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Growth, Sexual Dimorphism, and Geographical Variation of Skull Dimensions of the Brown Bear *Ursus arctos* in Hokkaido

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Abstract. The growth, sexual dimorphism, and geographical variation in skulls of 596 brown bears (*Ursus arctos*) hunted in Hokkaido, Japan from 1971 to 1986 were investigated. Most cranial traits continued to increase after the age of sexual maturity, and in particular skulls became progressively wider with age. Skulls of males, even those of cubs and yearlings, were larger than those of females, and the difference became significant after two years of age. Skull dimensions tended to increase from south to north, in Hokkaido, and bears from the north-eastern region possessed higher brain cases and longer mandibles relative to skull length and width, than those in the southern region.

Key words: Growth; Sexual dimorphism; Bergman's rule; Brown bear.

Yoneda and Abe (1976), in a pioneering investigation of brown bear *Ursus arctos* skulls from Hokkaido, demonstrated that there was an obvious sexual dimorphism in cranial size favoring males and a geographical cline in cranial size which gradually increased from the south-west to the north-east in Hokkaido after eight years of age. They were, however, unable to analyze sexual dimorphism and geographic variation statistically because their sample sizes were too small.

In this paper, we take Yoneda and Abe's (1976) further, and from a large sample supply we statistically analyzed the growth, sexual dimorphism, and geographical variation of brown bear skulls from Hokkaido. We also conducted canonical discriminant analysis of geographical variation in cranial morphology.

Materials and Methods

We collected 702 skulls of brown bears which had been hunted in Hokkaido from 1971 to 1986, 63 of which had been killed between 1971 and 1981, and 639 between 1982 and 1986. After the investigation, most skull specimens were returned to hunters, and a few tens were deposited at the Department of Oral Anatomy, School of Dentistry, Hokkaido University. Initial sexing of bears had been made based on observation of external genitalia, however, when the sex had not been recorded by the hunters, only specimens which were obviously distinguishable by the sex criteria of their skulls (Yoneda & Abe, 1976) were used for the investigation. After damaged skulls had also been removed from the sample, 596 skulls of sexed bears were retained for the examination.

Age, in years, was determined by counting the number of annual layers of cementum of an upper right canine (Yoneda, 1976). Age determination of cubs (0-year) and yearlings (1-year) was based on the condition of permanent tooth eruption (Inukai & Mukasa, 1934). Bears were divided arbitrarily into the following eight age classes. Age class I, 0 to 5 months old (assuming that all bears were born on 31 January) ; class II, 6 to 11 months old ; class III, 12 to 17 months old ; class IV, 18 to 23 months old ; class V, 2 and 3 years old ; class VI, 4 to 7 years old ; class VII, 8 to 10 years old ; class VIII, 11+ years old.

Hokkaido has been divided into three regions ; southern, central and north-eastern regions (Fig. 1) for the purpose of analysis, based on the locations where bears had been hunted. The demarcation of these regions corresponds essentially with those of isolated populations of bears (Abe, 1980 ; Division of Conservation, Hokkaido, 1986), although the northern part of the line separating the central and north-eastern regions was drawn arbitrarily as there seem to be no obvious geographical barriers to the movements of bears.

Skulls were boiled for 1 hr, put in 60 °C water with protainerse for 12 hrs, cleaned, then dried under natural conditions for three days or more. After a series of these treatments, skulls were measured and tooth roots were sampled for age determination.

Eleven cranial traits were measured: greatest length of cranium (GL), palatal length (PL), rostral width (RW), zygomatic width (ZW), distance between mastoids (MD), width of brain case (BW), height of brain case (BH), length of mandible (ML), height of mandible (MH), length of upper molar row (UML), and thickness of upper canine root (CT) (see Fig. 2). Calipers were used for the measurement of BH, and vernier calipers were used for the measurement of the other traits. UML and CT were measured to the nearest 0.1 mm, and the other traits to the nearest 1 mm.

Growth curves of some cranial traits were drawn for visual comparison of cranial size among the three regions. First, three growth curve models were fitted for the data of four cranial traits (GL, ZW, BH, BW). Then, curves of the best fit model were drawn. The three models used were the monomolecular

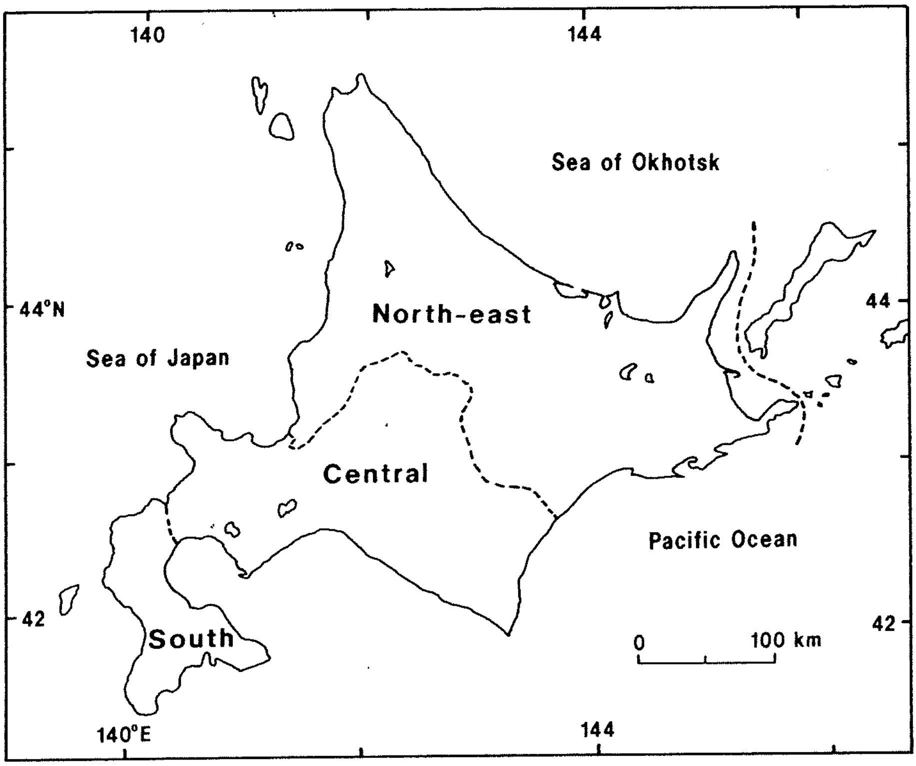

Fig. 1. The study area and the delineations of the southern, central, and north-eastern regions of Hokkaido, Japan.

curve, $L(t) = K - A \cdot \exp(-b \cdot t)$; the Gompertz curve, $L(t) = K \cdot A^{\exp(-b \cdot t)}$; and the logistic curve, $L(t) = K/(1 + A \cdot exp(-b \cdot t))$; where $L(t)$ is the size of a trait at age t (year), K the asymptotic size of the trait, A the constant of integration, and b the growth rate constant. These models were fitted using the corrected Gauss-Newton algorithm of the NLIN procedure of SAS[R] (Statistical Analysis System Institute, 1985). Here, the independent variable for the models was a bear's age in years, which we categorized as 0 (year) for 0 – 5 months of age, 0.5 for 6 – 11 months, 1 for 12 – 17 months, and 1.5 for 18 – 23 months.

The degree of sexual difference was expressed as the coefficient of difference (*CD* ; Mayr *et al.*, 1953). The formula for calculating *CD* is: $CD =$ (Mean of male − Mean of female) / (*SD* of male + *SD* of female). The growth rate of each trait was expressed as the ratio of the mean size in age class VIII (the most advanced class) to that in class V (sub-adult class).

To analyze the geographical variation in cranial morphology, canonical discriminant analysis was conducted on nine traits (GL, ZW, MD, BW, BH, ML, MH, UML, CT ; in natural-logarithm) of bears two or more years old, between the southern and north-eastern regions using the CANDISC procedure of SAS[R]

