# Cranial Variation in the Kodiak Brown Bear (*Ursus arctos middendorffi*): Implications for Age Prediction

By

Kalin Ann Kellie

In Partial Fulfillment of the Requirements for

Senior Honors Thesis

## Thesis Outline

## List of Figures

## List of Tables

## ABSTRACT

Three sources of variation were identified in the growth of brown bears. The relationship between age and growth was modeled and the model evaluated as a method of age prediction. Twenty-two cranial measurements were taken on a sample of forty-two subadult (2- to 6- year-old) brown bears (*Ursus arctos middendorffi*) from Kodiak Island. Using four criteria, seven variables were chosen for model selection. The single variable IB was selected as the best parameter for age estimation. Addition of the SEX variable to the model did not increase model accuracy. The assumption of linearity was not met; transformations and nonlinear regression were attempted to assess the nonlinear relationship. All models used in this analysis overestimated the ages of young subadult bears and underestimated the ages of older subadults. This nonlinear relationship was not adequately described by any of the models used in this study. Age cannot be accurately predicted using linear regression.

## INTRODUCTION

*"For wild animals there are no written birth certificates and we must therefore look within their own age structure for signs of age or any biological record of the passage of time (Morris 1972)."*

Age determination is an important tool for wildlife biologists. Determining the chronological age of individuals is necessary to ascertain life history characteristics of a population. For example, vital parameters for population modeling, such as age of first reproduction and survival, are based on age classes (Gotelli 1995). Because *cementum annuli* counts are accurate predictor of age, they are frequently chosen to estimate age in brown bears (Marks and Erickson 1966, Craighead et al. 1970, Crowe 1975). However, cementum analysis is dependent on the experience of the observer and exacting laboratory methods. Large samples of teeth can result in considerable financial investment and delay in obtaining results because often tooth samples are sent to commercial laboratories for analysis (Allen 1974, Fancy 1980, Roberts 1978, Root and Payne 1984). Alternative aging methods might provide a faster determination or minimally provide a preliminary estimate if cementum analysis is ultimately preferred.

Few robust alternative morphological methods of age determination exist. Morphological variation within age classes can blur the distinctions between ages to the point of confusion. Three types of morphological variation can complicate age determination: geographic variation, sexual dimorphism and individual variation (Rausch 1953, 1961). The effects of these variables must be considered when attempting to accurately predict age.

### ***Geographic Variation***

*"Geographic variation is nearly ubiquitous among organisms, occurring in most species of plants and animals.., affecting nearly any characteristic (Heins 1995)."*

Geographic variation may take two forms: (1) clinal or continuous variation, and (2) discontinuous variation. Within a species, geographic variation often results in the splitting of populations into several taxonomic groups. For example, the gray wolf (*Canis lupus*) was classified into 24 subspecies in North America (Goldman 1944, Nowak 1983). This classification was challenged, and suggested to be most likely the result of a continuum related to geographic differences (Rausch 1953, Jolicoeur 1959, Kelsall 1968, Banfield 1974).

Similar confusion led to the classification of brown bears (*Ursus arctos*) into 86 species in North America, some of which were described from the characteristics of a single skull (Merriam 1896, 1914, 1918). Merriam's 86 species were later challenged by Rausch (1953,

1963) and Kurtén (1973), who lumped all of them into one species, *U. arctos*. Rausch (1963) and Kurtèn (1973) determined that Merriam's work was based on inadequate sample size, and failure to account for the incredible clinal variation among populations of brown bears. Rausch (1963) suggested that this species was composed of two subspecies: (1) *U. a. middendorffi* on Afognak and Kodiak islands in Alaska, and (2) *U. a. horribilis* for all other North American brown bears. Kurtén (1973) added a third subspecies, *U. a. dalli,* from the southern coast of Alaska and west coast of British Columbia. Hall (1981) chose to ignore both Rausch and Kurtén's classifications, and preserved Merriam's 86 species in The Mammals of North America. He later classified Alaskan brown bears into five subspecies of *U. arctos*, retaining Kurtén's designations, but breaking *U. a. horribilis* into three groups: *U. a. gyas* on the Alaskan peninsula, *U. a. sitkensis* in southeast Alaska, and *U. a. alascensis* in interior Alaska and the Kenai peninsula (Hall 1984). All of these subspecies were challenged by Talbot and Shields (1996a, b) based on mitochondrial DNA sequencing. Agreeing with the earlier conclusions of Rausch (1953,1963), Paetkau et al. (1998b) separated the Kodiak Island bears from the mainland, using analyses based on nuclear microsatellite DNA variation.

According to Paetkau et al. (1998a, b), the Kodiak Island brown bears have been reproductively isolated from the mainland for a long time. This feature suggests that the island subspecies *U. a. middendorffi* may be much less variable than the widespread mainland bears. Earlier efforts based on morphometric measurement failed to age brown bears successfully (Sherwood 1981). Nevertheless, such an effort may succeed on the Kodiak Island population where geographic variation should be minimal.

### *Sexual Dimorphism*

*"Age-specific morphological variation was not parallel in males and females; different suites of variables were important to the age variation in each sex... (Davis and Choate 1993)."*

When examining criteria for age determination, one of the first questions to address is whether differences in morphology exist between males and females. Two individuals of similar age, origin, and diet may have different body sizes depending on their sex. Also, sexual dimorphism may result in a fundamental difference in shape. Morris (1972) cautions that not only are measurements in mammals usually smaller for females than males, but females may be more accurately aged by entirely different criteria than those used for males.

The difference in growth between the sexes is inherent in most mammals. Sexual dimorphism has been found in a variety of species: marine mammals such as the Antarctic fur seal (*Arctocephalus gazella*) and elephant seal (*Mirounga leonina*), terrestrial carnivores such as the timber wolf (*Canis lupus*) and African wild cat (*Felis lybica*) and small mammals such as the eastern mole (*Scalopus aquaticus*) ( Jolicoeur 1975, Kieser and Groeneveld 1991, Arnbom et al. 1992, Davis and Choate 1993). Because sexual dimorphism is an obvious aspect of growth in brown bears (Rausch 1969, Sherwood 1981), separate analyses of males and females will be necessary to build models of age determination in brown bears.

### *Individual Variation*

*"A general problem lies in the nature of individual variation among animals (Morris 1972)."*

Individual variation explains the differences among individuals that are related to genetic diversity within a population. When considering morphological methods of age determination, these individual differences act as "noise" in the sample, and decrease the resolution of the technique. The manifestations of individual differences are limitless. Lunn et al. (1993) found that individual differences among Antarctic fur seals may relate to variation in the foraging efficiency of their mothers. Rausch (1969) reported an inverse relationship between growth and duration of denning in Alaskan brown bears, suggesting that variation in individual behavior results in differences in growth. Chestin and Mikeshina (1998) concluded that individual variation in brown bears from the Caucasus Mountains may be due to behavioral "ecomorphs" of sub-populations.

To overcome the uncertainty of such variation, some studies do not attempt to explain the causes of individual variation; instead they focus on methods to minimize its effect on age estimation. For example, Sherwood (1981) restricted his study of brown bears to Yellowstone National Park in an effort to examine individuals with similar genetic background and behavior (e.g. a single "ecomorph").

Kodiak brown bears form a similarly restricted population. *U. a. middendorffi* is found only on the Kodiak Archipelago (Fig 1.), 35 km from the mainland at the closest point (Paetkau et al. 1998b). The islands have similar climate and habitat, suggesting that behavioral differences such as denning, fishing and breeding will be minimized. The low genetic diversity of this population may result in lower phenotypic variability in Kodiak bears than between mainland bears (Paetkau et al. 1998a).

