

BRAIN VOLUME OF TAIGA MOOSE (*Alces alces* sp.) IN
RELATION TO SKULL PARAMETERS - A PILOT STUDY

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Abstract: The ontogeny of the skull was studied by comparing brain case volume (BCV) and 13 cranial parameters of 30 male and 24 female moose of known age harvested in 1979. Results: (1) As with other cervid skulls, the males exhibited greater variability in brain growth than females; (2) Cohorts born in 1976 and 1977 had smaller BCV than those of 1978 and 1979; (3) The skull was fully developed by 40 months of age; (4) The height and width of the brain case related well with BCV; (5) A trend in sex dimorphism was evident, similar to that for the maximum upper orbital width; (6) Minimum frontal bone width was highly sex dimorphic, growing hyperbolically in males and linearly in females; (7) The eye angle enlarged during the first 3 years from $34^{\circ} \pm 6$ to $44^{\circ} \pm 8$. Four Alaskan male moose (older than 6 years of age) had eye angles of only 30° to 38° , i.e. less than any taiga moose over 2 years old. This could mean that stereopsis in mature taiga moose is better developed than in its tundra relatives; (8) No significant sex dimorphism was found in the relationships between maximum upper orbital width and the parameters of maximum and condylo-basal lengths, and maximum width of the brain case. Good correlation exists for maximum length (ML) vs. pedicle diameter. It seems that BCV could be a valuable tool for prediction of generation performance and population status. Dentition patterns in calves and yearlings point to a 3 month calving period.

It is common knowledge that undernourishment during pregnancy and/or the nursing period are major causes of a small and under-developed brain. Such brains have lower DNA content and fewer synapses, and the animals show impaired learning ability and extremely low thresholds for alarm stimuli (Barnes et al. 1970, Bronzino et al. 1975, Castellano and Oliverio

1975, Corah et al. 1975, Crile and Quiring 1940, Dobbing 1970, Engsner et al. 1970, Greenough 1975, Jerison 1973, Morgane et al. 1978, Sacher 1970, Sara et al. 1974, Sobotka et al. 1974, Stein et al. 1976, Van Marthens et al. 1975, Winick 1976, Wintzerith et al. 1974).

Our unpublished studies in different ungulate species (*Cervus elaphus*, *Capreolus capreolus*, *Odocoileus virginianus*, *Rupicapra rupicapra*) have shown great variability of brain volume, especially for males. This could be related to the finding that the growth of the brain, which has been found to correlate well with overall growth (Brody and Kibler 1941, Bronson 1979, Hahn et al. 1979, Mangold-Wirz 1966, Oboussier and Schleimann 1966), is impaired more in males than females by fetal malnutrition, and by social stressors to which the pregnant mother may have been exposed (Dahlof et al. 1977, Saal 1979, Sara et al. 1974). Such animals also have a lower life expectancy (Barnes et al. 1970, Stein et al. 1976). This could possibly explain why the demographic structures of free living animals often display a zig-zag, instead of a staircase-like build up, as would be expected from longevity curves (Bubenik 1979, Bubenik and Schwab 1977, Smith and Wishart 1978).

Based on this background information, we decided to examine the following variables in a pilot study: (1) brain growth in relation to age, (2) the individual differences in brain volume, (3) variability of brain volume in both genders, (4) variability in brain volume of different generations, and (5) which cranial parameters do and do not correlate with brain volume. Finally, we followed (6) the mineralization progress of both cartilages of the basisphenoids, as indicators of terminated growth of the brain case (Schuhmacher 1939), and (7) the progress of milk tooth replacement, to

determine if there were any relationships amongst the brain case, skull growth and the expected date of birth.

MATERIAL AND METHODS

During the first 20 days of the 1979 hunting season the following 53 moose skulls (Table 1) were collected from the Black Sturgeon River area of north central Ontario (Latitude 48°50', Longitude 88°23').

Table 1. Number, age and sex of moose collected in the Black Sturgeon area of Ontario, 1979.