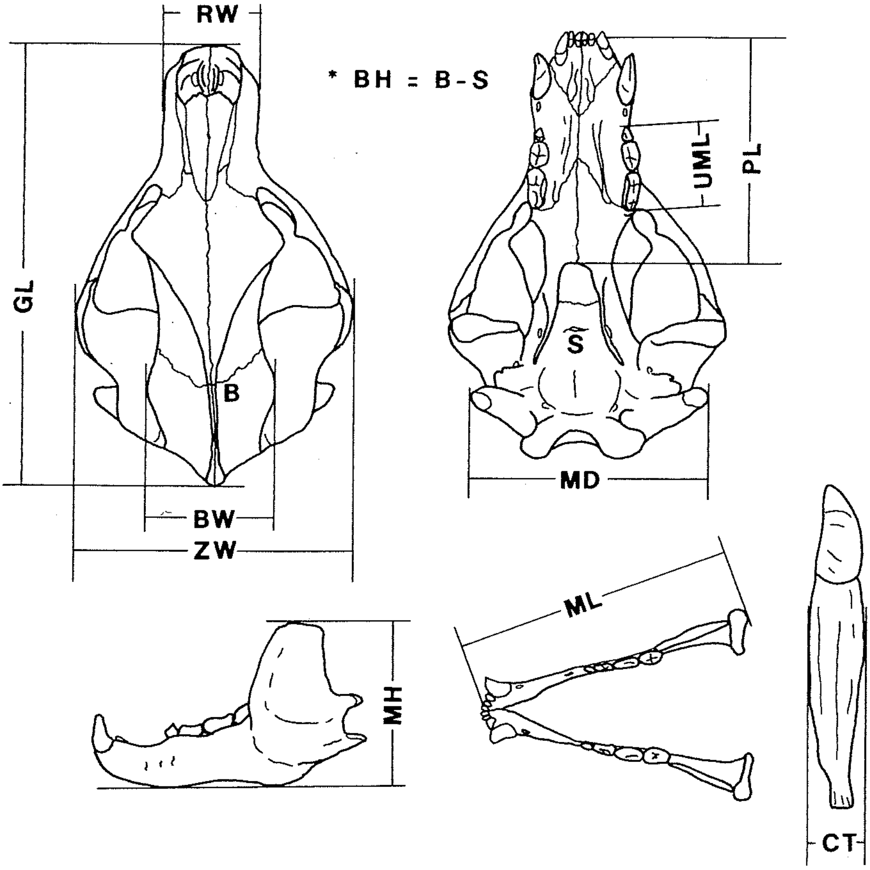

Fig. 2. Details of the 11 cranial traits measured in brown bears *Ursus arctos*. GL= greatest length of cranium; PL=palatal length; RW=rostral width; ZW=zygomatic width; MD=distance between mastoids; BW=width of brain case; BH=height of brain case; ML=length of mandible; MH=height of mandible; UML=length of upper molar row; and CT=thickness of upper canine root.

(Statistical Analysis System Institute, 1985).

Results

Most cranial traits increased with age, except for upper molar row length (UML), which showed no increase (Table 1). Of the former traits, growth rates were low in brain case width (BW) and canine thickness (CT), and high in zygomatic width (ZW) and the distance between mastoids (MD) (Table 1). Males had higher growth rates than females in almost all traits; the ratios varying from 0.99 to 1.56 in males and from 0.97 to 1.29 in females (Table 1).

The monomolecular growth curve proved the closest fit among the three

Table 1. Growth rates of 11 cranial traits in brown bears *Ursus arctos* in Hokkaido. Growth rates are calculated as the ratios of mean cranial size of age class VIII to that of age class V. South refers to the southern region, Central to the central region, and NE to the north-eastern region.

Trait	GL	PL	RW	ZW	MD	BW	BH	ML	MH	UML	CT
Male											
South	1.28	1.24	1.23	1.42	1.56	1.05	1.23	1.28	1.47	1.03	1.14
Central	1.23	1.17	1.20	1.42	1.52	1.05	1.22	1.22	1.37	1.00	1.13
NE	1.26	1.27	1.20	1.42	1.56	1.06	1.23	1.22	1.34	0.99	1.11
Female											
South	1.14	1.12	1.13	1.22	1.29	1.01	1.08	1.14	1.25	1.00	1.12
Central	1.12	1.12	1.11	1.21	1.23	1.02	1.07	1.12	1.19	0.99	1.11
NE	1.15	1.14	1.14	1.26	1.29	1.01	1.03	1.13	1.23	0.97	1.12

See Fig. 2 for abbreviations. Sample sizes are given in Appendices 1 and 2.

growth models (monomolecular, Gompertz, and logistic). All curves generated using the three models proved to be significant at the five percent level and showed only trivial deviations among them. Sums of squares of the residuals were smallest, however, in the monomolecular curves and largest in the logistic curves for most traits, except for height of brain case (BH) of both sexes in the north-eastern region (largest in the monomolecular curve and smallest in the logistic curve). The monomolecular growth curves for the greatest length (GL), zygomatic width (ZW), height of brain case (BH), and width of brain case (BW) are drawn in Figs. 3 and 4.

The greatest length (GL) and brain case height (BH) of females grew rapidly until eight to ten years of age and then slowly, while zygomatic width (ZW) and BH of males continued to increase until 15 – 20 years of age (Figs. 3 and 4). By contrast, brain case width (BW) nearly stopped increasing after four to six years (Fig. 4).

Skulls were found to become progressively wider with age and brain cases taller. Proportions of zygomatic width (ZW) and distance between mastoids (MD) against greatest length (GL) increased with advancing age class, while that of palatal length (PL) slightly decreased (Fig. 5). The proportion of brain case width (BW/GL) clearly decreased with age class, while that of brain case height (BH/GL) decreased only slightly (Fig. 6). The proportions of brain case height (BH/GL) of males, in age classes V – VIII, in the north-eastern region were significantly ($p<0.01$) greater than those in the southern region (analysis of variance with arcsine-transformation, two tailed; Sokal & Rohlf, 1981). Other proportions, however, showed no significant differences between the two regions.

Most cranial traits showed marked sexual dimorphism favoring males, and the dimorphism had already become significant after only two or three years of age. Skulls of males were significantly larger than those of females in all traits in age class V and more advanced age classes (Table 2). In addition, by

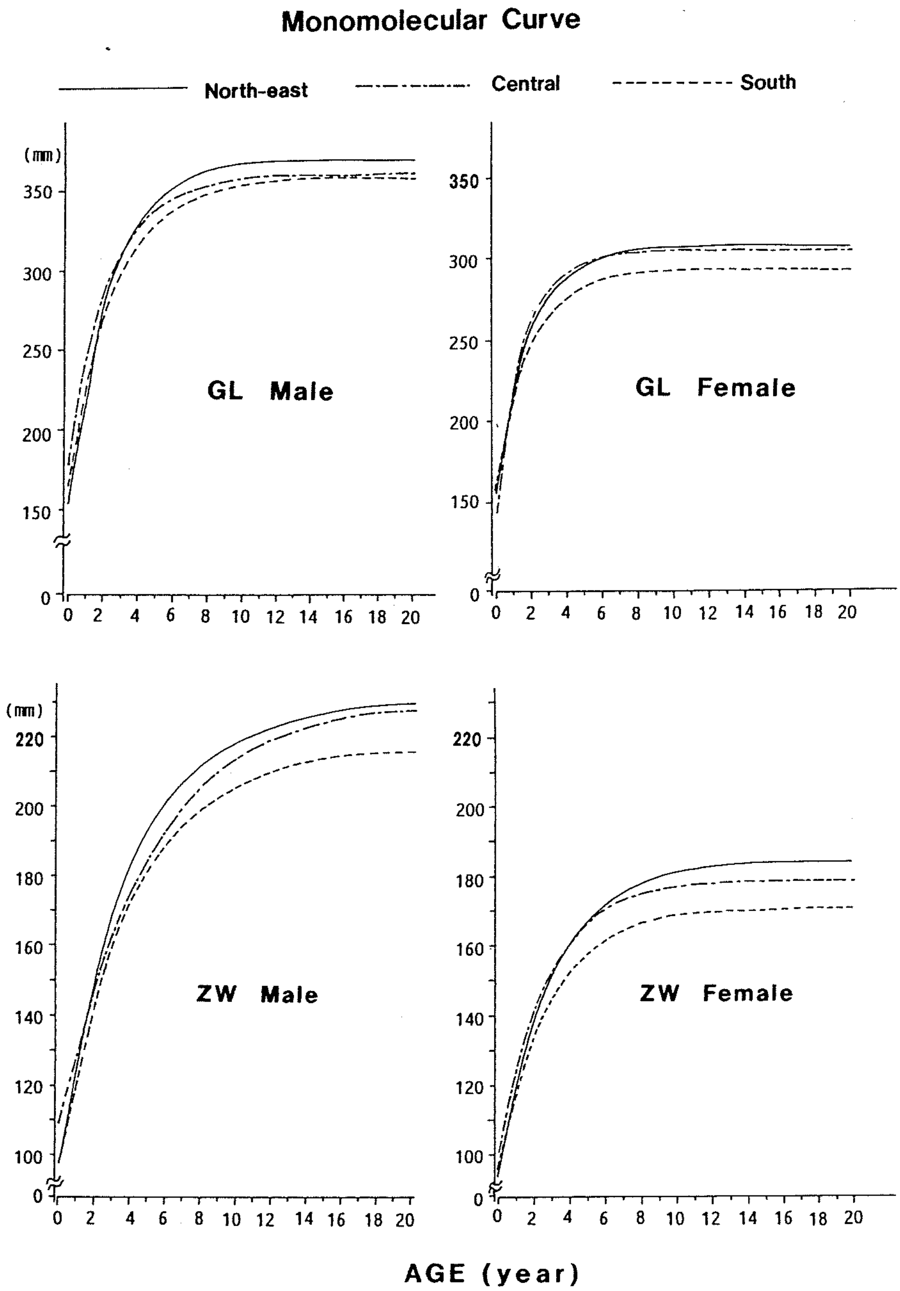

Fig. 3. The monomolecular growth curves of greatest length of cranium (GL) and zygomatic width (ZW) in brown bears *Ursus arctos* in Hokkaido.