### ***Review of Morphological Aging Techniques***

Rausch (1963) recognized the high amount of morphological variation in brown bears of Alaska, particularly in skull dimensions. He measured and cementum aged a large sample of brown bear skulls from throughout Alaska. Much of his work, however, concentrated on the analysis of a single measurement (Rausch 1963, 1969). Zygomatic breadth, condylobasal length, and size of canine tooth have also been reported as single-measurement indicators of bear age (Mundy and Fuller, 1964; Sauer, 1966, Nagy et al., 1977). Age classes have been described using cranial characteristics for bears up to 6 years of age (Stickley, 1957, Manning, 1964, Sherwood 1981, Zavatsky 1988). None of these studies was able to accurately predict the age of an unknown bear skull. Cranial measurements, including suture closure, were unreliable due to the high within-class variation among skulls and the lack of additional development in female skulls after maturity. Spencer (1961) concluded that morphometrics cannot be used to determine the age of black bears (*Ursus americanus*), based on a sample size of 170 black bears from Maine. Because he had no known-age bears, uncertainty of actual ages prevented him from drawing any definitive conclusions.

## METHODS

### *Study Design*

There were three objectives for this study. First, I describe the effects of variation on the growth of the skull and make predictions about how this will influence age. Secondly, I attempt to model the relationship between skull growth and age in subadult brown bears using methods that avoid variation. Finally, I evaluate the accuracy of the model in predicting the age of brown bears using cranial morphometrics.

With the exception of Rausch (1963), previous studies used small sample sizes drawn from large geographic regions. My study avoids much of the reported geographic variation in cranial morphology by concentrating on a single, geographically isolated subspecies (*U. a.*

*middendorffi*). Because genetic diversity is lower (Paetkau et al. 1998a), it is possible that the individual variation between Kodiak brown bears is also reduced. In addition, Kodiak Island bears enjoy a relatively homogeneous climate, which further reduces individual variation in denning and foraging behavior.

Most morphometric studies report a changing rate of growth with an increase in age (Morris 1972, Sherwood 1981, Manning 1964, Rausch 1961). Figure 2 shows extremely rapid growth during the newborn/yearling stage, a steady increase during the subadult years (2-6 in the brown bear), and a slowing of growth past sexual maturity. Sexual dimorphism also becomes increasingly pronounced after maturity (Sherwood 1981). My study focuses on subadult individuals. Because this age class represents the majority of bears harvested, it has the two-fold appeal of large sample size and increased importance to wildlife management. Subadult bears are also easier to age using cementum analysis: the two to six cementum rings are usually clearly defined and easy to count. Because only a small number of samples of mature brown bears are available, they are difficult to model.

### *Measurements*

Cranial measurements were taken on a sample of 46 brown bear skulls, 20 female and 26 male, collected from Kodiak Island between 1962 and 1977. Skulls were previously aged using *cementum annuli* techniques described by Rausch (1961). All samples were within the subadult age group (Table 1).

Twenty-two cranial measurements were taken with electronic calipers to the nearest 0.01mm. Two other measurements were made with slide calipers* to the nearest 1.0mm (Figure 3). The measurements (adapted from Sherwood 1981) were as follows:

BB. Breadth of braincase: greatest breadth recorded between the parietal-squamosal sutures.

BC. Breadth of canines: greatest breadth of the rostrum at or above the canines. This is normally 5 to 10mm. above the aveoli of the canines, but in young bears with permanent canines only partially erupted, it is distinctly higher up.

BOC. Breadth of the occipital crest: greatest width across the exoccipital processes.

CBL* Condylobasal length: from the anterior extremity of the premaxilla (not teeth) to the posterior extremity of the condyle.

CH. Coronoid height: with the bar of the calipers at right angles to the long axis of the mandibles, one caliper jaw was placed on the top of the coronoid process, the other at the bottom of the angle.

CL. Cranial length: from the inion to the midpoint between the supraorbital processes. A line can be drawn on the skull joining the extremities of the processes. The inion here is defined as the most posterior point on the skull at or near the junction of the lamboidal and sagittal crests.

CPL. Condylopalatal length: from the left condyle to the posterior border of the palate. The palatal notch that occurs in some skulls was not included.

FL. Facial length: from the midpoint between the supraorbital processes to the extremity of the premaxillae.

GLS* Greatest length of skull: greatest distance from the anterior-most extremity of the skull (including the teeth) to the posterior-most extremity of the sagittal crest.

HSC. Height of the sagittal crest: distance between the lowest extremities of the occipital condyles to the highest point on the dorsal surface of the sagittal crest in adults or highest point of the inion in young grizzly bears with undeveloped sagittal crests.

IB. Interorbital breadth: minimum width between the orbits measured across the frontals.

LCB. Least cranial breadth: the least width of the cranium posterior to the supraorbital processes.

LM1. Crown length of M1: from the posterior border of the cingulum near the midline to the anterior border in line with the two outer cusps.

LM2. Crown length of M2: from the posterior border of the cingulum near the midline to the anterior border in line with the two outer cusps.

LP4M2.Length P4 to M2: distance between anterior extremity of the cingulum of P4 and the posterior border in line with the two outer cusps.

LSC. Length of sagittal crest: from the posterior extremity of the sagittal crest to the anterior-most extremity of the sagittal crest. This point is usually located at the bifurcation of the temporal ridges.

MB. Mastoid breadth: greatest breadth across the mastoid processes.

MPL. Molar-premaxilla length: one jaw of the calipers was placed across the posterior border of both M2's either at the widest point of the cingula or the aveoli, whichever gave the greatest measurement.

MSH. Maxilla-supraorbital height: distance between the highest part of the lower border of the left maxilla posterior to M2, and a point on the dorsal surface of the frontal immediately above this. This point is approximately at the intersection of a line joining the extremities of the supraorbital processes and a line tangent to the inner border of the orbit.

PB. Palatal breadth: distance between the outer borders of the alveoli of the posterior root of M1.

SB. Supraorbital breadth: maximum breadth across the supraorbital processes.

ZB. Zygomatic breadth: greatest breadth across the zygoma. Where the squamosal and jugal has parted, the squamosal was assumed to give the correct breadth.

### *Variable Selection*

From these twenty-two measurements seven were chosen for model selection using the rule of 6-10 samples for each variable in model selection (Neter et al. 1989). Predictor variables were removed from the analysis based on the following criteria: (1) low measurement reproducibility, (2) low sample size, (3) no apparent relationship to age, and (4) effectively duplicated by another variable (Neter et al. 1989). In a pilot study, twenty-four skulls from the Alaska Department of Fish and Game were measured using the complete list of measurements. Each skull was measured three times, and the mean and standard error determined for each skull-measurement combination. The measurements with ambiguous or high standard error among the twenty-four skulls were removed (CL, LCB, CPL, MPL, BB, BOC, and MSH). Measurements PB, CH and BC were unavailable for a large number of samples due to damage and were removed. Tooth measurements LM1, LM2 and LP4M2 were removed after plots against age showed no relationship. Measurement GLS was removed because it was redundant with CBL. As suggested by Brunner (1998a, b), all remaining measurements were divided by the CBL measurement to decrease effects of individual size variation in the data. Using the PROC REG procedure (Cary 1989), multivariate regression was calculated using these variables and the results were examined for outliers and validity of model assumptions. A correlation matrix was also examined for multicolinearity effects.

