylobasal length of males equal to that of class IX; development of femur equal to that in class VII—VIII; basioccipital-basisphenoid suture closed but well defined; root of upper canine closed, similar to condition in class VII.	VII
V	1 male	4 years, 1 month	Basioccipital-basisphenoid suture closed; still visible; development of femur comparable to that of class VIII—IX; root of canine with cementum layer comparable to that in class VIII.	VIII
	1 female	4 years, $2^1/_2$ months		
VI	None			
VII	1 male*	7 years, $2^1/_2$ months	Basioccipital-basisphenoid suture obliterated; thick cementum layer over root of canine; ends of femur completely fused with shaft.	IX
VIII	1 male	8 years, 2 months	Similar to foregoing.	IX
	1 female*	10 years, 5 months		

[1] Assuming a birth date of February 1. – [2]A male killed on January 14 not included. Also not included in this table are 4 animals from 10 to 12 months old.

(1951) measured the temperature of a denning black bear in captivity and recorded a range of 31° to 34° C. On February 17, 1959, I shot an adult male in a den, taking care to avoid any prior disturbance of the animal; a rectal temperature of 33° C. was recorded immediately after death. Since the body temperature of active black bears is about 38° C. (Irving and Krog, 1954, and unpublished data), these observations indicate a decreased metabolic rate during the denning period.

Young animals are particularly well suited for the study of comparative growth, because changes in size and in dentition can be more easily discerned. Through the first summer of life, up to the time the wild bears enter the dens, the two groups (wild and captive) differed little in size. For in males killed between August 1 and October 31, the mean condylobasal length of captives exceeded that of the wild specimens by 5 per cent (6 skulls in each sample). No differences were noted in the development of the dentition up to this time; thereafter the eruption of the permanent canines took

Table 5

Skull dimensions (in mm) of captive bears according to age class; data on 5 specimens killed during the winter are not included

Age Class	Sex	N	Range Length	$\overline{M}$	Range Width	$\overline{M}$
I	♂	6	142—192	168	92—118	105
	♀	8	151—180	167	91—102	97
II	♂	3	230—238	233	132—138	135
	♀	3	210—225	220	128—129	128
III	♂	2	259—264	261	152—174	163
	♀	1	262	—	164	—
IV	♂	3	260—283	269	153—164	159
	♀	—	—	—	—	—
V	♂	1	264	—	155	—
	♀	1	251	—	147	—
VII	♂	1	269	—	172	—
	♀	—	—	—	—	—
VIII	♂	1	288	—	192	—
	♀	1	247	—	164	—

place rapidly in the captives. In a female killed on November 12, the upper canines already had emerged 9 mm beyond the alveolar margins[2], and the same value was obtained from a male skull dated November 19. This dimension was 16 mm for a female on December 28, and 19 mm for a male on February 3; in the latter, the extent to which the upper canine had emerged was equal to that recorded for wild bears at the end of the second summer, and the condylobasal length (221 mm) exceeded any recorded for wild bears in class II. The condylobasal length of a captive male killed on May 14 (second summer) was greater than the mean for wild males in class III (232/227 mm). The disparity in size between the two groups increased thereafter, as suggested in Fig. 9; additional data on relative growth in the captives are presented in Table 4.

Growing steadily throughout the year, the captives would be expected to attain maximum size in about half the time required by animals living under natural conditions if both grew at the same rate. However, since differences in average size were already evident in first-year animals, time was not the only variable involved. Not only did the captives grow at a more rapid rate, but there was an indication that they would become larger than wild bears. The skull dimensions of captive bears are summarized in Table 5. Comparative data on body weights are presented in Table 6.

Two bears, captured when 3 to 4 months old, regularly denned for at least 6 months of the year and, in the pattern of their annual cycle, were the only captives that might be considered comparable to wild animals. These bears, a male and a female, were maintained for 7 and 10 years, respectively, and thus would be assigned to age classes VII and VIII. The layers of dentin in the upper canine of the male corresponded with chronological age, but the most recently formed layers could not be interpreted in the tooth from the female. Irrespective of the findings in the teeth, the characteristics of the skull and long bones were in both cases typical of wild bears of class IX (see Table 4). These two animals seemed to provide evidence that the captives grow at an accelerated rate, whether they den or not.

Nutritional factors evidently were responsible for the aforementioned differences in growth rates. According to Chatelain (1950), and from my own observations, the diet of black bears in south-central Alaska is much the same as has been reported for these animals at lower latitudes (Bigelow, 1922; Murie, 1937; Cottam et al.,

[2] Measured along the medial side of the canine from the point at which the ventral border of the premaxilla joins the maxilla.

Table 6

Weights of captive and wild bears according to age class

Age Class	Captive				Wild			
	Sex	Date	Age	Weight (kg)	Sex	Date	Age	Weight (kg)
I	♂	14 August	6½ months	24.0	♂	28 June	5 months	11.6
	♂	4 Oct	8 months	38.6	♂	28 June	5 months	12.5
	♂	13 Oct	8½ months	41.0	♂	8 August	6 months	11.4
					♂	1 Oct	8 months	22.3
					♂	4 Oct	8 months	12.7
					♂	28 Oct	9 months	13.6
	♀	12 August	6½ months	25.0	♀	6 June	4 months	8.9
	♀	27 August	7 months	29.5	♀	8 August	6 months	11.8
	♀	22 Oct	9 months	19.0	♀	17 August	6½ months	18.2
	♀	31 Oct	9 months	18.2				
Intermediate I/II	♂	3 Feb	12 months	66.0				
	♀	12 Nov	10½ months	31.8				
	♀	28 Dec	11 months	35.4				
II	♂	14 May	15½ months	57.7				
	♂	27 May	16 months	62.7				
	♀	25 May	16 months	63.6				
	♀	27 August	19 months	54.5				
Intermediate II/III	♂	14 Jan	23½ months	104.5				
III	♂	9 May	2 years, 3 months	88.6				
	♂	3 Nov	2 years, 9 months	126.0				
	♀	3 Nov	2 years, 9 months	123.6				
IV	♂	5 June	3 years, 4 months	80.4				
	♂	21 June	3 years, 5 months	73.2				
	♂	27 August	3 years, 7 months	147.7				
V	♂	1 March	4 years, 1 months	102.3				
	♀	9 April	4 years, 2½ months	109.1				
VI					♂	6 August	5 years, 6 months	100.0
VII	♂	13 April	7 years, 2½ months	159.0	♂	21 June	—	73.2
VIII	♂	7 April	8 years, 2 months	165.0				
	♀	28 June	10 years, 5 months	91.8				
IX					♂	16 Feb	—	91.0
					♂	27 April	—	93.2
					♂	3 August	—	112.3
					♀	28 June	—	72.7
					♀	6 July	—	69.0
X					♂	October	—	76.0