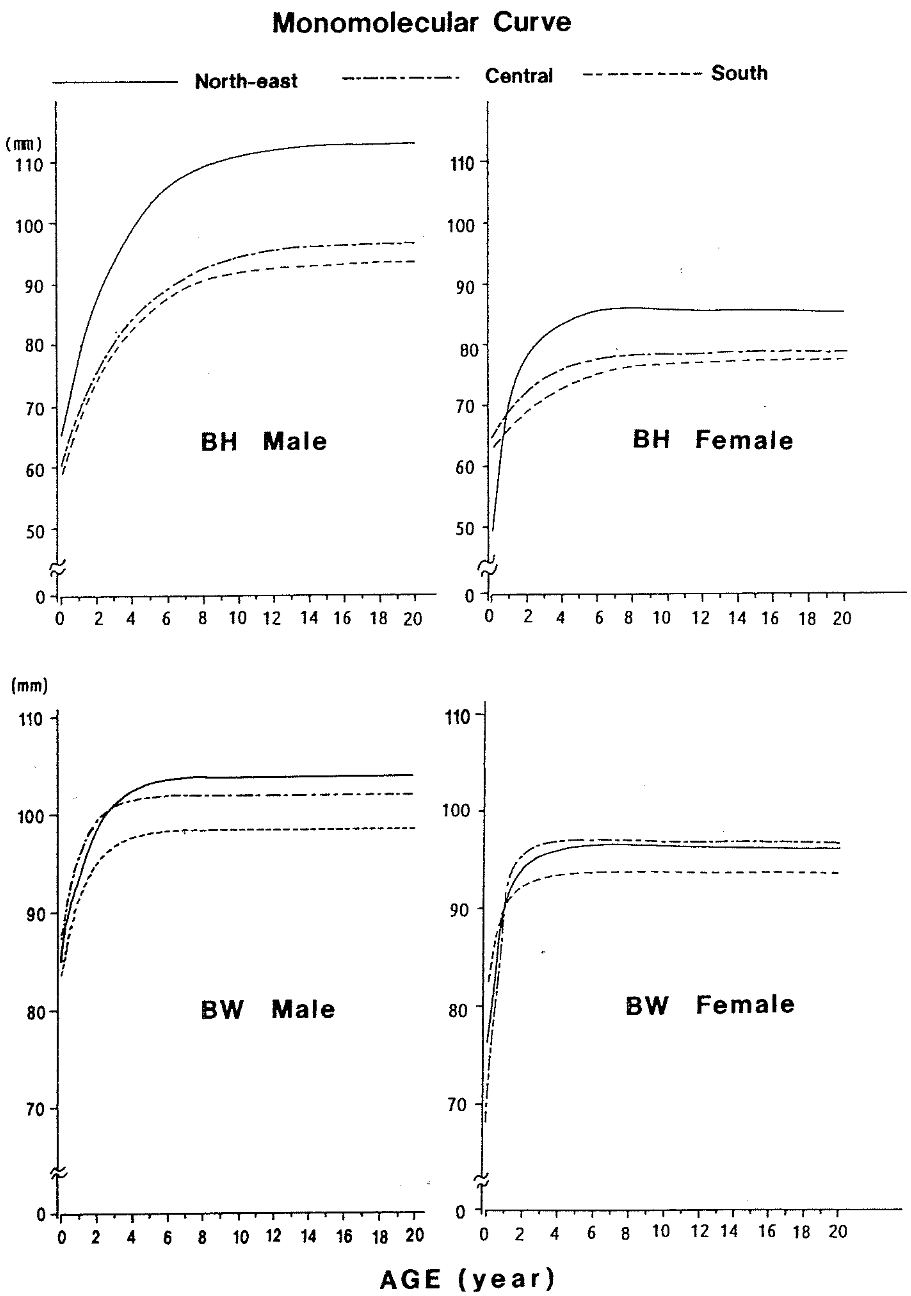

Fig. 4. The monomolecular growth curves of brain case height (BH) and brain case width (BW) in brown bears *Ursus arctos* in Hokkaido.

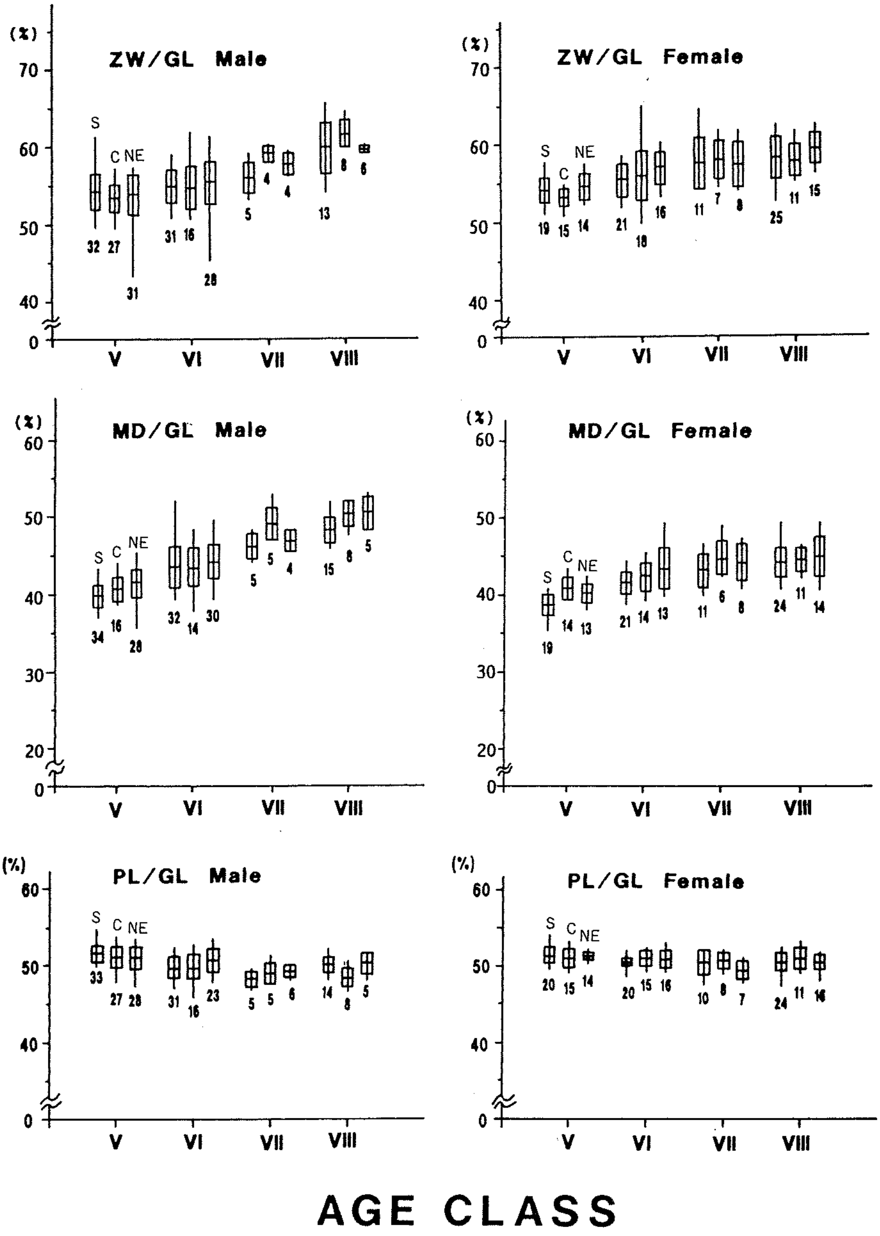

Fig. 5. Proportions of zygomatic width (ZW), distance between mastoids (MD), and palatal length (PL) against greatest length of cranium (GL) in brown bears *Ursus arctos* in Hokkaido. Median horizontal lines are means, boxes are *SD*, and vertical lines ars ranges. S=southern region; C=central region; and NE=north-eastern region. Numerals are sample numbers.