### *Model Selection*

The regression equation was determined using four different methods of model selection (Table 2): maximum R-squared improvement (MAXR), adjusted R-squared (ADJRSQ), Mallow's Cp (CP) and backward elimination (BACKWARD). When methods gave multiple results, the best five models were ranked (Cary 1989). In order to minimize sexual dimorphism, female and male skulls were also analyzed separately. Separate analysis ensured that no sex-specific characters were dropped because they inadequately predict age for the combined sexes.

### *Regression*

The PROC STANDARD procedure in SAS was used to standardize all continuous variables used in the final regression. Using PROC UNIVARIATE procedure, simple linear regression was used on the chosen model. The validity of five regression assumptions was assessed: (1) linear relationship, (2) constant variance, (3) independent samples, (4) no outliers, and (5) data are normally distributed. Because sexual dimorphism may play a role in subadult growth, the variable SEX was added to the model and the full model regressed using the PROC REG procedure (Cary 1989). An F-test was used to determine if the additional variation explained by sex gave the model closer fit with age (Neter et al. 1989). Squared and cubed transformations of IB were regressed in an effort to mimic a nonlinear relationship (Neter et al. 1989). Finally, an inverse regression was used on a nonlinear model (Figure 3) in order to examine the possibility of the growth rate described by Shirakihara et al. (1993). Variables 'a', 'b' and 'd' were determined using the PROC NLIN procedure, with the Gauss-Newton method specified (Cary 1989).

## RESULTS

A correlation matrix of variables chosen for model selection found that all cranial measurements were highly correlated (Table 3). Using the four methods for model selection listed above, the aggregate choice for best model was the following:

$$\varepsilon[\text{Age}] = \beta_0 + \beta_1(\text{IB/ CBL}) + \epsilon$$

where $\beta_0 = 4.513$ and $\beta_1 = -41.698$.

The addition of SEX as a variable led to the full model:

$$\varepsilon[\text{Age}] = \beta_0 + \beta_1(\text{IB/CBL}) + \beta_2(\text{SEX}) + \epsilon$$

where $\beta_0 = 4.292$, $\beta_1 = -49.432$ and $\beta_2 = 0.494$.

The SEX variable is not highly correlated with IB /CBL ($R^2 = 0.473$), thus multicolinearity was not a concern. Both the full and reduced models met the assumptions of equal variance, independent samples, no outliers and normality. Using an F-test to compare the two models, the reduced model was selected as the best linear model for describing age. The reduced model shows a significant relationship between IB/ CBL and age ($p = 0.0004$).

The cementum ages were plotted against the transformed IB and the predicted ages added to examine the assumption of a linear relationship (Figure 5).

Two transformations were explored in an effort to linearize the nonlinear relationship. The first model,

$$\varepsilon[\text{Age}] = \beta_0 + \beta_1(\text{IB/ CBL}) + \beta_2(\text{IB/ CBL})^2 + \epsilon$$

where $\beta_0 = 4.513$, $\beta_1 = -51.766$ and $\beta_2 = 25.282$, transforms a logistic relationship into a linear relationship.

The second,

$$\varepsilon[\text{Age}] = \beta_0 + \beta_1(\text{IB/ CBL}) + \beta_2(\text{IB/ CBL})^2 + \beta_3(\text{IB/ CBL})^3 + \epsilon$$

where $\beta_0 = 4.513$ and $\beta_1 = 1835.300$, $\beta_2 = - 9404.229$ and $\beta_3 = 15624.000$, transforms a sigmoidal relationship into a linear relationship. These models failed to remove the effect seen in Figure 5.

The final model used to describe the relationship between age and IB/CBL (Figure 3). Parameters had estimated as follows: $\boldsymbol{a} = 18.453$; $\boldsymbol{b} = 0.287$; and $\boldsymbol{d} = -13.396$. The high standard errors of 194, 0.53 and 118, respectively, suggest that this model was marginal. When the ages predicted by this model were overlain with the cementum ages against IB (Figure 6), the unstable nature of the model is readily noted.

## DISCUSSION

Because the same multicolinearity pattern is found in both age and growth, correlation between the cranial measurements does not greatly influence selection when building a model to describe age (Neter et al. 1989). Selection of IB, a width measurement, indicates that a width/length ratio more accurately describes skull growth than the ratio of two lengths (*i.e.* frontal length and condylobasal length). This ratio of infraorbital breadth to condylobasal length decreases with an increase in age (Figure 5), suggesting that lateral growth of the skull may slow toward maturity or, alternatively, longitudinal rate of growth is increasing. Braincase development is rapid early in the life of bears (0-2 years) because the brain and cranial nerves develop first and require protection (Moore 1981). It is possible that the cranial portion of the skull is slowing from that initial rapid development in the early subadult years (2.5 to 3.5). The rate of rostral growth either increases or remains the same in the later subadult years (5.0 to 6.5).

The combination of these two factors may be causing the decrease in IB/CBL as age advances.

Consistent underestimation of older bears (5.0-6.5 years) and overestimation of younger bears (2.5 to 3.5 years) showed that the relationship between IB/CBL and age was not linear. Thus the assumption of linear relationship was violated by both full and reduced linear models, as well as the two transformations. Violation of this assumption indicates that linear regression is not the best modeling technique for describing age because the rate of growth is not constant.

The nonlinear regression (Figure 6) bears little resemblance to the curve given in Figure 4. The majority of the steep logistical growth occurs in the most developmental years of life (0-2.5 years), slowing considerably prior to the subadult years. Subadult development of brown bears represents a small portion of logistical growth, falling out between '***b***' and '***b/2***' on the curve. The small curvature found in Figure 6 can be matched with this more gently sloping portion of the curve in Figure 4.

There are two main areas that warrant further study in the estimation of subadult age of brown bears using cranial measurements. First, though it was not accurately described, this study did detect a nonlinear relationship between age and growth. The models used in this analysis consistently underestimated older bears and overestimated young bears. Although transformations and nonlinear regression did not elucidate the nature of the interaction between growth and age, calculation of this curved relationship may lead to accurate age prediction.

Secondly, some age/sex combinations are not well represented by the sample. For instance, three-year-old males are well represented by eleven individuals, whereas two-year-old males are not represented at all. The small amount of data available for some of these groups may be causing more representative groups to unnaturally influence the regression model.

Future studies should include a larger sample of all age groups in order to avoid this effect.

Due to multiple sources of morphologic variation, populations of brown bears have been reportedly difficult to describe using morphometrics (Rausch 1963, Sherwood 1981). This study attempted to remove the maximum amount of variation in the sample population by focusing on a single, geographically isolated population. The Kodiak Archipelago is small enough to have a relatively homogeneous climate, reducing variation originating from a variety of denning and foraging behaviors. I had hoped to avoid the fast growth of the very young and imperceptible growth of the old by restricting the study to subadult brown bears. Because most differences in growth between males and females occur after maturity, the subadult sample was also less susceptible to variation due to sexual dimorphism. Finally, dividing all cranial measurements by skull length served to standardize the measurements, reducing individual variation. Yet even with this reduced level of variation, brown bear populations remain difficult to describe through morphometric methods. Individual variation is inherent in the population, and prevents accurate descriptions of age-related physical characteristics.

## ACKNOWLEDGMENTS

I would like to thank Joseph Cook, Eric Rexstad, Robert Rausch, Sylvia Brunner and Tom Seaton for their technical advice; the UA Museum and John Hechtel for use of the skulls measured in this study; and Erich Follmann, Gordon Jarrell and Amber Bethe for reviewing this manuscript.