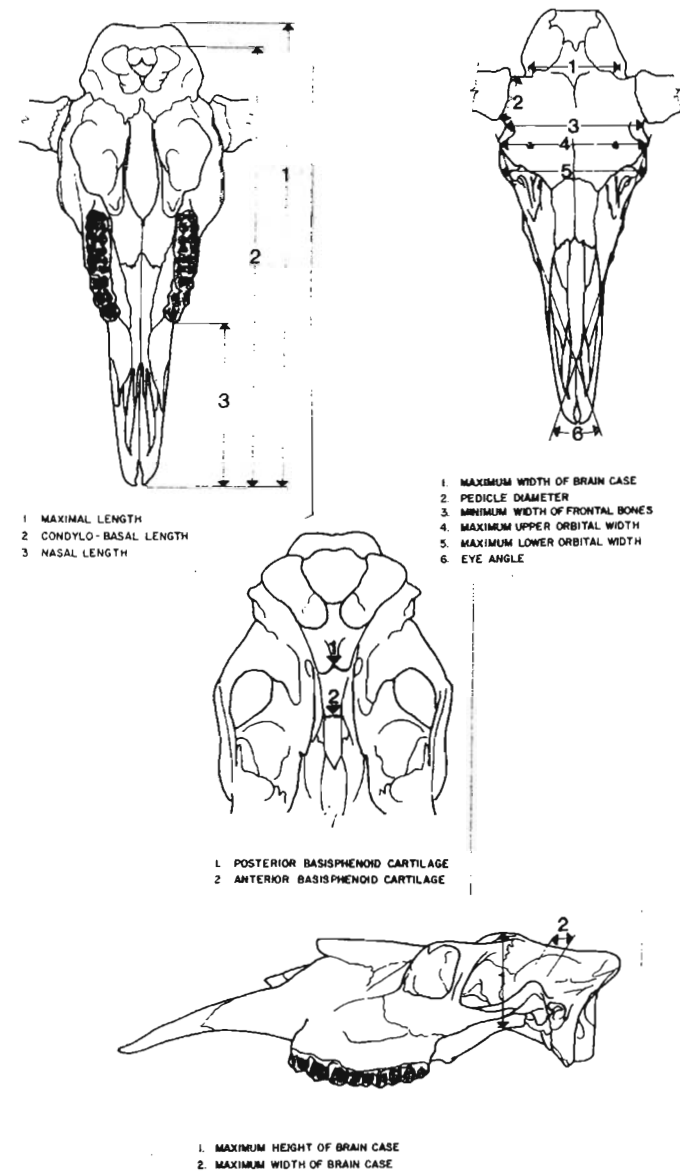
Age (years)	Males	Females
0.5	11	7 (includes one pair of twins)
1.5	10	6
2.5	2	7
3.5	4	3
4.5 to 15.5	2	1
Alaskan > 6 years	4	

One skull of a well-developed Alaskan moose (*A.a.gigas*) was used for comparison, along with the eye angles of three additional Alaskan moose.

The brain volume measurements were replaced by measurements of the brain case volume (BCV) using a new measuring technique developed by Bubenik and Bellhouse (in prep) which provides a highly reliable approximation of the brain volume.

All cranial measurements were done with calipers (accuracy to 1 mm) and protractor (accurate to 1°). The following variables were measured (Fig. 1):

Figure 1.



maximum length (ML), condylo-basal length (CBL) and nasal length (NL), maximum width of the brain case (MWBC), maximum upper orbital width (MUOW), maximum lower orbital width (MLOW), minimum width of frontal bones (MFBW). Other measurements included the diameter of the pedicle bases (PD), the maximum height of the brain case (MHBC), and the eye-angle (EA).

In order to follow the growth of the brain case, we checked the progress of mineralization of the anterior and posterior cartilages of the basisphenoid bone (ABC, PBL) (Fig. 1). These sites permit a longitudinal growth of the BC (Schuhmacher 1939). The progress of mineralization is expressed on a scale of 0 to 5. A value of 1 means that the first mineralized bridge was observed and a value of 5 represents skulls in which no traces of the suture could be seen.

The progress of the tooth eruption pattern (TEP) was also expressed as an index, using the following formula: each individual tooth on one side of the lower and upper jaw was assigned a score of -4 if it was not visible at all, -3 if the tooth was not erupted but the bone over the tooth was open, -2 if the tooth was barely protruding from the jaw, -1 if a tooth was half erupted, and 0 if fully erupted. The summed index is the total of the scores for all incisors, the canine, premolars and molars. An index of 0 represents fully established permanent dentition and a value of -20 indicates the most retarded pattern for calves shot between October 11 and 31. Ranges between -14 and -16 for calves, and between 0 and -2 for yearlings were considered as normal for the age according to Peterson's (1955) description of tooth development of moose.