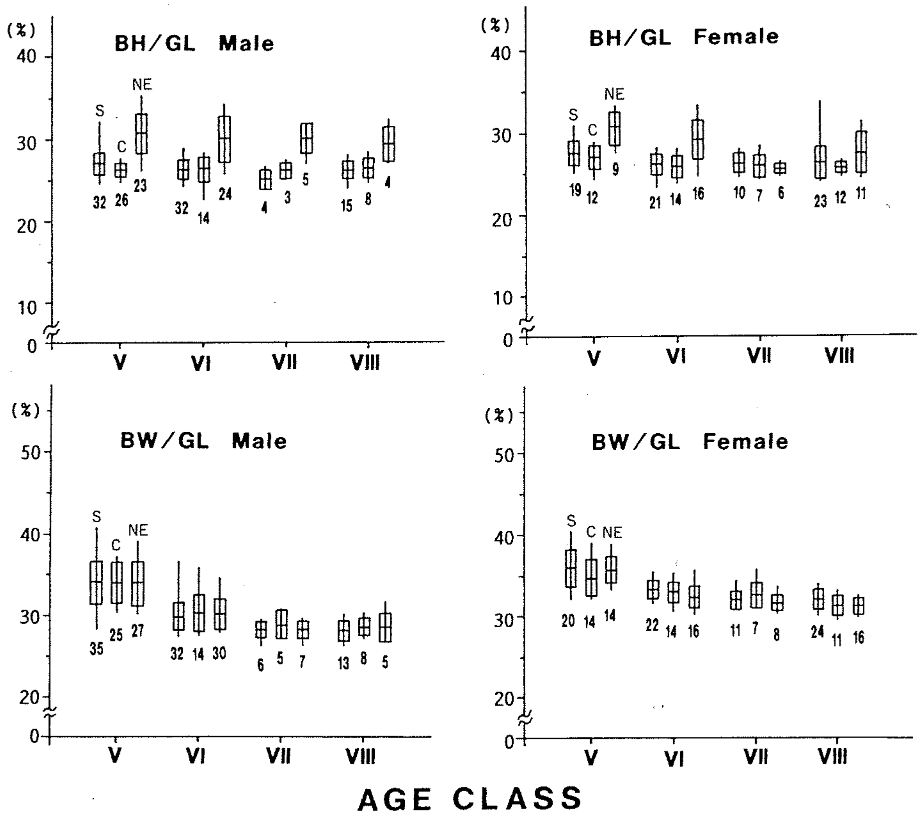

Fig. 6. Proportions of brain case height (BH) and width (BW) against greatest length of cranium (GL) in brown bears *Ursus arctos* in Hokkaido. Median horizontal lines are means, boxes are *SD*, and vertical lines are ranges. S=southern region; C=central region; and NE=north-eastern region. Numerals are sample numbers.

though not yet significant (Table 2; see also Appendices 1 and 2). The degree of sexual difference (*CD*) tended to increase with advancing age class. There were no obvious deviations in the degree of sexual difference between the southern and north-eastern regions (Table 2).

Cranial size was found to increase gradually from south to north in Hokkaido, although the cline was not observable in 0 and 1 year old individuals. Mean sizes of most traits, except upper molar row length (UML) in the north-eastern region, were significantly greater than those in the southern region in age classes V – VIII (Table 3), while no significant differences were found in a number of traits in age class III (and also in age classes II and IV; Appendices 1 and 2). Furthermore, mean cranial size tended to increase from the southern via the central to the north-eastern region (Figs. 3 and 4; see also Appendices 1 and 2).

Table 2. Sexual differences of 11 cranial traits, and the results of analysis of variance (two tailed), in brown bears *Ursus arctos* in Hokkaido. Sexual difference is expressed as the coefficient of difference (*CD*) between sexes. Calculation for the coefficient of difference is given in the text. ns=non-significant ($p \geq 0.01$) ; *=significant ($p < 0.01$).

Age class	III	V	VI	VII	VIII
Southern region					
GL	0.16 ns	0.66 *	1.61 *	2.26 *	3.00 *
PL	0.23 ns	0.71 *	1.41 *	1.78 *	2.53 *
RW	0.34 ns	0.97 *	1.60 *	1.76 *	2.29 *
ZW	0.28 ns	0.65 *	1.15 *	1.26 *	2.22 *
MD	0.12 ns	0.60 *	1.15 *	2.02 *	2.98 *
BW	0.10 ns	0.46 *	0.62 *	0.86 *	1.07 *
BH	0.40 ns	0.54 *	1.18 *	1.33 *	1.60 *
ML	−0.04 ns	0.58 *	1.36 *	1.37 *	2.58 *
MH	−0.02 ns	0.47 *	1.03 *	1.73 *	2.44 *
UML	0.17 ns	0.87 *	0.94 *	1.04 *	1.30 *
CT	—	1.27 *	2.63 *	1.92 *	2.27 *
North-eastern region					
GL	0.36 ns	0.82 *	1.01 *	1.63 *	2.63 *
PL	0.22 ns	0.83 *	1.30 *	1.33 *	4.29 *
RW	0.70 ns	1.06 *	1.15 *	1.89 *	2.12 *
ZW	0.47 ns	0.71 *	0.65 *	1.92 *	2.17 *
MD	0.34 ns	0.92 *	0.56 *	1.66 *	2.54 *
BW	0.31 ns	0.78 *	0.54 *	0.89 *	1.68 *
BH	0.50 ns	0.68 *	0.73 *	2.90 *	1.83 *
ML	0.27 ns	0.99 *	1.54 *	1.86 *	5.38 *
MH	0.23 ns	0.78 *	0.99 *	1.25 *	2.78 *
UML	0.61 ns	0.64 *	1.15 *	1.05 *	0.97 *
CT	—	1.92 *	2.54 *	1.96 *	2.17 *

See Fig. 2 for abbreviations. Sample sizes are given in Appendices 1 and 2.

Bears in the north-eastern region had taller brain cases and longer mandibles, relative to skull length and width, than those in the southern region. In the canonical discriminant analysis, the first canonical variable chiefly contributed to the geographical difference of cranial morphology between the southern and north-eastern regions (Fig. 7). The first canonical variable was largely affected by brain case height (BH) and mandible length (ML) (positively) and by the greatest length (GL) and distance between mastoids (MD) (negatively) in males (Table 4) ; therefore, the positive direction of the first canonical valuable can be interpreted as 'relatively tall brain case and long mandible to the length and width of skull'. A similar trend was demonstrated

Table 3. Regional comparison of mean sizes of 11 cranial traits between the southern (S) and north-eastern (NE) regions and the results of analysis of variance (two tailed) in brown bears *Ursus arctos* in Hokkaido. ns=non-significant ($p \geq 0.05$) ; Asterisks for significance (*=$p<0.05$; **=$p<0.01$; and ***=$p<0.001$).

Age class	III	V	VI	VII	VIII
Male					
GL	S>NE ns	NE>S *	NE>S *	NE>S ns	NE>S *
PL	S>NE ns	NE>S *	NE>S ***	NE>S *	NE>S ***
RW	NE>S **	NE>S ***	NE>S ***	NE>S *	NE>S *
ZW	NE=S ns	NE>S *	NE>S *	NE>S *	NE>S *
MD	NE>S ns	NE>S ***	NE>S *	NE>S ns	NE>S ***
BW	NE>S ns	NE>S ***	NE>S ***	NE>S **	NE>S **
BH	NE>S **	NE>S ***	NE>S ***	NE>S ***	NE>S ***
ML	NE>S **	NE>S ***	NE>S ***	NE>S ns	NE>S *
MH	S>NE ns	NE>S **	NE>S **	NE>S *	NE>S ns
UML	S>NE ns	NE>S ns	NE>S ns	NE>S ns	S>NE *
CT	–	NE>S **	NE>S **	NE>S ns	NE>S ns
Female					
GL	S>NE ns	NE>S ns	NE>S ***	NE>S *	NE>S ***
PL	–	NE>S *	NE>S ***	NE>S *	NE>S ***
RW	NE>S ns	NE>S **	NE>S ***	NE>S ns	NE>S ***
ZW	S>NE ns	NE>S *	NE>S ***	NE>S *	NE>S ***
MD	NE>S ns	NE>S *	NE>S ***	NE>S **	NE>S ***
BW	–	NE>S *	NE>S ***	NE>S *	NE>S *
BH	NE>S ns	NE>S ***	NE>S ***	NE>S *	NE>S **
ML	S>NE ns	NE>S *	NE>S ***	NE>S ns	NE>S **
MH	S>NE ns	NE>S *	NE>S ***	NE>S ns	NE>S *
UML	–	NE>S *	NE>S ns	S>NE ns	S>NE ns
CT	–	NE>S *	NE>S *	NE>S ns	NE>S *

See Fig. 2 for abbreviations. Sample sizes are given in Appendices 1 and 2.

in females, although the absolute values of the canonical coefficients were low (Table 4).