1939; Bennett et al., 1943). After emerging from the dens in early spring, the bears commonly tear open logs and dead trees in order to obtain carpenter ants, *Camponotus herculeanus* (Linnaeus), which also are eaten throughout the summer. They feed upon new growth of grasses and sedges in the spring and early summer and, as the season progresses, an increasing proportion of their diet is comprised of berries; these include the fruits of *Vaccinium* spp., *Empetrum nigrum* L., *Viburnum edule* (Michx.), and *Streptopus amplexifolius* (Linnaeus). Carrion is consumed when available, as are any animals that can be captured.

The young bears are probably weaned when about 5 months old. I examined three cubs which, with their mother, had been struck by an auto on June 28. The stomachs of all four animals contained adults, larvae, and pupae of the carpenter ant, along with a small amount of vegetation. No trace of milk was found in the stomachs of the cubs, although a small amount could be expressed from the mammary glands of the old female. Lactation had essentially stopped in another female, also with three cubs, that was killed on July 6; again, carpenter ants comprised the bulk of the stomach contents. Consequently, whatever fat the cubs accumulate prior to denning is deposited after they have been weaned.

The diet of the captive bears was composed essentially of cereal (maize meal) cooked with meat and, from time to time, supplemented with uncooked meat or fish and leafy vegetation. A commercially prepared "dog food," consisting mainly of cereals and limited amounts of animal tissues, was also fed occasionally. Unweaned bears received milk and cereals. Water was available *ad libitum*. Although these data are of little value for detailed comparisons, it is evident that the diet of the captives had a much higher caloric content than that of the wild bears. This may account for the more rapid growth in the former and for the greater size attained by them.

Abnormal growth of bone, in the form of hyperostosis, was noted to varying degrees in some of the captive animals. Attention was drawn to such cases by the unusual weight of the skulls as compared with those of wild individuals. When such skulls were sawed longitudinally, it was found that certain bones, particularly the parietals, the basilar part of the occipital, and the body of the sphenoid, were much thickened. Further investigation also disclosed considerable thickening of the compact bone in the shaft of the femora in such animals, but it was not determined whether the entire skeleton was so affected. This condition was perhaps related to the high phosphorus content of the artificial diet. It is of interest that an apparently identical condition has been described in captive lions by Howell (1925).

Although subject to some modification by local conditions, the denning period of black bears at lower latitudes is relatively short. In the State of Washington, for example, the animals spend about 5½ months in dens situated at higher altitudes, but only 2½ to 3 months in dens in the lowlands (Dalquest, 1948). The denning period is about 4 months in Pennsylvania (Gerstell, 1939), and becomes increasingly short toward the south. Hamilton (1943) indicated that bears may fast briefly even at the southern limits of their geographic range, but Baker (1956) cited limited evidence to the contrary. In any event, if diets are comparable, black bears in the southern United States might be expected to attain full growth in about half the time required in south-central Alaska; thus, they would closely resemble non-fasting captives in pattern of growth. Although regional differences are to be expected, they may also resemble the captives in the failure of the canine teeth to develop annulations correlated with extended periods of fasting; if so, segregation of younger animals by age class might be difficult. Whether longevity is affected by the duration of the annual fasting period remains to be determined; however, long-term studies of marked wild bears will be necessary to clarify some of these questions.

VII. Reproduction

Although too little material was available to permit a detailed study, the general reproductive pattern of the black bear in south-central Alaska was determined. The little information previously published on reproduction in this species was acquired much farther south.

Males

Penile bones were collected from 30 bears, of which 17 were captives. In the youngest animals, this bone is slightly curved and more or less cylindrical, with the greatest diameter near the proximal end; the dorsal ridge is already visible. The bone evidently grows at a rather uniform rate until it reaches a length of about 135 mm. At this stage, the development of the distal end is nearly complete, and most of the subsequent growth takes place in the proximal half of the bone. A curve representing the development of the os penis is obtained when length is correlated with weight (Fig. 10). It may be seen from this curve that weight begins to increase at a more rapid rate about at the time the aforementioned length has been attained. Since it occurs in wild bears in the 5th or 6th summers (3rd or 4th summers in captives), the change in rate