# Literature Cited

1. Allen, SH. 1974. Modified techniques for aging red fox using canine teeth. *The Journal of Wildlife Management* 38: 152-54.
2. Arnbom, TA, N. J. Lunn, I. L. Boyd, and T. Barton. 1992. Aging live antarctic fur seals and sourthern elephant seals. *Marine Mammal Science* 8: 37-43 .
3. Banfield, AWF. 1974. <u>The mammals of Canada.</u>. Toronto, Ont.: Univ. of Toronto Press.
4. Brunner, S. 1998a. Skull development and growth in the southern fur seals *Arctocephalus forsteri* and *A. pusillus doriferus* (Carnivora: Otariidae). *Australian Journal of Zoology* 46: 43-66.
5. Brunner, S. 1998b. Cranial morphometrics of the southern fur seals *Arctocephalus forsteri* and *A. pusillus* (Carnivora : Otariidae). *Australian Journal of Zoology* 46: 67-108.
6. Cary, NC. 1989. <u>*SAS/STAT User's Guide, Version 6, Fourth Edition, Volume 2*</u>. SAS Institute Inc. 846 pp.
7. Chestin, IE, and N. G. Mikeshina. 1998. Variation in skull morpholgy of brown bears (*Ursus arctos* ) from Caucasus. *Journal of Mammalogy* 79: 118-30 .
8. Craighead, JJ, F. C. Craighead, and H. E. McCutchen. 1970. Age determination of grizzly bears from fourth premolar tooth sections. *Journal of Wildlife Management* 34: 353-63.
9. Crowe, DM. 1975. Aspects of aging, growth and reproduction of bobcats from Wyoming. *Journal of Mammalogy* 56: 177-98 .
10. Davis, FW, and J. R. Choate. 1993. Morphologic variation and age structure in a population of the eastern mole, *Scalopus aquaticus*. *Journal of Mammalogy* 74: 1014-25 .

11. Fancy, SG. 1980. Preparation of mammalian teeth for age determination by cementum layers: a review. *Wildlife Society Bulletin* 8: 242-48 .

12. Goldman, EA. 1944. The Wolves of North America. In Classification of wolves., Am. Wildl. Inst. Washington, D. C. 636 pp.

13. Gotelli, NJ. 1995. A primer of ecology. Sunderland, MA: Sinauer Assoc., Inc.

14. Hall, ER. 1981. The Mammals of North America.. New York, NY: John Wiley and Sons.

15. Hall, ER. 1984. Geographic variation among brown and grizzly bears (*Ursus arctos*) in North America. *University of Kansas Museum of Natural History Special Publication* Vol. 13: .

16. Jolicoeur, P. 1959. Multivariate geographical variation in the wolf *Canis lupus* L. *Evolution* 13: 283-99.

17. Jolicoeur, P. 1975. Sexual dimorphism and geographical distance as factors of skull variation in the wolf *Canis lupus* L. In *The wild canids*, ed. Fox, M. W.p. . New York, NY: Van Nostrand Reinhold.

18. Keiser, JA, and H. T. Groeneveld. 1991. Craniodental allometry in the African wild cat, *Felis lybica. Journal of Mammalogy* 72: 578-82 .

19. Kelsall, JP. 1968. The migratory barren-ground caribou of Canada. *Can. Wildl. Serv. Monogr.* 3: 340 pp.

20. Kurtén, B. 1973. Transberingian relationships of *Ursus arctos* Linn, (brown and grizzly bears). *Commentat. Biol.* 65: 10 .

21. Lunn, NJ, I. L. Boyd, T. Barton , and J. P. Croxall. 1993. Factors affecting the growth rate and mass at weaning of Antarctic fur seals at Bird Island, South Georgia. *Journal of Mammalogy* 74: 908-19 .

22. Manning, TH. 1964. Age determination in the polar bear, *Ursus maritimus* L. *Canadian Wildlife Service Occasional Papers* 5: 1-12 .

23. Marks, SA, and R. W. Erickson. 1966. Age determination in the black bear. *The Journal of Wildlife Management* 30: 389-410 .

24. Merriam, CH. 1896. Preliminary synopsis of the American bears. *Proc. Biol. Soc. Wash.* 10: 65-83 .

25. Merriam, CH. 1914. Description of thirty apparently new grizzly and brown bear species from North America. *Proc. Biol. Soc. Wash.* 27: 173-96 .

26. Merriam, CH. 1918. Review of the grizzly and big brown bears of North America. In *North Am. Fauna,* Vol. 41, p.. Washington D. C.: U. S. Gov't Printing Office.

27. Moore, WJ. 1981. *The Mammalian Skull*. New York, NY: Cambridge University Press.

28. Morris, P. 1972. A review of mammalian age determination methods. *Mammal Review* 2: 69-104 .

29. Mundy, KR, and W. A. Fuller. 1964. Age determination in the grizzly bear. *Journal of Wildlife Management* 28: 863-66.

30. Nagy, JA, R. H. Russell, A. M. Pearson, M. C. S. Kingsley, and B. C. Goski. 1977. Ecological studies of grizzly bears in the arctic mountains, Northern Yukon Territory, 1972 to 1975. *Canadian Wildlife Service Report* :95 pp. (Abstr.)

31. Neter, J, M. H. Kutner, C. J. Nachtsheim, and W. Wasserman. 1989. *Applied linear statistical models.*. Chicago, IL.: Irwin Publishing

.

32. Nowak, RM. 1983. A perspective on the taxonomy of wolves in North America. *Canadian Wildlife Service Report Series* No. 45:

33. Paetkau, D, G. F. Shields, and C. Stobeck. 1998a. Gene flow between insular, coastal and interior populations of brown bears in Alaska. *Molecular Ecology* 7: 1283-92.

34. Paetkau, D, L. P. Waits, and P. L. Clarkson . 1998b. Variation in the genetic diversity across the range of North American brown bears. *Conservation Biology* 12: 418-29.

35. Raucsh, RL. 1953. On the status of some arctic mammals. *Arctic* 6: 91-148 .

36. Raucsh, RL. 1961. Notes on the Black bear, Ursus americanus Pallas, in Alaska, with particular reference to dentition and growth. *Z. Saugetierk* 26: 77-107 .

37. Raucsh, RL. 1963. Geographic variation in size in North American brown bears, *Ursus arctos* L. as indicated by condylobasal length. *Canadian Journal of Zoology* 41: 33-45 .

38. Raucsh, RL. 1969. Morphogenesis and age-related structure of permanent canine teeth in the brown bear, *Ursus arctos* L., in arctic Alaska. *Z. Morph. Tiere* 66: 167-88 .

39. Roberts, JD. 1978. Variation in coyote age determination from annuli in different teeth. *The Journal of Wildlife Management* 42: 454-56 .

40. Root, DA, and N. F. Payne. 1984. Evaluation of techniques for aging gray fox. *The Journal of Wildlife Management* 48: 933-38 .

41. Sauer, PR. 1966. Determining sex of black bears from the size of the lower canine tooth. *New York Fish and Game Journal* 13: 140-45.

42. Sherwood, HW. 1981. Morphological variation of grizzly bear skulls from Yellowstone National Park. *MS Thesis, Univ. of Montana, Missoula* 96pp.

43. Shirakihara, M, A. Takemura, and Kunio Shirakihara. 1993. Age, growth, and reproduction of the finless porpoise, *Neophocaena phocaenoides*, in the coastal waters of western Kyushu, Japan. *Marine Mammal Science* 9: 392-406.