We also checked all possible indices of winter severity (Monthly Record: Meteorological Observations in Ontario) in December to April of the years 1973 to 1979, to determine if there was a correlation to the

brain case values. Under extreme winter conditions, energy losses, food shortage and impaired lactation in exhausted mothers could be expected (Sobotka et al. 1974), which could adversely affect brain case growth of fetuses and neonates.

Because of the generally low number of specimens per class, especially those moose over 2 years old, we did not attempt statistical evaluation. Our findings to date have undergone graphical interpretation only, and we have attempted to draw by hand the approximations of expected confidence limits of the skull development.

RESULTS

Growth of the BCV (Fig. 2) in both genders, followed a hyperbolic curve, with an unknown beginning because newborn specimens were lacking. The most striking finding was that, of the generations of 1979 and 1978, about 50% were above the BCV of those born in 1977, 1976 and 1975. This we conclude from the fact that the 1978 yearlings whose skulls are still

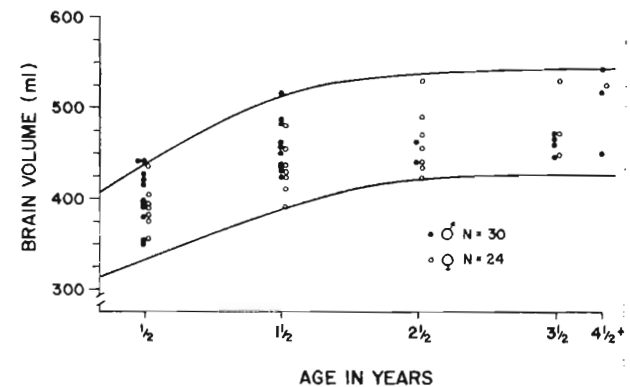
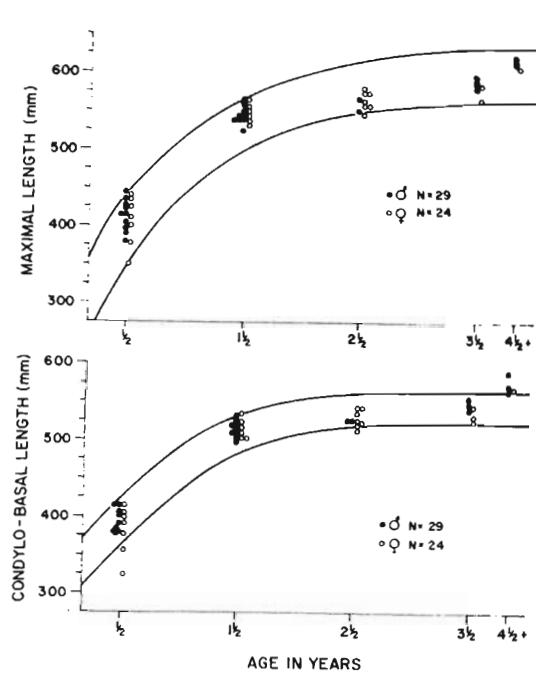


Figure 2.

growing, have the BCV almost as large as the 2½ year old cohorts. Therefore, there is a distinct possibility that the 1978 and 1979 generations will grow larger BCV than those that are now 2½ years old. The BCV of some of the calves from 1979 presumably lie on the growth curve of that expected for *Alces a. gigas*. Considering only the calves and yearlings we notice that the generation from 1978 shows a much greater variability in males than in females when compared to the generation born in 1979, which appears quantitatively the best. The growth of the skull in length (Fig. 3a,b) is similar to the trend in Fig. 2. The generations of 1978 and 1979 should have obviously longer skulls than those of 1976 and 1975. The two female twin calves which match the trend expected for years 1977 and 1976 are an exception. Each member of twin calves are generally lighter in weight than single calves (Heptner et al. 1974).



MWBC (Fig. 4a) grows nearly linearly up to about 3½ years. There was a similar difference between the generations of 1979, 1978 and 1977, 1976, as there was with BCV, ML and CBL. In view of this index, the calving year of 1977 appears to have been the worst. Some of the calves of 1979 have BCV as large as the 2½ year olds. The 15 year old bull fits into the trend of the good generation.