Discussion

Skulls of brown bears from Hokkaido appear to attain their maximum size after the age of physiological sexual maturity, which is at 2 – 5 years old for males and 3 – 4 years old for females (Tsubota, 1988). Some cranial traits, such as greatest length (GL), grew rapidly until 8 – 10 years old and other traits, such as zygomatic width (ZW), continued to grow rapidly until 15 – 20 years old (Figs. 3 and 4). These traits reached ca. 80 – 90% of their asymptotic size, however, just before the age of sexual maturity. For example, the mean greatest length of female skulls from the southern region was 257.6

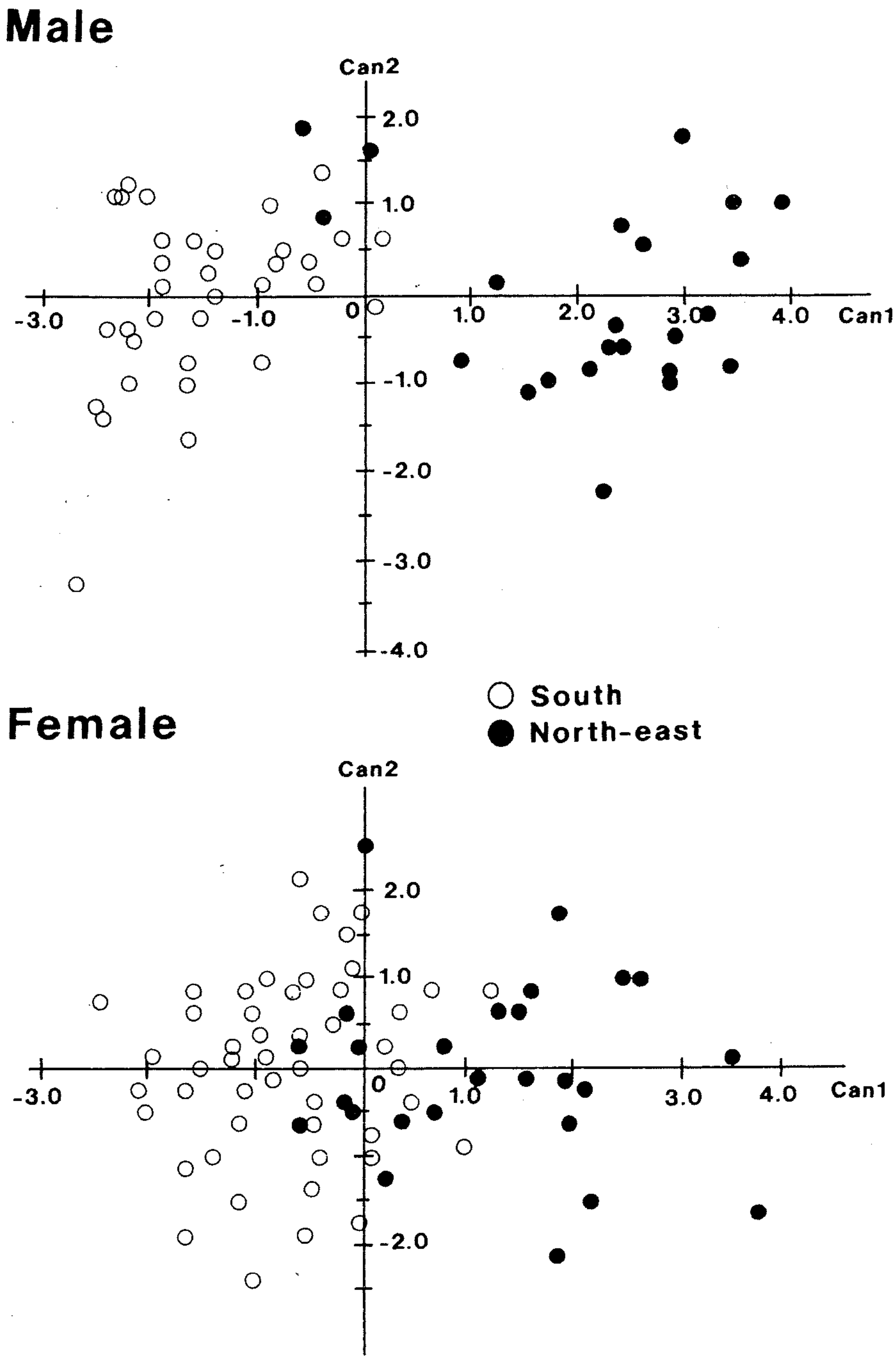

Fig. 7. Plots of canonical discriminant functions on the first by the second canonical variable plane (Can 1 by Can 2) in the canonical discriminant analysis of nine cranial traits between the southern region (open circles) and the north-eastern region (solid circles) in 2+ years brown bears *Ursus arctos* in Hokkaido. The canonical functions are plotted by using raw canonical coefficients.

Table 4. Standardized canonical coefficients of nine cranial traits (in natural-logarithm) for the canonical discriminant analysis between the southern and north-eastern regions in 2+ years brown bears *Ursus arctos* in Hokkaido. Can 1=first canonical variable; Can 2=second canonical variable. The coefficients for the third–ninth canonical variables are omitted.

Trait	Male		Female	
	Can 1	Can 2	Can 1	Can 2
GL	−1.615	−1.205	−0.167	−2.536
ZW	−0.945	0.916	−0.070	−1.945
MD	−1.188	−2.095	0.211	2.560
BW	−0.026	−1.160	0.268	−0.482
BH	2.361	0.306	1.235	0.259
ML	2.591	2.669	0.305	1.824
MH	−0.224	0.110	−0.274	0.107
UML	−0.012	0.240	−0.030	0.049
CT	0.287	−0.007	−0.237	0.173

See Fig. 2 for abbreviations.

mm in age class V (sub-adult class) and 292.7 mm in age class VIII (the most advanced class); the percentage of the former to the latter thereby being 88.0% (from Appendix 2). A similar phenomenon has previously been reported from North America, where Kingsley *et al.* (1988) reported that the body length of female brown bears in northern Canada and northwest Alaska reached 90% of the asymptotic size just before sexual maturity, but continued to increase after that.

The present study has demonstrated explicitly that skulls of brown bears become wider with age, although it has been implicitly shown previously by allometric growth. Mukasa (1934) and Suenaga (1972), for example, reported that Hokkaido brown bear skulls showed positive allometric growth in dimensions of width, such as zygomatic width and distance between mastoids, against dimensions of length, such as greatest length and condylobasal length. Similar allometric growth has been reported for the American black bear *U. americanus* (Rausch, 1961) and the Japanese black bear *Selenarctos thibetanus japonicus* (Mukasa, 1934). In the present study, the proportions of width against length, such as ZW/GL and MD/GL, were found to increase with age class (Fig. 5), explicitly indicating that skulls become wider with age.

Sexual dimorphism in cranial size favoring males was found among juveniles and became significant after two or three years of age; this is consistent with the dimorphism of some external body measurements of brown bears reported by other authors. Blanchard (1987), for example, reported that in the grizzly bear *U. arctos horribilis*, sexual dimorphism in body length and chest

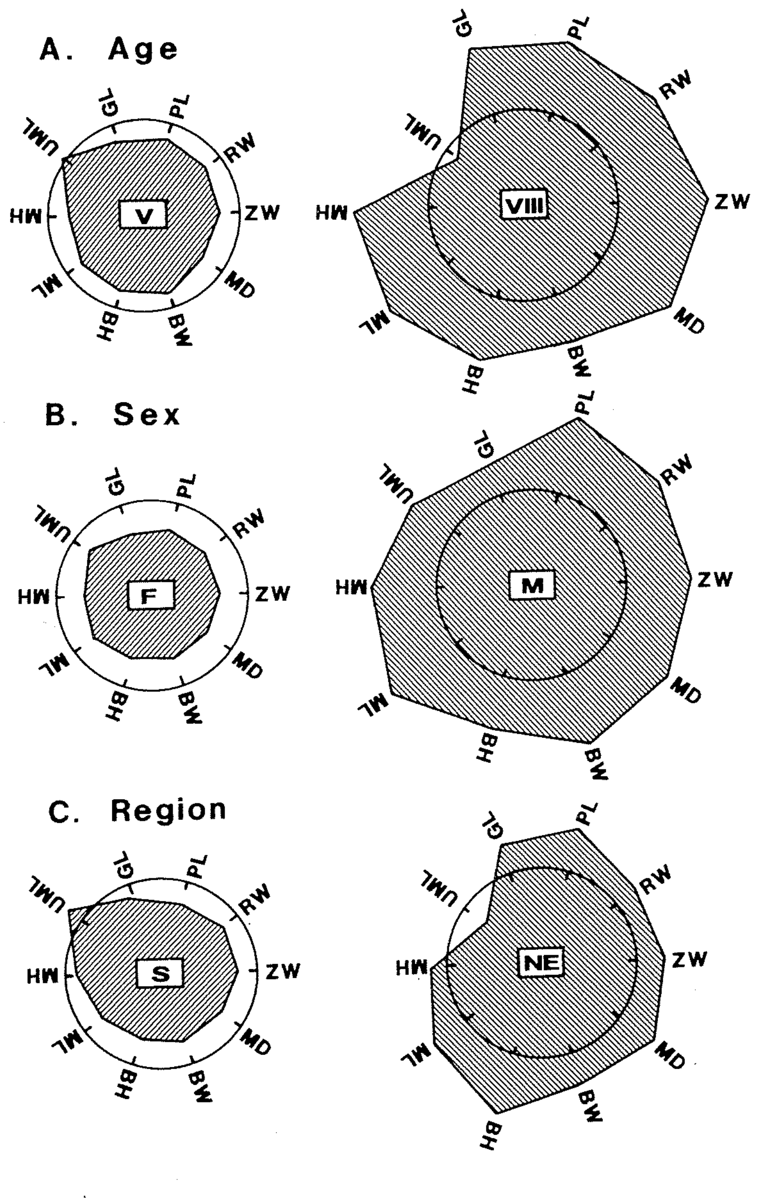

Fig. 8. Morphograms drawn of the Z-score between age classes (A; age class V versus class VIII, of males in the southern region), between sexes (B; female vs. male, of age class VIII in the southern region), and between regions (C; southern region vs. north-eastern region, of males in age class VIII) in brown bears *Ursus arctos* in Hokkaido.