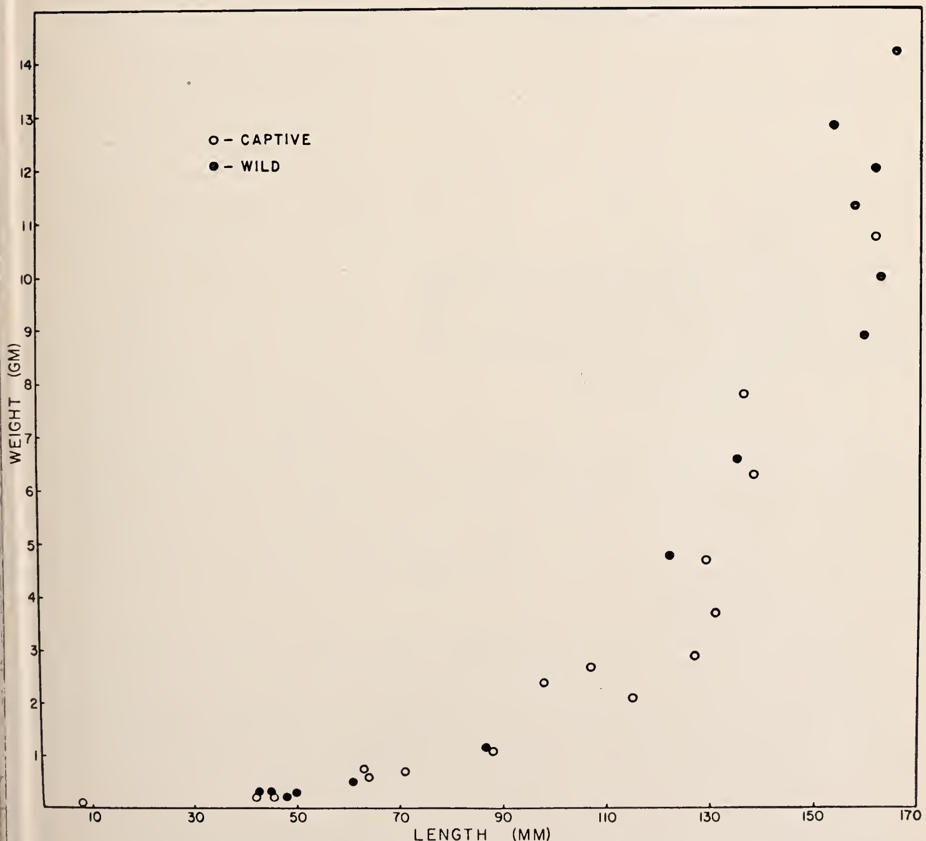


Figure 10. Pattern of growth in the penile bone of the black bear

probably coincides with the onset of puberty. Since the longest and heaviest bone was taken from the oldest available animal, it seems possible that the os penis may continue to grow throughout the life of the individual. In this connection, it has been found that the weight of the penile bone increases with age in the mink, *Mustela vison* Schreber (Elder, 1951). The os penis of the black bear is relatively straight, but considerable individual variation in shape was noted. Penile bones from wild and captive bears are shown in Fig. 11.

The relationship between age and the development of the os penis is best understood in certain species of small carnivores (mustelids) which, compared with the black bear, mature rapidly (Wright, 1947; Fryley, 1949; Elder, 1951; Wright and Rausch, 1955). Immature individuals can be distinguished from adults by the weight of the penile bone, and, in some cases, it has been found that the growth of this structure is much accelerated with the initiation of spermatogenesis. Wright (1950) demonstrated experimentally that the development of the penile bone in the longtailed weasel, *Mustela frenata* Lichtenstein, is controlled by androgens, particularly testosterone. As might be expected, the growth of this bone appears to be similarly regulated in the black bear. A 10-month-old bear was castrated by me and was killed early in the 5th summer of like (March 1), at the age of about 4 years. The penile bone of this animal was strikingly slender, measuring 115 mm in length, with a weight of only 2.1 Gm (see Fig. 11, F). Compared with bones from captives killed a Summer earlier (class IV), it was only 10 to 15 % shorter, but weighed from 60 to 75 % less. Increase in the length of the penile bone is evidently controlled only partially by androgens, but its growth otherwise appears to be entirely dependent upon these hormones. As far as could be determined from the available material, the growth of the penile bone in wild black bears is not influenced by androgens before the third summer.

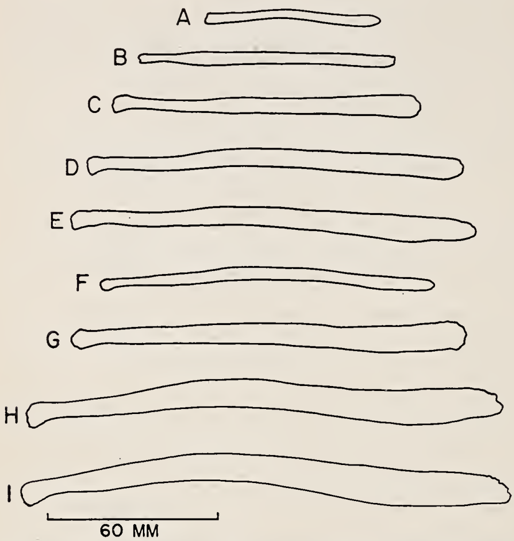


Figure 11. Outlines of representative penile bones from black bears, by age class: A, October 28 (I), wild; B, February 3 (I/II), captive; C, May 27 (II), captive; D, May 9, (III), captive; E, August 27 (IV), captive; F, March 1 (V), castrated captive; G, August 6 (VI), wild; H, April 27 (IX), wild; I, August 31 (X), wild

Findings in the reproductive organs of 23 male bears are summarized in Table 7. Although the critical age classes are inadequately represented, these data tend to support the earlier inference that puberty is attained by wild males in the 5th or 6th summer. Spermatozoa were found in the epididymis of a wild bear killed in the 6th summer, and in the testes of a captive killed early in the third summer; the latter is regarded as the physiological equivalent of a wild bear of class VI (see Table 4).

The time of maximum sexual activity in the male could not be determined in my material. Spermatozoa were found in the testes and/or epididymides from about the middle of April until late August, but observations on captive animals indicate that breeding usually takes place in late June. There is no evidence that wild males differ from captives in the pattern of their reproductive cycle, nor did captive animals that denned appear to differ in this regard from those that remained active. Captive males sometimes attempted to copulate when the females were unreceptive; such behaviour was noted as early as April 13 and as late as early June.