44. Spencer, HE, Jr. 1961. The black bear and its status in Maine. *Maine Dept. Inland Fisheries and Game, Game Division Bulletin* 4: 55pp.

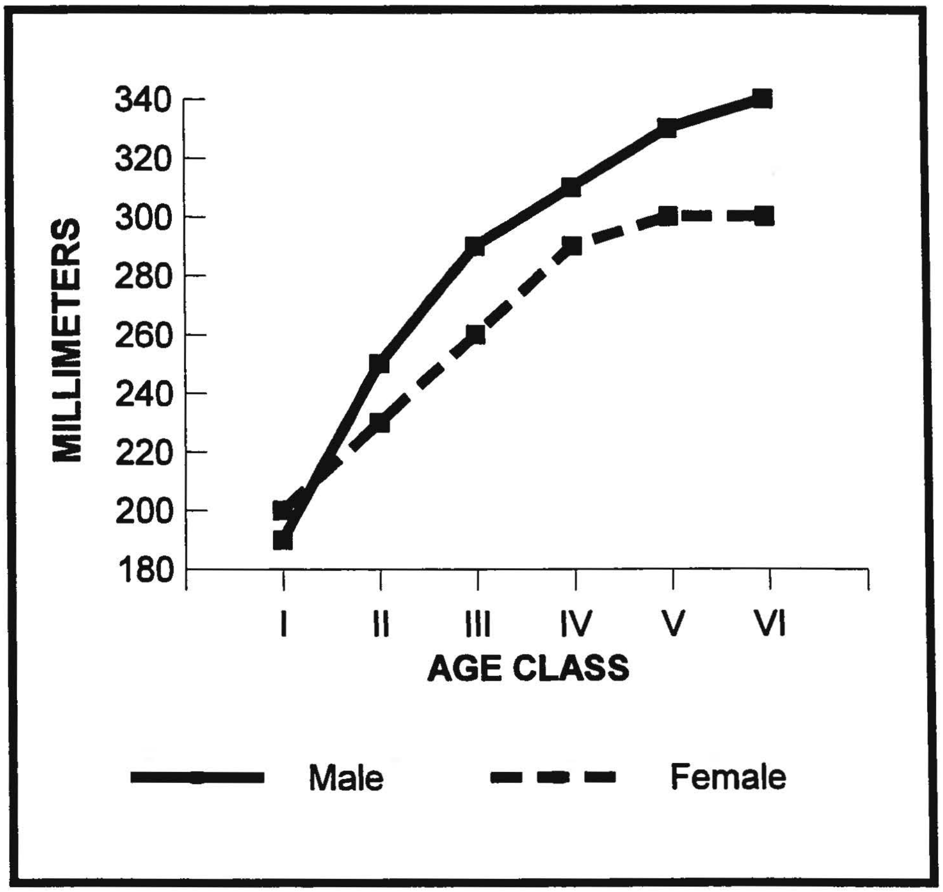
45. Stickley, AR. 1957. The status and characteristics of the black bear in Virginia. *M. S. Thesis Virginia Polytech Inst., Blackburg.* 101pp.

46. Talbot, SL, and G. F. Shields. 1996a. Phylogeography of brown bears (*Ursus arctos*) of Alaska and paraphyly within the Ursidae. *Molecular Phylogenetics and Evolution* 5: 477-94.

47. Talbot, SL, and G. F. Shields. 1996b. A Phylogeny of the bears (Ursidae) inferred from complete sequences of three mitochondrial genes. *Molecular Phylogenetics and Evolution*` 5: 567-75.

48. Zavatsky, BP. 1975. The use of the skull in age determination of the brown bear. *Third International Conference on Bears* 25: 275-79.

**Figure 2.** Representative growth curves by age class of condylobasal length (CBL) measurements from grizzly bears in Yellowstone National Park. Age classes are as follows: (I.) 0-1 years; (II.) 1.0-1.9 years; (III.) 2.0-2.9 years; (IV.) 3.0-5.9 years; (V.) 6.0-11.9; and (IV.) 12+ years. Adapted from Sherwood 1981.



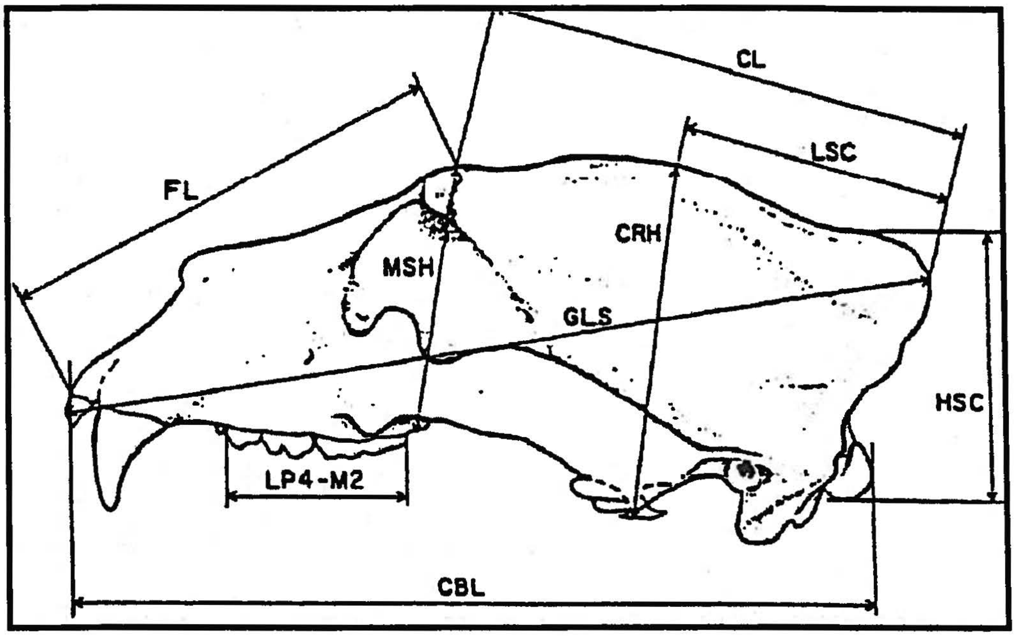


**Figure 3.** Cranial measurements of brown bears used in this study. B = breadth at supraorbital processes; BB = breadth of braincase; BC = breadth at canines; BOC = breadth at nucal crest; CBL = codylobasal length; CL = cranium length; FL = front length (rostrum length); GLS = greatest length of skull; HSC = height of sagittal crest; IB = interorbital breadth; LCB = length of cranial braincase; LM1 = length of molar 1; LM2 = length of molar 2; LSC = length of saggital crest; MB = mastoid breadth; PB = palatal breadth; ZB =zygomatic breadth. NOTE: Measurments CPL, CRH, LP4-M2, MPL and MSH were not taken in this study. Illustrations from Sherwood, 1981.