Z-score of a trait for group i (Z_i) is calculated as follows: $Z_i = (X_i - M) / SD$; where X_i is the mean of the trait for group i, M is the total mean of the trait, and SD is the total standard deviation of the trait. Z-scores of each trait are plotted along the radius of a circle, and the length of the radius is two (scaled by the Z-score). The circumference expresses the total mean for each trait ($Z_i = 0$), and the Z-score becomes negative toward the inside of the circumference and positive toward the outside. See Fig. 2 for abbreviations.

girth was apparent even in cubs and became significant after three years of age. In addition, sexual dimorphism favoring males, in some body measurements of captive Hokkaido brown bears, has been found as early as one year of age, and the differences became significant after four years of age (Maeda & Ohdachi, in press).

Sexual dimorphism in brown bear cranial size might result from male-male competition for females, although the genetic effects on the differences in cranial size are not known yet. In brown bears, male-male combat (direct fighting) in the mating season is severe, and it is supposed that larger males have a greater likelihood of reproductive success than smaller ones (Pulliainen *et al.*, 1984).

Cranial size was found to increase in a cline from south to north in Hokkaido, supporting Yoneda and Abe's (1976) conclusion, and several factors are thought to cause this geographical variation. One factor is the geographical difference in dietary condition (both quantitative and qualitative) which would affect overall growth rate. Rausch (1963) and Yoneda and Abe (1976) have both suggested that the availability of salmon and trout as food was one of the most important factors causing geographical variation in cranial size in brown bears. Salmon and trout, however, occupy only a small part of the present diet of bears in Hokkaido (Abe *et al.*, 1987 ; Kadosaki, 1983 ; Ohdachi & Aoi, 1987), and thus it seems less plausible that the geographical cline is solely as a result of differences in the availability of fish today. Instead, a general effect of differences in dietary condition could be the main factor involved, since food items and their consumption vary between various regions of Hokkaido (Abe *et al.*, 1987 ; Ohdachi & Aoi, 1987). A further factor potentially affecting geographical variation in cranial size is climatic difference. In general, the period of snow-cover is shorter, and temperatures are higher in southern parts of Hokkaido than in northern and eastern parts. Hence, geographical variation in cranial size might be explained in the context of climatic adaptation such as reduction of heat loss (e. g., McNab, 1971 ; Scholander, 1955, 1956).

The ontogenetic pattern of cranial growth may relate to the geographical variation in skulls. The pattern of the deviation of morphograms from young to old individuals was similar to the pattern from the southern to north-eastern regions, although the degree of increase with age, of mandible height (MH), was much greater than the degree of difference from the southern to north-eastern regions (Fig. 8). Generally, those traits whose growth rates were high also demonstrated large increases from the southern to north-eastern regions, as Yoneda and Abe (1976) pointed out. In contrast, however, upper molar row length (UML) was much larger in males than in females, while there was only a little deviation of UML between age classes or between regions (Fig. 8), making the deviation pattern of sexual dimorphism different from those of growth and geographical variation. Thus, bears in the southern region could be said to be paedomorphic, and the geographical variation of the skulls seems to be concerned with cranial growth. In other words, geographical variation might be affected by adjusting the ontogenetic patterns of skulls in brown bears.

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References

Abe, H. 1980. Distribution of the brown bear. *In* The Report on the Second Survey of Distributions of Wildlife (Mammals) (Japasese Agency of Environment, ed.) pp. 87–96. Japan Wildlife Research Center, Tokyo (in Japanese).

Abe, H. *et al.* 1987. The Report on Ecological Researches of Brown Bears. Division of Conservation, Hokkaido Government, Sapporo, 75 pp. (in Japanese).

Blanchard, B. M. 1987. Size and growth patterns of the Yellowstone grizzly bear. Int. Conf. Bear Res. and Manage., 7: 99–107.

Division of Conservation, Hokkaido. 1986. The Report on Distributions of Wildlife. Brown Bears and Sika Deer. Division of Conservation, Hokkaido Government, Sapporo, 115 pp. (in Japanese).

Inukai T. & K. Mukasa. 1934. Über den Zahnwechsel des Yesso Braunbären, *Ursus arctos yesoensis* Lyd. Separatabdruck aus Folia Anatomica Japonica, 7: 291–301.

Kadosaki, M. 1983. Food habits of the brown bear in Hokkaido (I). J. Mamm. Soc. Japan, 9: 116–127 (in Japanese with English abstract).

Kingsley, M. C. S., J. A. Nagy & H. V. Reynolds. 1988. Growth in length and weight of northern brown bears: differences between sexes and populations. Canad. J. Zool., 66: 981–986.

Maeda, N. & S. Ohdachi. In press. Growth and body measurements of the brown bear in captivity. Proceedings of the Second Asiatic Bear Conference 1991.

Mayr, E., E. G. Linsley & R. L. Usinger. 1953. Methods and Principles of Systematic Zoology. McGraw-Hill, New York, 428 pp.

McNab, B. K. 1971. On the ecological significance of Bergman's rule. Ecology, 52: 845–854.

Mukasa, K. 1934. The growth of the crania of Yezo brown bear. Trans. Sapporo Nat. Hist. Soc., 15: 96–111.

Ohdachi, S. & T. Aoi. 1987. Food habits of brown bears in Hokkaido, Japan. Int. Conf. Bear Res. and Manage., 7: 215–220.

Pulliainen, E., Y. Luukkonen & T. Hietajärvi. 1984. Formation of a dominance hierarchy among wild brown bears (*Ursus arctos*). Zeit. Säugetierkunde, 49: 58–59.

Rausch, R. L. 1961. Notes on the black bear, *Ursus americanus* Pallas, in Alaska, with particular reference to dentition and growth. Zeit. Säugetierkunde, 26: 1–31.

Rausch, R. L. 1963. Geographic variation in size in North American brown bears, *Ursus arctos* L., as indicated by condylobasal length. Canad. J. Zool., 41 : 33−45.

Scholander, P. F. 1955. Evolution of climatic adaptation in homeotherms. Evolution, 9 : 15−26.

Scholander, P. F. 1956. Climatic rules. Evolution, 10 : 339−340.

Sokal, R. R. & F. J. Rohlf. 1981. Biometry. The Principles and Practice of Statistics in Biological Research. 2nd ed. W. H. Freeman & Co., New York, 859 pp.

Statistical Analysis System Institute. 1985. SAS User's Guide : Statistics. Version 5 ed. SAS Institute Inc., Cary, North Carolina, 956 pp.

Suenaga, Y. 1972. Morphological studies on the skull of the Yezo brown bear I. Growth of the skull size. Jap. J. Vet. Sci., 34 : 17−28 (in Japanese with English abstract).

Tsubota, T. 1988. Studies on Reproductive Physiology of Hokkaido Brown Bears. Ph. D. Dissertation, Hokkaido University, Sapporo, 90 pp. (in Japanese).

Yoneda, M. 1976. Age determination and age structure of the Ezo brown bear. J. Mamm. Soc. Japan, 7 : 1−8 (in Japanese with English abstract).

Yoneda, M. & H. Abe. 1976. Sexual dimorphism and geographic variation in the skull of the Ezo brown bear (*Ursus arctos yesoensis*). Mem. Fac. Agr., Hokkaido Univ., 9 : 265−276 (in Japanese with English abstract).

Appendix 1. Renults of skull measurements of male brown bears *Ursus arctos* in Hokkaido. S, southern region; C, central region; NE, north-eastern region. Abbreviations for cranial traits are given in Fig. 2