Females

Excluding several first-year animals, the genital organs from 14 female bears were studied. A well developed os clitoridis is present. This bone is largest at the proximal end, with a somewhat curved, laterally compressed shaft and a well defined knob at the distal end; in general form it is much like a small os penis. A fully ossified bone from a 3-year-old captive measured 39 mm in length and weighed 0.5 g. The development of this structure is perhaps controlled by the sex hormones in much the same way as is its homologue in the male. The occurrence of an os clitoridis in *Ursus* has been reported previously (see Layne, 1954). The bicornate uterus is relatively small and has a rather short, somewhat flattened body. In adults, the common lumen extends about 50 mm from the cervix to the bifurcation of the cornua; the latter measure up to 130 mm in length, with a maximum diameter of about 10 mm. Uteri containing implanted embryos were not examined.

The ovaries varied in shape, but usually were more or less oval in outline and somewhat flattened. They measured up to about 27 mm in greatest diameter in non-pregnant females and had a maximum weight of about 2 Gm. Histologically, the ovaries of black bears are characterized by the abundance of luteinized theca cells that occur throughout the stroma as well as in corpora lutea and corpora atretica.

In first-year females, killed when 9 or 10 months old, the ovaries contained large numbers of primary follicles measuring about 50 μ in diameter; where some epithelial proliferation had occurred, follicles up to 180 μ in diameter were seen. Except for these first-year animals, the younger age classes were poorly represented. A captive bear killed early in the second summer (May 25) had ovaries measuring about 18 mm in greatest diameter and weighing about 1 Gm each; many follicles, up to 1 mm in greatest diameter, were present, as were numerous atretic follicles (corpora atretica). A captive that was killed late in the third summer (Nov. 3), presumably the physiological equivalent of wild bears of age class VI, had not been kept with a male. The ovaries of this animal weighed about 1.8 Gm and contained atretic follicles which differed in the degree to which they had been replaced by connective tissue; ovulation might have occurred during the previous spring. In a wild bear of class VII, killed on August 6, the ovaries weighed about 2 Gm and contained numerous atretic follicles.

A captive female produced a single cub early in 1957, and the male was removed the following April. When killed two years later, on June 28, 1959, at the age of $10^1/_2$ years, one ovary was found to contain a mature follicle measuring 12 by 9 mm. Numerous corpora atretica were also present. The second ovary was lost.

Two wild females of class IX were killed on June 28 and July 6, respectively, after each had produced 3 cubs a few months earlier. The ovaries of the former measured about 23 mm in greatest length. Theca lutein cells were abundant and showed no signs of degeneration. In the one ovary that was sectioned serially, a single corpus albicans, measuring about 2 mm long, was identified; corpora atretica were numerous. There were many developing follicles, measuring up to 2 mm in diameter. In the second animal, the ovaries showed little evidence of activity. They were smaller, with a well defined cortex, and contained only a few follicles measuring less than 1 mm in greatest diameter. Theca lutein cells were abundant. In the one ovary sectio-

Table 7

Summary of data on reproductive organs of male black bears

Age Class	Date	Weight of os penis (Gm.)	Weight of testis (Gm.)	Weight of epididymis (Gm.)	Histological findings
WILD					
I	28 June	0.25	1.3	0.8	Interstitial cells abundant in testes of younger animals, becoming fewer in late summer and fall. Seminiferous tubules with mean diameter of 50 to 65 μ. Cells undifferentiated, lumina lacking.
I	28 June	0.25	1.3	1.0	
I	8 August	0.20	1.5	1.4	
I	1 Oct	0.29	1.2	0.7	
I	25 Oct	0.50	1.4	0.5	
IX	16 Feb	12.8	19.0	4.6	Seminiferous tubules comparatively acellular, with only spermatogonia present; lumina large. Ducts of epididymis full of fluid.
IX	27 April	10.0	17.9	5.3	Similar to next above.
VII	21 June	4.8	35.2	7.0	Spermatozoa few in seminiferous tubules; numerous in ducts of epididymis; epithelium of latter degenerating.
IX	3 August	11.3	22.0	5.5	Spermatozoa present in ducts of epididymis, none in seminiferous tubules; testes becoming inactive.
VI	6 August	6.6	17.5	4.7	Spermatozoa numerous in ducts of epididymis, none in seminiferous tubules.

ned serially, a corpus albicans measuring about 1 mm in diameter was found; corpora atretica were numerous.

Corpora lutea were found in the ovaries of only two bears. One, unaccompanied by cubs, was shot on September 27; the skull was not obtained, but the animal was described as old by the hunter. The left ovary contained one corpus luteum, and the right ovary contained two; these bulged above the ovarian surface, and measured 8, 8, and 7 mm in greatest diameter, respectively. These corpora lutea were about 3 months old if ovulation had occurred during latter June. They had well organized cores of connective tissue and exhibited little vascularity; theca lutein cells were scattered throughout the ovarian stroma. The cytoplasm of the granulosa lutein cells was quite granular. No blastocysts were found when the opened cornua were examined under the dissecting microscope, but, since these would have collapsed in the preserved material, this was not unexpected. No effort was made to section the cornua serially. These corpora lutea did not closely resemble the inactive corpora observed in the ovaries of the wolverine, *Gulo gulo* Linnaeus, prior to implantation of the blastocysts (Wright and Rausch, 1955), nor those described from the ovaries of badgers, *Meles meles* Linnaeus, in which unimplanted blastocysts were found (Neal and Harrison, 1958). It is presumed that the uterus of this bear contained unimplanted blastocysts.