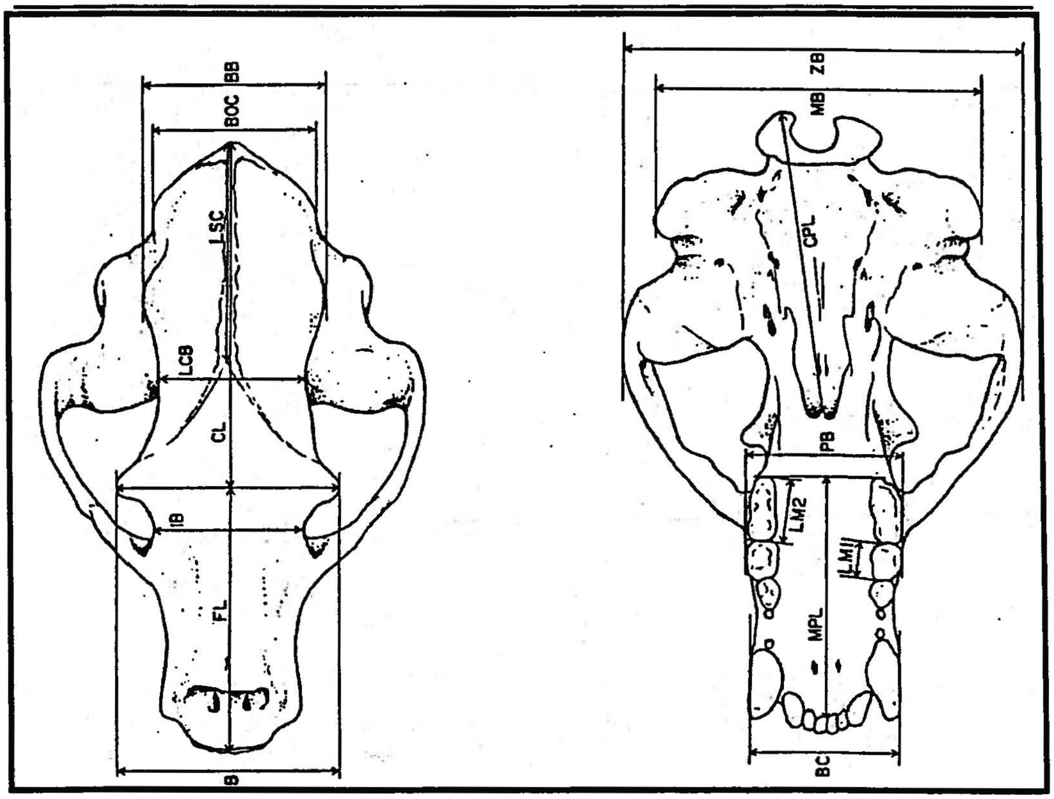
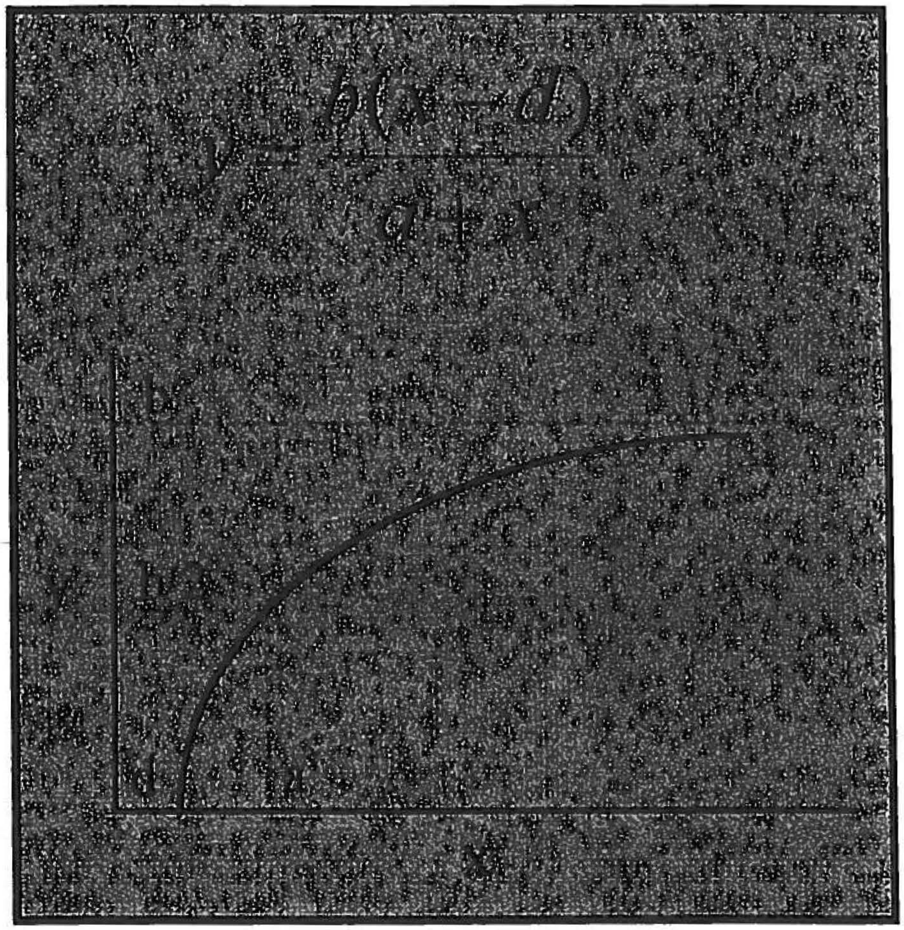


**Figure 4. Equation and graph of growth curve used to predict age in the nonlinear inverse regression model.**



Graphic courtesy of E. Rexstad.