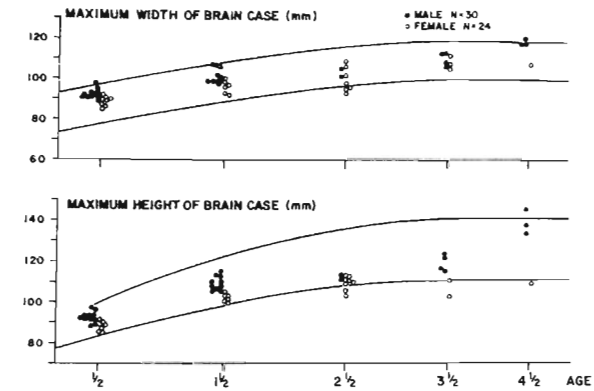


Figure 4.

The MHBC (Fig. 4b) is growing faster than MWBC and may be a better indicator of the qualitative differences between generations. Again, the 1977 generation appeared to be the worst.

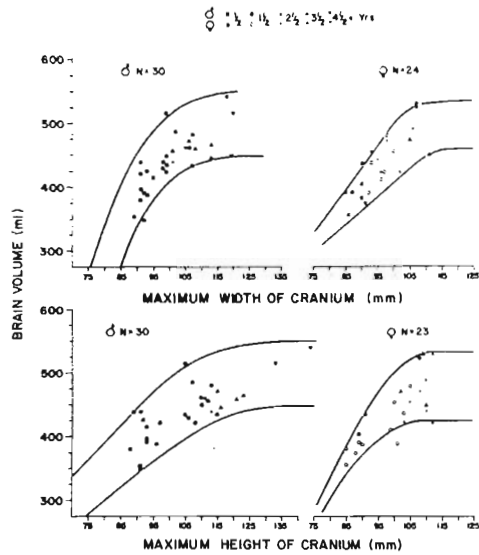


Figure 5. Relationships between BCV vs. MWBC and BCV vs. MHBC show relatively wide distributions of values which appear smaller in females than in males.

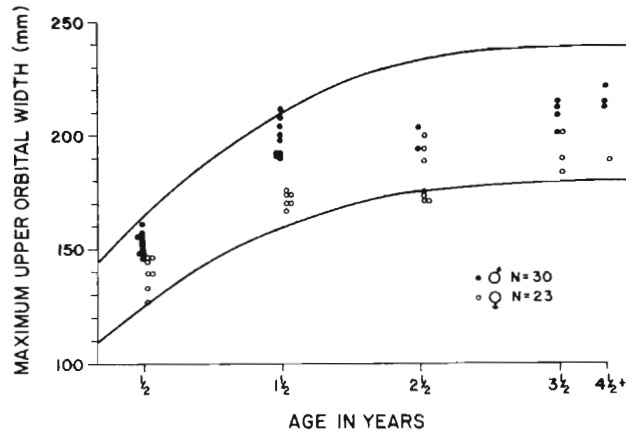


Figure 6. The MUOW parameter is obviously sex dimorphic. Males have larger and faster growing MUOW than females.

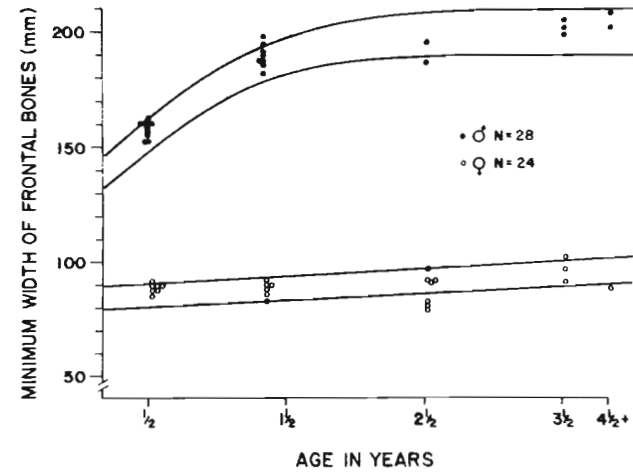


Figure 7. MFBW is a perfectly sexually dimorphic parameter. It is surprising that in females, the relationship is practically linear, and yet, apparently hyperbolic in males. Again, values for the calves and yearlings of both sexes show better development than the 2 1/2 year olds.