The second animal with corpora lutea also was a solitary female (age class IX), killed during the week of September 7–13. The right ovary could not be found, pre-

Fortsetzung Tabelle 7

Age Class	Date	Weight of os penis (Gm.)	Weight of testis (Gm.)	Weight of epididymis (Gm.)	Histological findings
CAPTIVE					
I	14 August	0.75	—	—	Similar to findings in class I (Wild) above.
I	1 Sept	0.2	—	—	
I	4 Oct	0.7	1.8	—	
I	3 Oct	—	1.8	0.7	
I	15 Oct	0.2	—	—	
I/II	3 Feb	1.1	1.4	0.8	—
II	14 May	2.4	5.7	2.2	Primary spermatocytes present.
II	27 May	2.7	10.0	3.0	Seminiferous tubules with mean diameter of about 175 μ. Interstitial cells few. Primary spermatocytes present.
II/III	14 Jan	2.9	7.2	2.2	Similar to next above.
VII	13 April	10.7	36.8	5.5	Seminiferous tubules with mean diameter of about 250 μ; many spermatids, few spermatozoa. No spermatozoa in ducts of epididymis.
III	9 May	4.7	37.0	5.8	Few spermatozoa in seminiferous tubules. None in ducts of epididymis.
IV	27 August	6.3	21.7	3.7	No spermatozoa in seminiferous tubules, testes becoming inactive. Ducts of epididymis filled with fluid; spermatozoa very few.
III	3 Nov	3.7	8.2	2.3	Seminiferous tubules average about 150 μ in diameter, comparatively acellular; testes inactive. Interstitial cells numerous.

sumably having been destroyed by one of two large tumors, described below, that involved the right cornu and accessory structures. The left ovary contained two corpora lutea which measured 8 and 6 mm in greatest diameter. Macroscopically, these structures appeared darker in color than those from the aforementioned animal; they also were more deeply situated and did not bulge above the ovarian surface. It was found in sections that both the corpora and the surrounding connective tissue were highly vascular. The granulosa cells were more deeply eosinophilic than those described above, and their cytoplasm was less granular. Essentially, however, the ovaries of the two animals were the same histologically. Since it was desirable to retain the specimen intact, no search for blastocysts was made.

The age at which females become sexually mature probably differs with latitude, in accordance with expected differences in the rate of growth. Accurate information for wild bears in Alaska is lacking, and few observations have been made on captive animals. Two young bears, a female and a male, born in 1949 and 1950, respectively, were placed together in a large enclosure at Anchorage, where they remained until the male was killed in April, 1957. They excavated a deep den in which they spent 6–7 months annually. Successful breeding took place in the spring of 1956, when the female was about 6 years and 4 months old (age class VII), and one cub was born late in the following winter. As mentioned earlier, these animals were regarded as approximately the same as wild bears in their pattern of development, but the female might have conceived earlier had a sexually mature male been present. In a second case, bears captured as cubs were maintained at Fairbanks by Dr. Raymond J. Hock, who provided the following observations. The female, born in 1955, denned little, if at all; the male, born in 1951, denned regularly. The two animals were first put together in June, 1957, when the female was about 2 years and 4 months old; the male attempted copulation, but the female was unreceptive. A year later, however, breeding was successful, and young were produced about January 25, 1959, when the female was 4 years old. The latter was killed on April 19, 1959; although actually of age class V, it was later concluded that this animal was physiologically equivalent to a wild bear of age class VIII. It is of interest that three captive females in Ohio all produced their first litters at the age of 4 years (Baker, 1912).

The time of year at which oestrus occurs in the black bear seems not to differ from region to region, nor does there appear to be much difference between wild and captive animals in this regard. Three captive females in Ohio produced 28 litters over a 21-year period, and their reproductive history was accurately documented (Baker, 1912). The male, usually kept separately, was placed with the females each year about the first of June, but copulation was observed only during the last 10 days of June and the first week of July. Black bears were observed *in coitu* in Yosemite Valley, California, on June 25 (Grinnell et al., 1937).

The duration of oestrus in the black bear is not known, but the few available data suggest that it may be comparatively short. Murie (1944) noted that a pair of brown bears copulated repeatedly over a period of about two weeks, and remained together for at least 23 days (south-central Alaska). Prell (1930) reported the occurrence of pseudoestrus following true oestrus, and separated from it by an interval of variable length, in the brown bear and polar bear. Additional observations on this condition were reported by Lindemann (1954) and by Steinbacher (1958). However, Schneider (1953), from many observations on captive animals, concluded that pseudoestrus does not occur in the polar bear, but rather that true oestrus is of long duration. Long-term observations on both wild and captive black bears will be necessary to determine the length of the breeding time.

The corpora lutea of pregnancy involute rapidly after parturition, but the findings in the ovaries of the aforementioned females killed in early summer with cubs of the year, indicated that postparturient ovulation had not taken place. This is in accord with the commonly held belief that black bears produce young only in alternate years. According to Baker (1912), oestrus could be induced annually at the usual time in captive females if the cubs of the year were taken away in May. Postparturient oestrus might therefore be expected to occur in wild bears if the young died soon after birth. It is possible that ovulation is inhibited during the period of lactation.

Convincing evidence of delayed implantation in species of *Ursus* was furnished by Prell (1930), as a result of observations on brown bears and polar bears. Hamlett (1935) concluded that implantation is also delayed in the black bear, but it is apparent from the recent review by Canivenc (1960) that little information on this point has been acquired subsequently. Implantation of the blastocyst may occur in late November according to Hamlett, who reported the finding of a 2-mm embryo in a bear killed on December 2 in Pennsylvania. However, Gerstell (1939), also in Pennsylvania, found embryos about 20 mm long in animals killed in late November and early December. The black bear evidently has a gestation period of about 220 days, according to the data of BAKER (1912), BROWN (1936), and others. However, SCHNEIDER (1953) found that the length of the gestation period varies to a remarkable degree in the polar bear, and a similar variation might be expected in other species of *Ursus*.

Black bears in Alaska usually produce two or three cubs, according to observations made after emergence of the litters from the dens. The average number is probably just in excess of two, as was found to be the case for the large number of litters reported from captive animals by BAKER (1912).

VIII. Parasites and Diseases

Parasites

All of the wild bears obtained with viscera were examined for parasitic helminths, of which 5 species were recorded. Since a detailed report on the parasites of bears is planned, they are considered only briefly here.