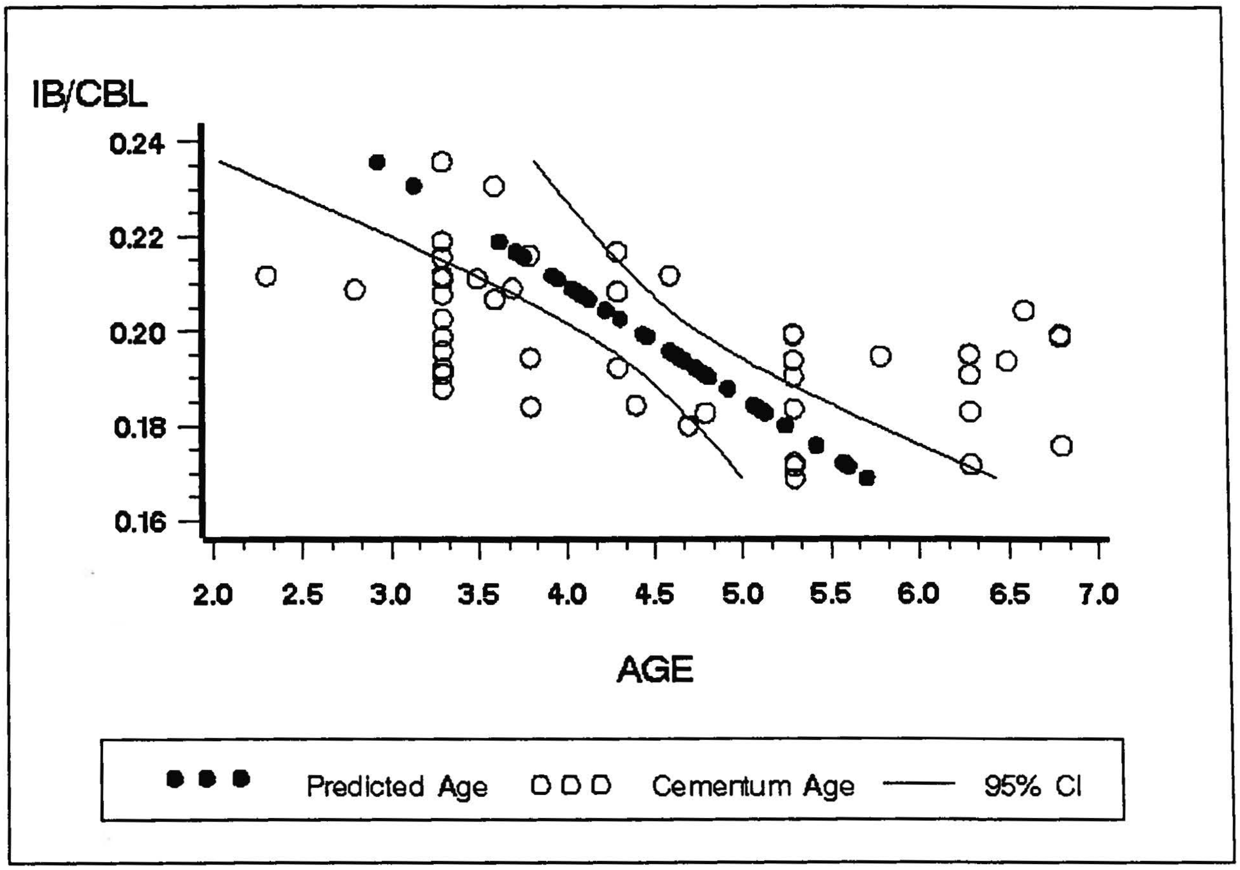


**Figure 5.** Predicted ages using the simple linear regression model $\varepsilon[\text{Age}] = \beta_0 + \beta_1(\text{IB/CBL}) + \epsilon$.

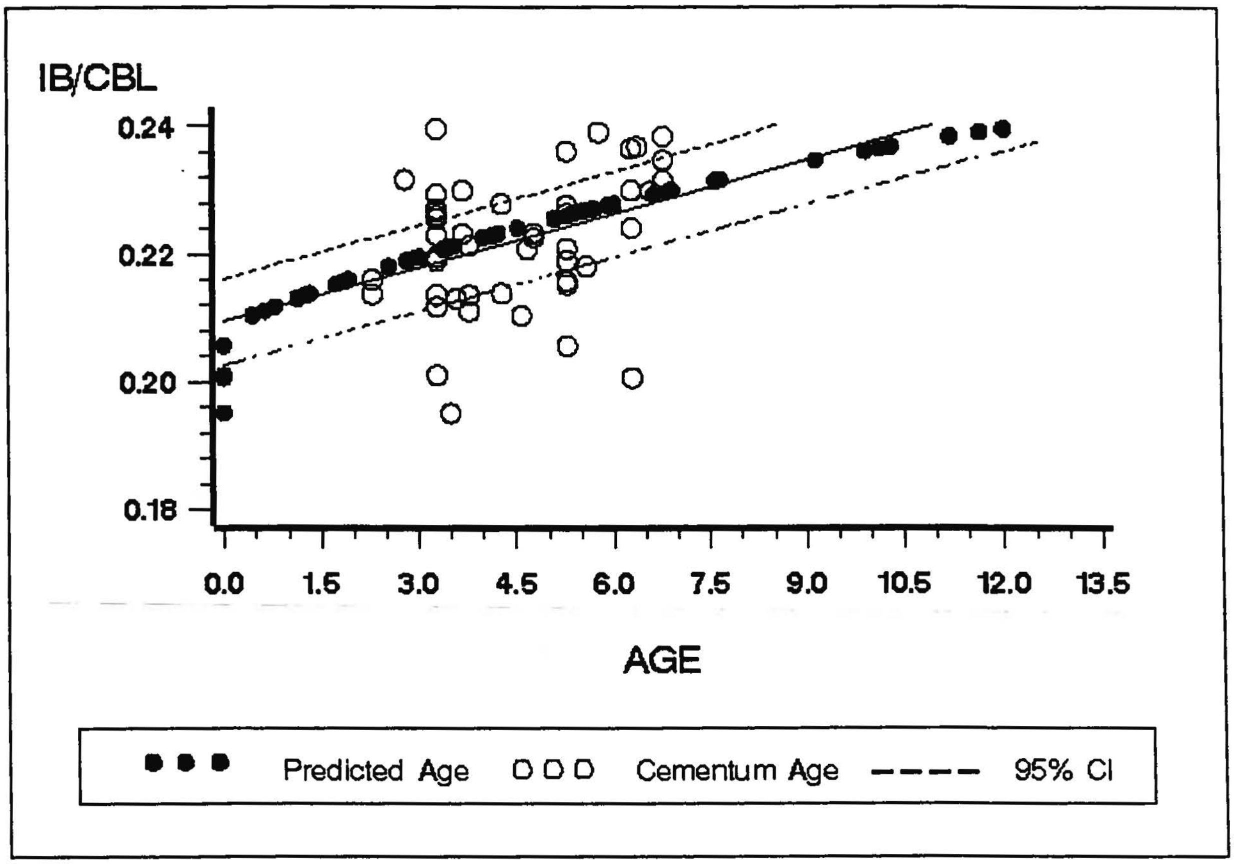


**Figure 6.** Predicted ages using the nonlinear regression model $\varepsilon[\mathrm{IB/CBL}] = \dfrac{b \times (\mathrm{AGE} - d)}{(a + \mathrm{AGE})}$.