Age class		I				II				III				IV			
		N	Range	Mean	SD	N	Range	Mean	SD	N	Range	Mean	SD	N	Range	Mean	SD
GL	S	2	145-150	147.5	3.54	9	166-231	204.6	20.98	15	197-265	223.9	20.10	6	239-270	250.8	11.79
	C	0	-	-	-	5	186-228	210.0	15.15	4	186-238	224.0	15.35	6	257-282	270.5	9.20
	NE	0	-	-	-	2	188-203	195.5	10.61	9	209-240	222.6	11.05	2	289-304	296.5	10.61
PL	S	2	75-76	75.5	0.71	10	88-114	103.9	8.62	14	101-136	115.6	10.23	7	116-142	127.4	8.12
	C	0	-	-	-	5	94-117	106.2	8.32	4	93-121	113.0	13.37	6	136-149	141.5	5.36
	NE	1	-	73.0	-	2	95-103	99.0	5.66	9	103-121	113.0	6.20	2	151-156	153.5	3.54
RW	S	3	37-40	38.3	1.53	10	40-51	46.2	4.02	15	45-59	51.9	4.53	7	53-66	57.6	4.72
	C	0	-	-	-	5	43-51	47.6	2.97	4	45-58	51.8	5.32	6	61-67	64.5	2.17
	NE	1	-	42.0	-	2	50-52	51.0	1.41	9	49-59	53.3	3.28	2	68-71	69.5	2.12
ZW	S	2	92-92	92.0	0.00	10	94-125	111.8	8.97	13	108-139	123.2	10.61	6	123-139	131.0	6.78
	C	0	-	-	-	4	106-117	112.3	4.65	3	105-131	120.3	13.61	5	133-148	142.0	6.04
	NE	0	-	-	-	2	108-116	112.0	5.66	9	117-132	123.2	5.65	2	156-157	156.5	0.71
MD	S	2	68-68	68.0	0.00	9	70-93	80.3	7.33	12	78-105	87.3	7.77	6	87-106	96.3	8.66
	C	0	-	-	-	4	74-87	82.8	5.97	3	79-99	90.7	10.41	4	103-122	110.5	8.10
	NE	1	-	70.0	-	2	77-86	81.5	6.36	9	80-99	90.0	5.77	2	118-121	119.5	2.12
BW	S	3	80-81	80.7	0.58	9	80-97	88.4	4.33	14	87-95	92.4	2.62	6	88-97	93.5	3.02
	C	0	-	-	-	5	88-98	91.6	3.91	3	97-100	98.3	1.53	5	94-100	96.6	2.41
	NE	1	-	87.0	-	2	88-90	89.0	1.41	10	85-100	92.7	4.55	2	102-102	102.0	0.00
BH	S	2	57-57	57.0	0.00	8	63-70	66.1	2.54	14	66-77	69.2	3.14	6	68-73	70.3	2.25
	C	0	-	-	-	5	61-71	65.4	4.34	4	64-69	66.8	2.06	6	69-78	72.2	3.31
	NE	0	-	-	-	0	-	-	-	6	70-90	77.7	7.28	2	80-98	89.0	12.73
ML	S	2	104-109	106.5	3.54	7	117-159	141.7	15.42	11	142-173	156.6	8.70	7	158-193	172.9	10.68
	C	0	-	-	-	5	133-159	146.4	9.79	3	127-169	153.3	22.94	5	176-196	187.2	7.69
	NE	0	-	-	-	2	133-149	141.0	11.31	7	145-170	156.7	9.94	1	-	212.0	-
MH	S	3	44-45	44.3	0.58	10	47-70	61.9	5.93	15	60-82	69.7	6.82	7	68-81	75.0	5.63
	C	0	-	-	-	5	60-69	65.6	3.36	4	60-78	70.5	7.72	6	79-93	83.8	4.96
	NE	1	-	45.0	-	2	60-68	64.0	5.66	8	63-75	69.4	4.21	2	95-97	96.0	1.41
UML	S	0	-	-	-	0	-	-	-	9	64.8-78.1	70.87	3.916	7	63.5-77.5	70.17	4.930
	C	0	-	-	-	0	-	-	-	1	-	72.40	-	6	68.3-77.2	73.20	3.936
	NE	0	-	-	-	0	-	-	-	8	67.1-74.1	70.59	2.619	2	74.3-77.9	76.10	2.546
CT	S	0	-	-	-	0	-	-	-	1	-	14.60	-	4	13.4-15.1	14.03	0.741
	C	0	-	-	-	0	-	-	-	0	-	-	-	6	10.7-15.2	14.22	1.749
	NE	0	-	-	-	0	-	-	-	0	-	-	-	2	15.8-16.0	15.90	0.141

(to be continued)

Appendix 1 (continued).

Age class		V				VI				VII				VIII			
		N	Range	Mean	SD	N	Range	Mean	SD	N	Range	Mean	SD	N	Range	Mean	SD
GL	S	37	237-329	282.7	21.38	33	277-363	329.5	18.54	6	327-367	348.7	12.85	15	333-380	360.5	13.31
	C	28	257-333	298.7	22.20	17	265-369	332.2	28.59	5	354-375	364.8	7.66	8	336-396	367.8	19.42
	NE	32	252-356	297.3	27.01	31	274-386	340.6	24.01	7	337-392	366.9	20.40	7	348-395	374.6	17.33
PL	S	36	126-165	145.1	10.28	33	141-181	164.2	9.06	7	156-178	169.9	8.55	14	168-193	180.6	7.15
	C	29	132-169	152.0	10.90	17	140-187	165.4	14.05	6	173-182	177.8	3.97	8	170-188	177.9	7.68
	NE	30	119-175	152.3	13.20	26	157-200	176.5	10.18	7	169-194	181.9	11.42	7	188-200	192.7	4.31
RW	S	43	53-74	64.1	4.70	36	64-80	71.4	3.85	10	71-83	75.6	4.20	14	71-84	78.8	3.70
	C	30	60-80	69.0	4.68	17	63-80	73.8	5.00	6	70-82	78.2	4.45	8	77-87	82.5	3.66
	NE	34	57-78	68.3	5.05	36	62-82	75.0	4.44	7	73-87	80.7	5.19	9	76-88	82.1	3.44
ZW	S	35	130-179	151.7	11.56	33	158-209	181.7	13.06	6	185-217	195.8	12.22	13	187-236	214.7	12.58
	C	28	140-182	159.9	11.82	17	143-201	180.8	16.00	5	209-223	214.2	5.63	8	217-241	226.4	8.85
	NE	32	131-188	159.8	14.33	30	152-224	189.8	16.24	6	195-235	217.8	15.09	7	207-245	227.7	12.16
MD	S	37	93-135	112.0	10.89	32	116-186	143.6	15.01	5	152-175	161.6	9.86	15	158-190	174.3	8.16
	C	16	99-143	122.2	13.33	14	110-162	144.3	17.68	5	171-192	179.8	8.58	8	173-206	185.3	12.38
	NE	29	100-152	124.1	13.20	32	113-184	151.8	16.60	6	154-203	175.5	16.84	8	169-216	193.6	14.26
BW	S	38	90-102	95.4	3.12	32	91-104	97.5	2.86	6	96-101	98.2	2.32	13	95-105	100.6	3.40
	C	26	94-114	100.0	4.87	14	93-105	98.4	4.07	6	96-109	104.3	5.05	8	99-112	104.9	4.02
	NE	29	94-108	100.2	4.00	31	91-110	102.1	4.45	9	100-109	103.9	2.80	8	100-111	106.1	3.91
BH	S	35	69-88	76.1	4.82	33	74-103	85.9	6.05	5	80-88	85.0	3.00	15	83-99	93.7	4.56
	C	26	67-87	79.0	5.66	15	70-98	86.6	8.44	4	90-100	95.5	4.12	8	90-103	96.5	5.35
	NE	24	75-105	91.2	9.25	25	80-121	102.1	11.85	6	102-117	108.0	5.29	6	100-119	111.8	7.19
ML	S	25	170-209	191.0	11.17	23	192-245	221.8	11.61	4	220-254	235.0	14.09	9	230-254	244.6	8.88
	C	27	181-225	203.0	13.82	18	187-246	224.8	17.57	6	235-253	244.8	6.85	8	231-269	247.1	12.32
	NE	19	161-238	210.6	17.85	23	213-253	234.3	11.44	5	231-255	245.8	9.55	4	255-260	257.5	2.38
MH	S	42	72-110	88.1	9.93	36	91-135	109.9	9.96	9	116-130	121.4	5.27	15	112-137	129.1	6.89
	C	29	81-130	97.9	12.44	18	89-132	115.1	11.43	6	118-144	131.0	10.10	8	125-147	133.9	8.25
	NE	35	79-115	95.6	10.06	33	95-130	117.6	8.75	8	118-144	131.1	10.12	10	123-137	132.5	4.72
UML	S	44	67.2-80.5	72.98	3.153	35	68.9-79.2	73.73	2.921	10	68.5-78.4	74.08	2.869	14	70.7-79.2	74.89	2.247
	C	21	70.3-81.0	75.42	2.898	16	66.3-82.1	73.49	4.202	6	69.8-79.7	75.43	3.263	8	68.9-82.1	75.63	3.744
	NE	33	65.5-80.0	73.58	2.975	34	68.2-80.1	75.06	3.103	7	68.4-79.5	74.34	4.011	9	69.7-76.1	72.64	2.346
CT	S	39	9.7-19.0	14.39	1.567	35	13.9-17.3	15.62	0.870	9	15.2-19.7	16.68	1.446	15	14.7-17.6	16.43	0.883
	C	21	12.6-18.8	15.26	1.326	14	12.9-16.5	14.93	1.300	6	14.0-18.3	15.83	1.528	8	15.7-19.2	17.25	1.241
	NE	28	11.4-16.8	15.38	1.169	28	14.0-17.7	16.26	0.866	7	15.3-19.2	16.79	1.364	8	15.4-18.1	17.05	0.805

Appendix 2. Results of skull measurements of female brown bears *Ursus arctos* in Hokkaido. S, southern region; C, central region; NE, north-eastern region. Abbreviations for cranial traits are given in Fig. 2