Diphyllobothrium sp. was recorded once, from an adult bear killed on the lower Talachulitna River. Since only a portion of the cestodes could be preserved, the number comprising the infection was not determined. The fatal outcome of an experimentally induced *Diphyllobothrium* infection in a young black bear has been reported (RAUSCH, 1955).

Another cestode, *Taenia hydatigena* Pallas, 1776, was reared experimentally in a young bear. Two large strobilae were recovered when the animal was killed 47 days after ingesting the larvae. Although ostensibly normal in development, these were found to be sterile. This tapeworm occurs naturally in the wolf, *Canis lupus* Linnaeus.

Nematodes representing 4 species were collected. The larvae of *Trichinella spiralis* (OWEN, 1835) were found in 5 of 23 animals that were appropriately examined (RAUSCH ET AL., 1956). Infections probably are acquired through eating carrion. *Dirofilaria ursi* Yamaguti, 1941, was collected only once from this host, although it is a common parasite of the brown bear in Alaska. Ascarids, *Toxascaris transfuga* (RUDOLPHI, 1819), were found, particularly in late summer and early fall. Black bears seem often to become infected during their first summer. Hookworms, *Uncinaria yukonensis* (WOLFGANG, 1956), occur widely in bears in Alaska.

The relationships between mammals that hibernate *s. str.* or, in the case of bears, that fast during the winter, and their intestinal helminths are complex and poorly understood. It has been observed that brown bears eliminate large numbers of cestodes *(Diphyllobothrium)* in late summer and fall, prior to denning; this may result from a change in diet (RAUSCH, 1954). Ascarids may be found in considerable numbers in bears during the fall, but they are evidently lost prior to denning (unpublished data). According to DUBININ and LESHKOVICH (1945), marmots, *Marmota bobak sibirica* Radde, which are true hibernators, lose their ascarids before hibernation begins. The examination of a bear killed in the den on February 16, 1959, revealed 279 hookworms in the small intestine. The fasting of the host presumably would have no effect on these nematodes, since they feed on blood.[6]

[6] After completion of the study, I obtained an adult female black bear that had been killed at its den on February 26, 1961. The intestine contained 78 hookworms and 3 small specimens of *Diphyllobothrium* sp. Although the strobilae of the latter were little developed, they must have been acquired prior to the time of denning. This finding suggests that such tapeworms may survive by means of destrobilization.

No ectoparasites were found on the animals examined. JELLISON and KOHLS (1939) reported a flea, *Arctopsylla ursi* (ROTHSCHILD, 1902), from black bears in south-central Alaska. I have collected this flea several times from brown bears.

Diseases

Excluding dental disorders, which are seen rather commonly in the older animals, there was little evidence of disease in the available material. Findings in two bears were of unusual interest.

Two large, more or less ovoid tumors involving the right horn of the uterus and the accessory structures were found in the old bear mentioned above. The right cornu appeared to be much elongated, with the tumors in tandem position; the distance from the point of bifurcation of the cornua to the anterior surface of the second tumor was 480 mm. The right ovary and its surrounding structures could not be identified and presumably had been destroyed. The first (posterior) tumor was situated about 130 mm from the point of bifurcation of the cornua; it measured 150 by 135 mm, and weighed 786 Gm. The latter was separated from the anterior mass by a tubular structure 120 mm long which was histologically compatible with somewhat abnormal fallopian tube. The second tumor measured 210 by 140 mm, and weighed 1500 Gm. When cut, the tumors were found to consist of soft, multicystic tissue surrounded by a loosely attached, fibrous covering. The cyst cavities contained a clear fluid that had solidified with fixation, but in some areas considerable blood was present. The diagnosis of liposarcoma was made by Dr. M. J. WICKS, who undertook the histological study of the tissue sections. Since the entire animal was not obtained, observations on other organs could not be made.

The dying of an old male bear (age class IX) was observed and reported by hunters on April 27, 1957, a few miles west of Anchorage. Retrospectively, there was reason to believe that the death of this animal had been precipitated when it was pursued by the hunters in an airplane, but this was not confirmed. The animal could not be recovered until two days later, by which time considerable *post mortem* degeneration had taken place. The bear weighed 93 Kg, and was moderately fat ;a thick layer of subcutaneous fat was present over the rump. Dissection revealed severe inflammation of the lungs and pleura. On the right side, the pleural surfaces were covered by a fibrinous exudate, but this was lacking in the left side of the thorax. Macroscopically, the cut surfaces of the lungs had a mottled appearance, with large areas of pale yellowish, amorphous tissue interspersed with ostensibly normal areas. Both lungs were affected to about the same extent. Scattered, necrotic foci measuring 2–4 mm were present in the liver; the other organs were apparently normal. The histological findings, according to Dr. JAMES G. BRIDGENS, supported the conclusion that the changes in the lungs had resulted from an inflammatory process, and the condition was diagnosed as bronchopneumonia.

The probable origin of the pulmonary infection became evident after the skull of this animal was cleaned. Chronic suppurative inflammation within the left tympanic bulla had resulted in osteomyelitis with the formation of necrotic sinuses. The affected area was more or less circular, of about 40 mm in diameter (Fig. 12). The ventral wall of the tympanic bulla and the adjacent basilar portion of the occipital bone had been destroyed, leaving a sinus of about 20 mm in diameter. Exostoses were numerous on the surrounding surfaces, particularly on the paramastoid process. The stylo-mastoid foramen was involved, as were both the carotid foramen and the Eustachian opening. A sinus 25 mm in greatest diameter had perforated the medial

Figure 12. Diseased skull of a black bear. Two of the described areas are visible (arrows)

surface of the pterygoid bone on the right side, opening from the natural sinus cavities underlying the parietal and squamous temporal bones. The bone surrounding the foramen ovale was osteoporotic. A third necrotic sinus, about 10 mm in diameter, perforated the palatine process of the maxilla on the left side, immediately posterior to the second molar but not involving its alveolus, from where it drained into the nasal cavity. The pulmonary infection evidently followed the aspiration of purulent exudate draining from the necrotic sinuses into the pharynx. The probability that this would occur was no doubt enhanced during denning time, when the capacity of the bear to evacute such material must have been significantly reduced.