**Table 1.** Kodiak Island brown bears used in the analysis.

| No. | Cementum Age | Sex | IB | CBL | IB/CBL | Standardized | Museum Catalog Number |
|---|---|---|---|---|---|---|---|
| 1 | 3.3 | M | 64.82 | 296.0 | 0.2190 | 0.021189 | UAM 14113 |
| 2 | 3.3 | M | 73.33 | 306.0 | 0.2118 | 0.013989 | UAM 14090 |
| 3 | 3.3 | M | 72.70 | 331.0 | 0.1958 | -0.002011 | UAM 14223 |
| 4 | 3.3 | M | 64.34 | 320.0 | 0.2026 | 0.004789 | UAM 14157 |
| 5 | 3.3 | M | 68.14 | 300.5 | 0.2157 | 0.017889 | UAM 14086 |
| 6 | 3.3 | M | 76.32 | 337.5 | 0.1921 | -0.005711 | UAM 14190 |
| 7 | 3.3 | M | 79.14 | 345.0 | 0.1879 | -0.009911 | UAM 14105 |
| 8 | 3.3 | M | 74.51 | 339.5 | 0.1909 | -0.006911 | UAM 14092 |
| 9 | 3.8 | M | 71.24 | 333.5 | 0.1944 | -0.003411 | UAM 14072 |
| 10 | 3.8 | M | 77.88 | 352.0 | 0.1841 | -0.013711 | UAM 14191 |
| 11 | 3.8 | M | 63.34 | 300.0 | 0.2161 | 0.018289 | UAM 14163 |
| 12 | 4.3 | M | 72.07 | 337.0 | 0.1923 | -0.005511 | UAM 14076 |
| 13 | 4.4 | M | 84.44 | 351.5 | 0.1844 | -0.013411 | UAM 14218 |
| 14 | 4.7 | M | 79.48 | 360.0 | 0.1801 | -0.017711 | UAM 14082 |
| 15 | 4.8 | M | 78.91 | 354.5 | 0.1828 | -0.015011 | UAM 14153 |
| 16 | 5.3 | M | 83.18 | 376.5 | 0.1722 | -0.025611 | UAM 14170 |
| 17 | 5.3 | M | 87.33 | 383.5 | 0.1690 | -0.028811 | UAM 14169 |
| 18 | 5.3 | M | 76.86 | 325.5 | 0.1991 | 0.001289 | UAM 14095 |
| 19 | 5.3 | M | 81.39 | 378.0 | 0.1715 | -0.026311 | UAM 14081 |
| 20 | 5.3 | M | 71.18 | 325.0 | 0.1994 | 0.001589 | UAM 14152 |
| 21 | 5.3 | M | 72.60 | 353.0 | 0.1836 | -0.014211 | UAM 14070 |
| 22 | 5.8 | M | 79.62 | 333.0 | 0.1947 | -0.003111 | UAM 14186 |
| 23 | 6.3 | M | 68.14 | 339.5 | 0.1909 | -0.006911 | UAM 14135 |
| 24 | 6.3 | M | 84.48 | 377.0 | 0.1719 | -0.025911 | UAM 14101 |
| 25 | 6.8 | M | 87.84 | 368.5 | 0.1759 | -0.021911 | UAM 14142 |
| 26 | 6.8 | M | 75.48 | 326.0 | 0.1988 | 0.000989 | UAM 14079 |
| 27 | 2.3 | F | 65.42 | 306.0 | 0.2118 | 0.013989 | UAM 14067 |
| 28 | 2.8 | F | 71.94 | 310.5 | 0.2088 | 0.010989 | UAM 14155 |
| 29 | 3.3 | F | 62.45 | 275.0 | 0.2357 | 0.037889 | UAM 14117 |
| 30 | 3.3 | F | 65.60 | 307.0 | 0.2111 | 0.013289 | UAM 14168 |
| 31 | 3.3 | F | 71.80 | 339.0 | 0.1912 | -0.006611 | UAM 14196 |
| 32 | 3.3 | F | 70.88 | 312.0 | 0.2078 | 0.009989 | UAM 14068 |
| 33 | 3.3 | F | 73.55 | 326.0 | 0.1988 | 0.000989 | UAM 14100 |
| 34 | 3.5 | F | 59.91 | 307.0 | 0.2111 | 0.013289 | UAM 14132 |
| 35 | 3.6 | F | 66.82 | 313.5 | 0.2068 | 0.008989 | UAM 14225 |
| 36 | 3.6 | F | 67.66 | 281.0 | 0.2307 | 0.032889 | UAM 14232 |
| 37 | 3.7 | F | 71.29 | 310.0 | 0.2091 | 0.011289 | UAM 14071 |
| 38 | 4.3 | F | 71.81 | 299.0 | 0.2168 | 0.018989 | UAM 14075 |
| 39 | 4.3 | F | 70.88 | 311.0 | 0.2084 | 0.010589 | UAM 14112 |
| 40 | 4.6 | F | 64.38 | 306.0 | 0.2118 | 0.013989 | UAM 14077 |
| 41 | 5.3 | F | 73.48 | 340.5 | 0.1904 | -0.007411 | UAM 14107 |
| 42 | 5.3 | F | 75.72 | 334.5 | 0.1938 | -0.004011 | UAM 14156 |
| 43 | 6.3 | F | 78.53 | 332.0 | 0.1952 | -0.002611 | UAM 14193 |
| 44 | 6.3 | F | 81.43 | 354.0 | 0.1831 | -0.014711 | UAM 14123 |
| 45 | 6.5 | F | 80.66 | 334.5 | 0.1938 | -0.004011 | UAM 14129 |
| 46 | 6.6 | F | 72.88 | 317.0 | 0.2045 | 0.006689 | UAM 14219 |
| 47 | 6.8 | F | 76.28 | 325.0 | 0.1994 | 0.001589 | UAM 14089 |

**Table 2. Model Selection methods and rank of possible models. $\varepsilon[Y] = \beta_0 + \beta_1(IB/CBL) + \epsilon$ was chosen as the best model.**

| *p* | Variables Included | $R^2_p$ | $MSE_p$ | $C_p$ | Model Rank | | | |
|---|---|---|---|---|---|---|---|---|
| | | | | | Back | Cp | AdjR$^2$ | Max R$^2$ |
| 1 | IB | 0.24445 | 1.2675 | -0.76125 | 1 | 1 | | 1 |
| 1 | HSC | 0.24433 | 1.2677 | -0.75494 | | 2 | | |
| 1 | ZB | 0.24429 | 1.2678 | -0.75245 | | 3 | | |
| 1 | B | 0.24427 | 1.2678 | -0.75102 | | 4 | | |
| 1 | LSC | 0.24426 | 1.2678 | -0.75073 | | 5 | | |
| 2 | ZB MB | 0.27495 | 1.2440 | -0.46633 | | | 5 | |
| 2 | SEX IB | 0.27363 | 1.2463 | -0.39247 | | | | 2 |
| 3 | SEX ZB MB | 0.30294 | 1.2238 | -0.03116 | | | 1 | 4 |
| 3 | SEX HSC MB | 0.29784 | 1.2327 | 0.25384 | | 2 | | |
| 3 | SEX IB MB | 0.29636 | 1.2355 | | | | 3 | 3 |
| 4 | SEX HSC IB MB | 0.31118 | 1.2381 | | | | 4 | |
| 4 | SEX HSC ZB MB | 0.30702 | 1.2456 | | | | | 5 |

**Table 3.** Correlation matrix of all variables used in model selection. Where SEX = Sex; FL = frontal length; LSC = length of sagittal crest; HSC = height of sagittal crest; CBL = condylobasal length; B = breadth of braincase; ZB = zygomatic breadth; and AGE = cementum age.

| | **SEX** | **FL** | **LSC** | **HSC** | **CBL** | **IB** | **B** | **ZB** | **MB** | **AGE** |
|---|---|---|---|---|---|---|---|---|---|---|
| **SEX** | 1.000 | -0.4414 | -0.2194 | -0.3364 | -0.4905 | -0.3572 | -0.4111 | -0.3505 | -0.3312 | -0.1001 |
| **FL** | -0.4414 | 1.000 | 0.6792 | 0.8623 | 0.9293 | 0.8552 | 0.8722 | 0.8664 | 0.8743 | 0.5109 |
| **LSC** | -0.2194 | 0.6792 | 1.000 | 0.8296 | 0.7151 | 0.6956 | 0.6968 | 0.8133 | 0.7925 | 0.6078 |
| **HSC** | -0.3364 | 0.8623 | 0.8296 | 1.000 | 0.8894 | 0.8755 | 0.8869 | 0.9155 | 0.9125 | 0.5817 |
| **CBL** | -0.4905 | 0.9293 | 0.7151 | 0.8894 | 1.000 | 0.8326 | 0.8598 | 0.9013 | 0.9230 | 0.4914 |
| **IB** | -0.3572 | 0.8552 | 0.6956 | 0.8755 | 0.8326 | 1.000 | 0.9585 | 0.8897 | 0.8773 | 0.5677 |
| **B** | -0.4111 | 0.8722 | 0.6968 | 0.8869 | 0.8598 | 0.9585 | 1.000 | 0.9059 | 0.8982 | 0.5768 |
| **ZB** | -0.3505 | 0.8664 | 0.8133 | 0.9155 | 0.9013 | 0.8897 | 0.9059 | 1.000 | 0.9583 | 0.6693 |
| **MB** | -0.3312 | 0.8743 | 0.7925 | 0.9125 | 0.9230 | 0.8773 | 0.8982 | 0.9583 | 1.000 | 0.6426 |
| **AGE** | -0.1001 | 0.5109 | 0.6078 | 0.5817 | 0.4914 | 0.5677 | 0.5768 | 0.6693 | 0.6426 | 1.000 |