Age class		I				II				III				IV			
		N	Range	Mean	SD	N	Range	Mean	SD	N	Range	Mean	SD	N	Range	Mean	SD
GL	S	0	-	-	-	6	168-206	192.3	13.54	4	188-240	216.8	24.13	1	-	209.0	-
	C	0	-	-	-	0	-	-	-	3	203-230	218.7	14.01	0	-	-	-
	NE	0	-	-	-	0	-	-	-	8	193-229	214.1	12.32	3	229-263	247.7	17.24
PL	S	0	-	-	-	5	83-104	97.8	8.76	2	104-118	111.0	9.90	1	-	108.0	-
	C	0	-	-	-	0	-	-	-	3	103-119	112.3	8.33	0	-	-	-
	NE	0	-	-	-	0	-	-	-	12	102-126	110.7	4.48	4	120-138	130.8	7.89
RW	S	0	-	-	-	6	40-46	43.5	2.17	4	43-54	48.8	4.50	1	-	49.0	-
	C	0	-	-	-	0	-	-	-	3	48-55	51.0	3.61	0	-	-	-
	NE	0	-	-	-	1	-	46.0	-	14	45-53	49.4	2.31	5	50-69	58.6	8.02
ZW	S	0	-	-	-	6	97-116	108.3	7.61	3	109-124	118.0	7.94	1	-	119.0	-
	C	0	-	-	-	0	-	-	-	3	118-128	124.7	5.77	0	-	-	-
	NE	0	-	-	-	0	-	-	-	11	106-126	117.5	6.38	3	121-142	133.0	10.97
MD	S	0	-	-	-	6	69-88	78.5	6.53	3	73-97	85.0	12.00	1	-	86.0	-
	C	0	-	-	-	0	-	-	-	3	83-92	88.7	4.93	0	-	-	-
	NE	0	-	-	-	0	-	-	-	14	78-57	86.1	5.72	4	85-109	99.5	10.34
BW	S	0	-	-	-	6	82-91	87.0	3.58	2	91-93	92.0	1.41	1	-	92.0	-
	C	0	-	-	-	0	-	-	-	3	91-92	91.3	0.58	0	-	-	-
	NE	0	-	-	-	0	-	-	-	13	84-94	90.3	3.12	4	88-95	92.3	3.10
BH	S	0	-	-	-	6	59-75	65.3	6.00	3	63-71	66.3	4.16	1	-	66.0	-
	C	0	-	-	-	0	-	-	-	3	66-72	69.0	3.00	0	-	-	-
	NE	0	-	-	-	0	-	-	-	7	63-80	71.4	5.35	4	66-76	71.3	4.57
ML	S	0	-	-	-	4	133-142	136.8	4.11	4	148-169	157.3	10.87	1	-	150.0	-
	C	0	-	-	-	0	-	-	-	2	146-166	156.0	14.14	0	-	-	-
	NE	0	-	-	-	0	-	-	-	10	136-164	151.6	8.77	1	-	183.0	-
MH	S	0	-	-	-	6	49-63	59.5	5.32	4	65-76	70.0	5.35	1	-	69.0	-
	C	0	-	-	-	0	-	-	-	3	64-75	71.3	6.35	0	-	-	-
	NE	0	-	-	-	1	-	-	-	14	59-75	67.6	3.63	5	69-86	77.6	5.57
UML	S	0	-	-	-	0	-	-	-	2	67.2-72.1	69.65	3.465	1	-	64.60	-
	C	0	-	-	-	0	-	-	-	2	63.3-70.1	66.70	4.808	0	-	-	-
	NE	0	-	-	-	0	-	-	-	11	65.2-72.1	67.66	2.218	5	66.3-72.7	69.12	3.197
CT	S	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-
	C	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-
	NE	0	-	-	-	0	-	-	-	0	-	-	-	3	12.3-14.8	13.43	1.266

(to be continued)

Appendix 2 (continued).

Age class		V				VI				VII				VIII			
		N	Range	Mean	SD	N	Range	Mean	SD	N	Range	Mean	SD	N	Range	Mean	SD
GL	S	21	223-285	257.6	16.81	22	264-303	283.6	10.02	11	281-310	294.5	11.12	26	273-313	292.7	9.27
	C	15	246-308	277.4	17.86	18	277-320	296.1	11.83	8	268-311	298.5	13.53	12	296-340	311.2	12.27
	NE	15	240-284	265.7	11.62	17	286-341	302.4	13.70	8	297-344	309.3	14.85	16	291-327	306.6	8.50
PL	S	22	113-148	131.4	8.96	26	132-152	143.8	5.38	11	144-156	148.4	3.50	30	136-162	147.3	6.00
	C	16	130-152	141.5	7.38	16	136-158	151.3	6.17	10	141-158	150.5	5.90	12	147-177	158.5	7.93
	NE	17	123-146	136.6	5.80	20	144-201	154.7	6.59	8	144-169	155.0	8.86	21	141-161	155.3	4.41
RW	S	22	53-64	56.9	2.72	29	56-66	61.0	2.67	13	59-68	63.5	2.67	37	58-71	64.2	2.67
	C	16	58-65	61.9	2.38	20	72-84	64.9	3.16	7	60-68	64.8	2.78	15	63-77	69.0	3.66
	NE	19	53-64	59.9	2.87	22	61-75	66.0	3.36	10	61-69	65.7	2.75	25	62-74	68.0	3.22
ZW	S	19	127-157	139.3	7.62	23	142-172	157.5	7.98	12	152-184	169.8	8.44	31	156-185	170.5	7.29
	C	16	131-169	148.4	10.21	20	152-194	166.7	10.65	9	162-182	173.1	7.27	12	164-196	180.2	8.15
	NE	16	132-156	145.1	6.45	18	152-201	172.6	10.09	8	169-185	177.3	5.95	17	167-202	182.6	8.60
MD	S	19	86-115	100.4	8.53	23	105-135	118.6	6.79	11	112-138	127.5	7.01	25	112-145	129.6	6.83
	C	14	100-130	113.3	9.47	16	114-139	126.3	7.77	8	123-148	131.9	8.20	11	125-158	139.1	8.23
	NE	15	97-119	106.8	5.69	17	117-169	134.5	14.23	9	127-145	137.6	5.98	19	124-152	137.4	7.84
BW	S	20	87-101	92.4	3.47	23	90-99	94.3	2.27	12	90-97	94.3	2.22	25	87-98	93.4	3.33
	C	14	91-102	96.0	2.86	16	93-102	97.1	2.14	8	93-101	97.3	2.82	11	90-102	97.5	3.36
	NE	15	90-100	94.9	2.76	20	92-104	97.7	3.57	8	94-107	97.6	4.24	21	90-100	95.4	2.46
BH	S	19	66-86	71.0	4.67	22	66-80	74.1	3.97	10	72-82	76.9	3.07	24	67-99	76.8	5.97
	C	12	67-82	74.7	3.92	15	72-84	76.4	3.52	8	72-86	77.5	4.00	12	75-91	79.7	4.31
	NE	9	71-89	80.6	6.44	18	76-97	88.7	6.56	7	76-87	81.1	3.98	12	72-96	83.4	8.34
ML	S	15	159-200	177.5	11.96	21	183-210	196.4	7.04	10	192-219	204.6	8.03	30	187-214	202.6	7.40
	C	15	175-214	191.9	10.18	18	182-217	203.3	8.39	9	193-215	204.4	7.80	11	197-232	214.6	9.76
	NE	16	171-198	185.4	7.60	15	198-219	206.3	6.76	8	206-232	212.5	8.32	14	200-227	210.3	6.39
MH	S	23	68-94	80.3	6.77	30	81-104	93.7	5.84	14	90-114	100.7	6.73	35	91-107	100.1	4.98
	C	16	77-104	90.8	7.58	20	87-110	98.5	5.74	9	100-113	104.8	4.32	13	94-120	108.2	7.53
	NE	18	79-93	84.6	4.03	20	95-121	102.5	6.43	11	96-123	107.0	9.17	23	93-118	103.8	5.59
UML	S	24	63.6-74.1	68.15	2.382	29	59.9-73.7	67.99	3.171	14	62.7-71.4	68.11	2.894	35	62.5-75.2	68.10	2.958
	C	15	64.9-74.0	69.34	2.486	17	64.4-73.7	70.24	2.703	10	63.9-75.0	68.46	3.338	15	63.9-74.5	68.93	2.907
	NE	19	63.6-73.7	70.05	2.576	20	63.7-73.5	68.84	2.296	10	64.9-71.9	67.89	2.134	24	63.2-73.8	68.05	2.398
CT	S	24	10.2-13.2	11.47	0.725	28	10.3-12.5	11.77	0.585	13	10.7-13.6	12.52	0.726	32	11.4-14.4	12.80	0.719
	C	14	11.0-13.0	11.90	0.632	16	11.4-14.4	12.55	0.850	8	11.5-13.8	12.28	0.792	13	12.2-14.3	13.18	0.691
	NE	18	10.5-12.7	11.93	0.626	19	11.2-13.9	12.24	0.715	10	11.7-13.8	12.82	0.665	19	11.9-15.6	13.36	0.895