Black bears that survive to old age nearly always have badly worn molars, and often exhibit signs of periodontal disease. These disorders occur with greater frequency in brown bears and are largely a result of herbivorous habits. I have not observed any severely worn molars in a large series of skulls from polar bears, whose carnivorous propensities have been well documented.

Fourteen skulls, of the series studied, represented aged animals (class X), of which 11 exhibited severely worn molars and signs of periodontal disease. The latter ranged from slight osteoporosis of the alveolar margins to extensive involvement of the alveoli and surrounding bone, with loss of teeth and the formation of necrotic sinuses. Diseased teeth had been lost from 3 skulls, and rather extensive absorption of alveolar bone was noted in several instances. In 8 skulls, attrition had been so severe that one or more teeth were represented only by their roots, which remained in the alveoli. Such excessive wear is not always accompanied by periodontal disease, but usually some signs of inflammation are visible.

Signs of periodontal disease were noted in 7 of 35 skulls representing age class IX, and, compared with the older animals, the affected areas were much less extensive. In these specimens, injuries to single teeth had apparently given access to infection. There was no evidence of such disease in animals of age classes I through VIII.

Dental caries does not occur in wild bears, according to Colyer (1936, p. 617). However, Hall (1940) reported having found carious teeth in 8 skulls among 360 that he examined, and he suggested that the condition was caused by a natural diet that he regarded as rich in sugar. "Cup-like attrition," similar to that described by Colyer, is seen rather commonly on the appositional surfaces of molars in both black bears and brown bears in Alaska. Some teeth in old black bears had remarkably deep cavities with dark-stained walls, which apparently had resulted purely from abrasion. However, it was noted that organic matter, particularly plant fragments and small seeds, becomes impacted in deeply worn cavities that communicate with the pulp canals of the roots. The decomposition of such materials might lead to caries of the adjacent surfaces of the cavities, but histological study of properly prepared specimens will be necessary to evaluate these conditions. The canines of some of the aged animals had been broken off near the gingival surface, exposing the pulp cavity, and in such teeth infections were not observed. None of the captive bears showed any evidence of dental disease, although the canines in some were badly worn from their habitual biting of the metal rods of the cages.

Few signs of injuries were observed in the skulls of the black bears compared with findings in skulls of either brown or polar bears in Alaska. Two old animals (class X) had sustained transverse fractures of one mandible. Healing had been complete in both, but there was residual periodontal disease in one, with involvement of the posterior root of the second molar; the extent of the affected area could no be defined because the observed thickening of the ramus had in part resulted from the healing of the fracture. Old fractures of one zygomatic arch had healed in three animals (class IX) with no significant deformity. The right mandible of another bear (class IX) exhibited osteoporosis over the anterior half of its lateral surface with no evident cause. An injury sustained by an adult bear (class VIII) involved the proximal end of the left nasal bone and the adjacent portions of the left frontal bone and the maxilla; after healing a shallow concavity about 60 mm in diameter remained.

One case of unusual interest involved an old black bear (class X) shot during October, 1952, while raiding the provisions of a trapper near Skwentna. Local hunters noted the absence of tracks or other signs of activity while flying in the vicinity, but made no investigation until January, at which time the bear, shot through the head, was found outside the door of the cabin; the trapper's stores were in a state of disorder, and the trapper himself was dead, presumably as a result of injuries inflicted by the bear. The animal was very thin, weighing only 73 Kg, and its stomach contained food items consumed in the cabin. After the skull was cleaned, signs of an old injury became apparent; bilateral perforations involved the lacrimal bones and the orbital portion of the temporal bones around the openings of the lacrimal canals. The injury was not recent, as evidenced by the proliferation of bone, but an irregular perforation persisted in the medial wall of each orbit. In view of the circumstances, the animal might have been blinded by a bullet passing transversely through the head, which could explain its poor condition and failure to den, as well as its having been attracted to the provisions in the cabin. Another bear (class IX) was found to have sustained a similar, though unilateral injury, resulting in the perforation of the medial wall of the left orbit near the opening of the lacrimal canal. A fragment of lead, possibly a bird-shot, was found embedded in the nasal bone of another adult animal. Careless shooting is no doubt the primary cause of injury in bears, at least in populated areas.

The causes of natural mortality in the black bear in Alaska are obscure, except for those indications discussed above. Kurtén (1958) has called attention to the high winter mortality in cave bears, as evidenced by skeletal remains in the caves in which they denned, but comparable information on black bears is difficult to obtain, for their dens are used only a few years at most, so that the accumulation of a significant quantity of remains cannot be expected. Wright (1910, p. 67) remarked that he had found many carcasses of black bears „in dens and elsewhere," but he provided no further information. Winter at higher latitudes must be a rigorous time for individuals unable to build adequate reserves of fat. Kurtén stated, in reference to cave bears, that old animals with badly worn teeth enter the dens in poor condition and die during this period. Some old black bears have such badly worn teeth as to be, in effect, early edentulous, yet they are able to deposit what appears to be a normal amount of fat. However, the year to year fluctuations in abundance of food may be of critical importance to such individuals. Besides poor dental function, the aged animals are frequently afflicted with periodontal disease and, as noted by Colyer

(1936), aspiration of exudate may give rise to pulmonary infection. There is evidence that bears in poor physical condition do not attempt to den, instead remaining active into the late fall; such animals must soon starve. Solitary cubs appear to be unable to den alone in northern regions and must also starve soon after the first autumnal snows. ERICKSON (1959) found that two cubs released on islands in northern Michigan were able to survive the winter alone. In both cases at least a limited amount of food might have been available along the beaches. WEEKS (1888, cited in SILVER, 1957) expressed the opinion that many die during their first winter or soon after they emerge from the dens in the spring.