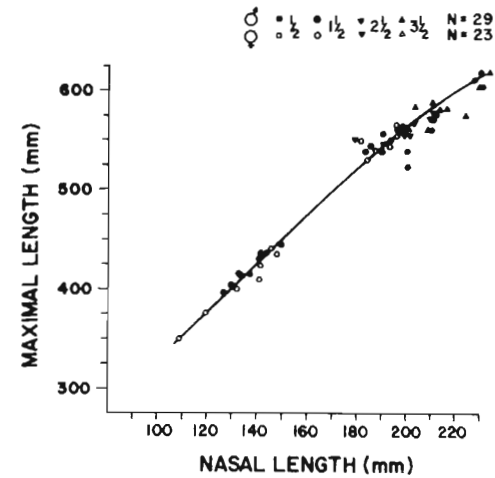


Figure 8. ML vs. NL shows a nearly linear relationship and indicates that bulls over 2 years of age have longer skulls than cows of the same age.

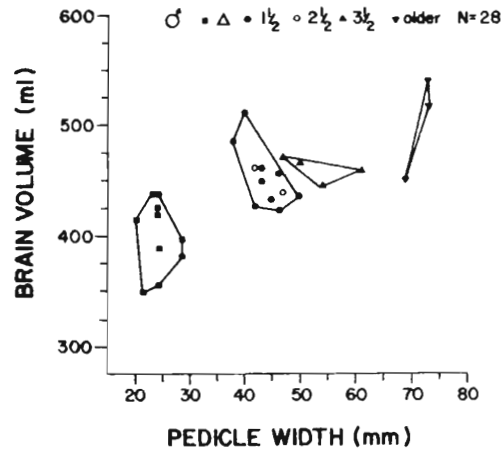


Figure 9. In comparison with other cervid species (Anderson et al. 1974, Bubenik et al. in prep.) we were surprised to find great variance in the relationship of BCV vs. PD.

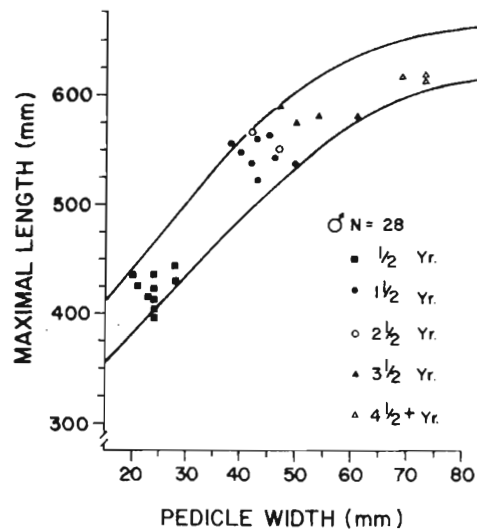


Figure 10. ML vs. PD correlates much better than BCV vs. PD. Pedicle growth is faster than that of the whole skull.

EA vs. Age (Fig. 11) shows great variance, with a pronounced trend for growth along an S-shaped curve, which is an unusual phenomenon in growth processes (Huxley 1972). In calves the EA is about $34^{\circ} \pm 6$ and in full grown specimens of taiga moose (3.5 years or more) the EA reaches an average value of $44^{\circ} \pm 6$. A comparison of 4 mature Alaskan bulls (*Alces a. gigas*) aged 6 to 14 years reveals that the EA of these tundra relatives shows little or no growth.

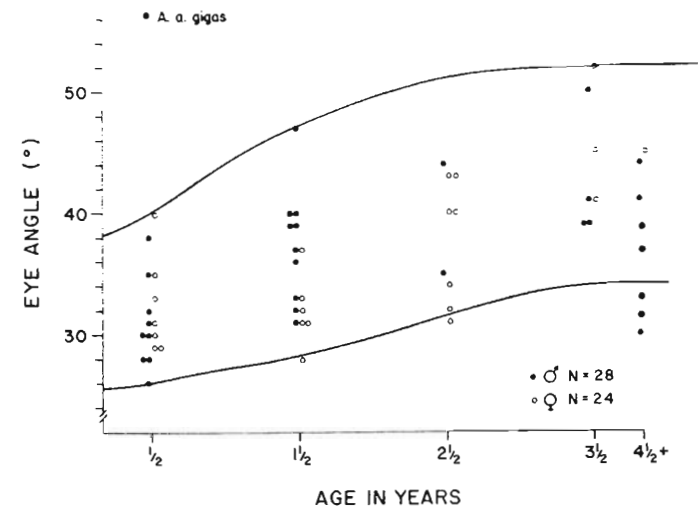


Figure 11.

Since there was a possibility that the horizontally oriented pedicles could influence the growth in the upper orbital region (i.e. that it may be sexually dimorphic), we compared the MUOW to the MLOW (Fig. 12). As the figure shows the growth of both of these parameters has the same trend in both sexes.