The significance of interspecific and intraspecific strife among these animals is unknown. However, there is a widespread belief in Alaska that brown bears prey upon black bears at every opportunity.

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Summary

In Alaska, where the winters are relatively long and severe, the denning period of the black bear, *Ursus americanus* Pallas, lasts 6 to 7 months. During this time, a body temperature of 32–33^0 C. persists; this represents a decrease of about 5–6^0 from that of active animals.

Growth in the black bear is correlated closely with the annual cycle and is limited largely to the period of activity. As a result of the interrupted growth, zones corresponding to the period of activity are laid down annually on the roots of the canines. The demarcation of the annual zones is visible as external, ring-like markings. The greatest amount of growth takes place during the first three summers of life, with the growth zones decreasing gradually in width thereafter until the roots of the canines are fully developed, usually in the 6th summer. These growth zones provide a means by which age in individual bears can usually be determined through the 6th summer of life. The first six age classes are designated I through VI in the present work. The remaining classes, designated VII through X, represent age groups that could be characterized only relatively by means of changes in the growing skull (closure of sutures; development of secondary sex characteristics), tooth wear, etc.

Comparative growth was also investigated in the skulls of wild and captive black bears. It was determined that captives that did not den grew about twice as fast as wild bears within the same period of time. The lenght of the growing time is particulary significant in this connection, but the artificial diet received by the captives was presumably also important.

In addition, some characteristics of dentition of the black bear have been described, including eruption times, sexual dimorphism, tooth wear, and variation. Reproductive biology has been discussed briefly, and findings on parasites and diseases have been presented.

Zusammenfassung

In Alaska erreicht die Winterruhe des Schwarzbären, *Ursus americanus* Pallas, eine Dauer von 6 bis 7 Monaten. Dies ist auf die Wirkung des strengen Winterklimas zurückzuführen. Während der ununterbrochenen Ruhezeit herrscht eine Körpertemperatur von 32 bis 33° C., d. h. ein Temperaturabfall von etwa 5 bis 6°.

Das Wachstum des Schwarzbären ist mit dem Jahreszeitenzyklus eng verknüpft und zu einem hohen Grad auf die Periode der Aktivität beschränkt. Als Folge des unterbrochenen Wachstumsprozesses lagern sich jährliche, in der Aktivitätsperiode auftretende Anwachszonen auf die Eckzahnwurzeln auf. In den ersten 3 Jahren ist das Wachstum am stärksten; danach wird der Zuwachs allmählich geringer, bis im 6. Sommer die Eckzahnwurzeln gewöhnlich vollkommen entwickelt sind. Die Abgrenzung der Jahreszonen ist durch äußerliche, ringförmige Markungen ersichtlich. Durch diese Wachstumszonen wird jährlich bis zum 6. Sommer die Altersbestimmung ermöglicht. In der vorliegenden Arbeit werden die ersten 6 der 10 Altersklassen römisch I bis VI bezeichnet. Die übrigen Altersklassen, römisch VII bis X, repräsentieren Altersgruppen, die nur relativ durch Veränderungen des wachsenden Schädels (Verwachsungsgrad der Nähte; Entwicklung der Geschlechtsmerkmale), Abnutzung der Zähne, usw., charakterisiert werden konnten.

Schädelwachstum bei wilden und bei gefangen gehaltenen Schwarzbären wurde vergleichend untersucht. Es wurde festgestellt, daß die gefangenen Bären, ohne beträchtliche Aktivitätsverminderung (keine Winterruhe), im gleichen Zeitraum ungefähr zweimal so viel wuchsen wie wilde Bären. In diesem Zusammenhang ist die Wachstumsdauer von besonderer Bedeutung, und die Einwirkung des Kunstfutters war vermutlich wichtig.

Neben den gemachten Beobachtungen wurden auch die Eigentümlichkeiten des Gebisses des Schwarzbären beschrieben, einschließlich Zahnwechsel, Geschlechtsdimorphismus, Abnutzung, und Variabilität. Die Fortpflanzungsbiologie wurde ebenfalls kurz besprochen, desgleichen Feststellungen über Parasiten und Krankheiten.

Résumé

En Alaska, où les hivers sont relativement longs et rigoureux, la période dans laquelle l'ours noir (*Ursus americanus* Pallas) reste dans sa tanière hivernale dure de six à sept mois. Pendant ce temps, la température corporelle des animaux est 32–33° C.; c'est une diminution de 5–6° de celle des animaux actifs.

La croissance dans l'ours noir est en accord avec le cycle annuel et arrive en grande partie dans l'époque d'activité. A cause de la croissance intermittente, des zones correspondantes à cette époque annuelle se trouvent sur les racines des canines. Les démarcations des zones annuelles sont visibles comme des marquages externes annulaires. La plupart de la croissance arrive pendant les trois premiers étés de la vie, et en suite les zones de la croissance se sont réduites en largeur jusqu'au moment où les racines des canines sont développées pleinement, usuellement dans le sixième été. Par ce moyen, on peut déterminer l'âge des animaux individus jusqu'au septième été. Les six premières classes de l'âge sont nommées I – VI dans cette étude. Les autres, désignées VII–X, représentent des groupes que l'on ne peut que caractériser relativement par moyen des changes du crâne croissant (fermeture des sutures; développement des caractères secondaires sexuels), l'usure des dents, etc.

La croissance comparative des ours noirs captifs et sauvages a été recherchée dans les crânes. On a trouvé que les captifs qui ne sont pas entrés dans leurs tanières hivernales sont crûs à peu près deux fois plus vite que les sauvages, dans le même espace de temps. Bien que la longueur du temps de la croissance soit signifiante ici, la diète artificielle est aussi importante.

En outre des caractéristiques de la dentition ont été décrits, y comprenant l'éruption, la dimorphisme sexuelle, l'usure des dents, et la variation. On a discuté brièvement la biologie reproductive et des faits sur des parasites et des maladies.

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