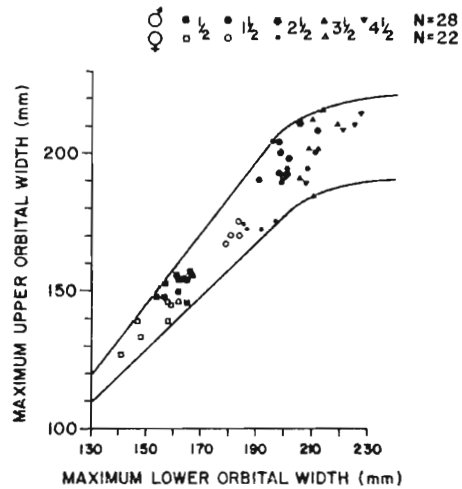


Figure 12

The tooth eruption patterns (Fig. 13) indicate that, of 9 male calves, 16% and 69% respectively were retarded. In the yearling group, 4 of 9 males and 2 of 5 females were behind the normal eruption pattern, if Peterson's description (1955) could be considered as a norm for North Central Ontario moose populations.

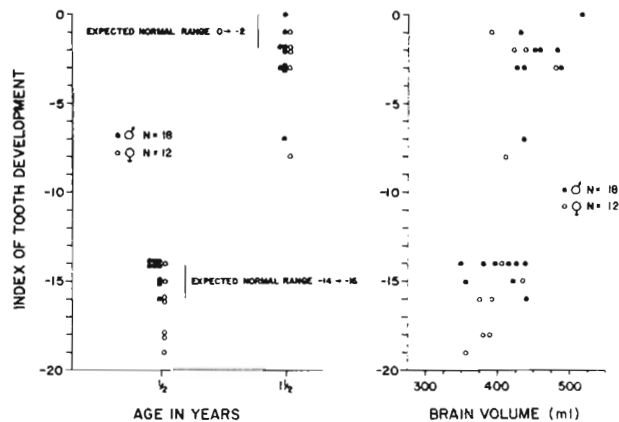


Figure 13



The progress of tooth eruption and mineralization of the anterior and posterior basisphenoid cartilages (ABC and PBC respectively) in relation to growth of BCV is displayed in Fig. 14. An overall comparison of these relationships in both genders reveal the following: The PBC was mineralized in all 10 male calves, but open in 3 of 7 females, and the ABC was open in 7 males and 6 females. In the yearling group the PBC was closed in both genders, while the ABC was open in 7 of 10 males and open in only 2 of 6 females.

In 2½ year olds, none of the 7 females, but one of the 2 males had the ABC open. In all other moose, the ABC and PBC were mineralized, but the closing process was faster in females than in males.

Mineralization of the basisphenoid cartilages did not appear to be related in any way to the size of the BCV. The TEP was closer to the expected norm in male calves and yearlings than in females. The delayed TEP appears to be slightly related to the BCV and mineralization of ABC.

Some environmental factors which could be considered as environmental stressors causing the malnutrition of unborn fetuses are shown in Fig. 15 (a,b).

After looking at these factors for December to April of the years of birth of the animals studied (1973 to 1979), we did not find any substantial differences in winter severity. We did not find any substantial temperature differences for the latter half of pregnancy, nor that snow, which was greatest in 1978 and 1979, could be considered as stressors. Therefore fetal malnutrition of the 2½ year old moose carried as fetuses in 1976-77 may not be attributed to environmental factors, and must have some other cause.

Figure 14

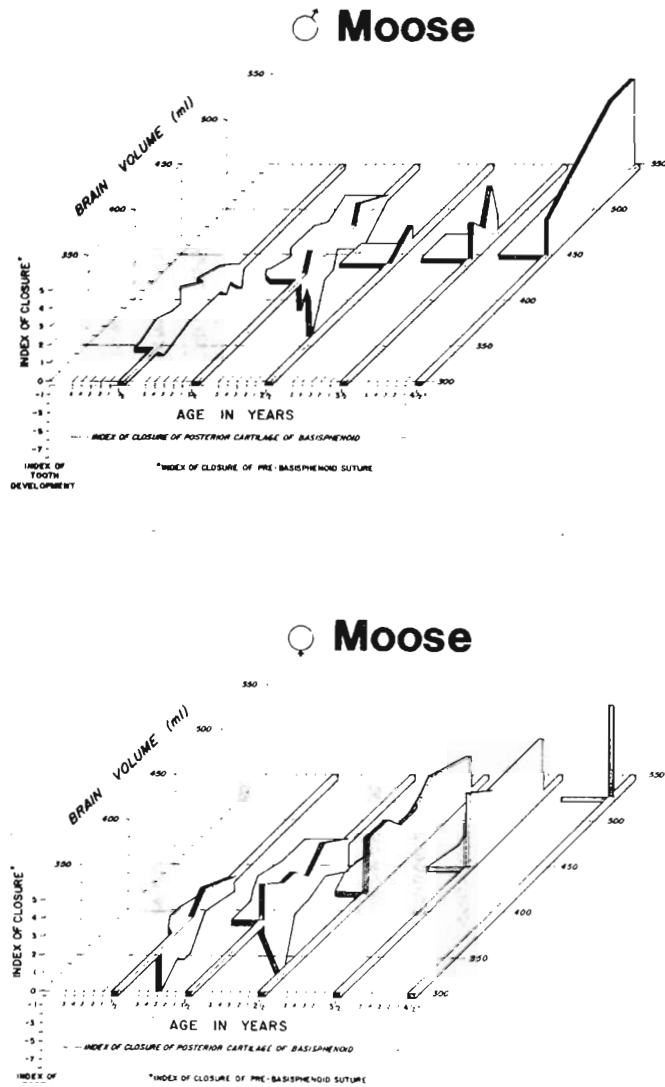
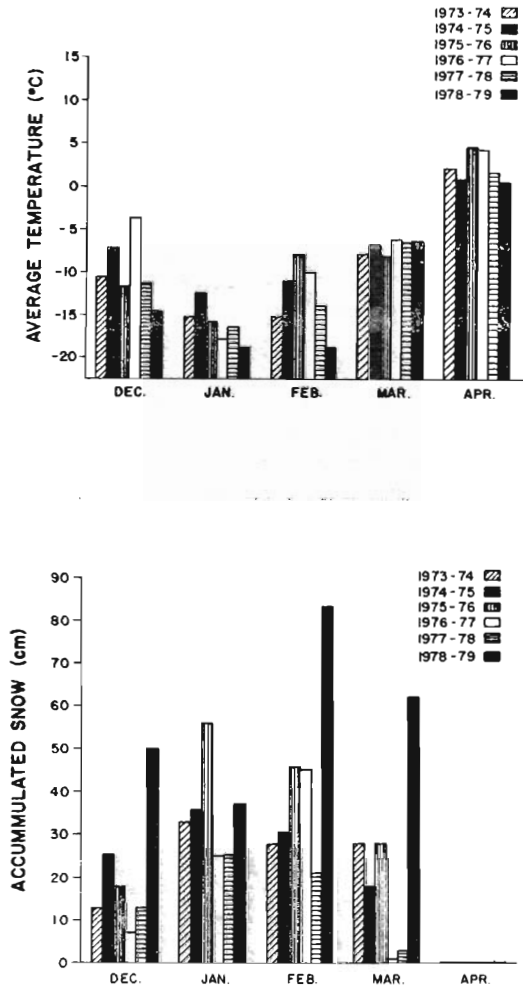


Figure 15



CONCLUSIONS

The low number of skulls available certainly does not allow us to make firm conclusions regarding the performance of each generation, nor for the entire North Central Region. But our findings do raise some interesting questions which warrant further study. (1) The BCV exhibited great variation, which could be caused by: (a) a prolonged calving period, (i.e. up to 3 months), (b) undernourishment during pregnancy and the nursing period, (c) different ages of the mothers, because progeny of primiparous females are generally smaller at birth (Brüggemann et al. 1973, Bubenik 1965). (2) The different sizes and growth of the BCV are not sex dimorphic, and did not correlate well with ML and CBL. Similar discrepancies have been found in white-tailed deer *A. virginianus* and mule deer *O. hemionus* (Anderson et al. 1974, Bubenik et al. in prep.). It is interesting that sexual dimorphism is exhibited in body size of moose (Hermansson and Böethius 1975), but not in BCV or ML. (3) The BCV is fully developed by approximately 3½ years of age. The suggestion by Anderson et al. (1974) that, in mule deer the brain can grow until an age of about 10 years, may not be correct in view of the mineralization of the basisphenoid and other sutures associated with the brain case. Since the cartilages of the basisphenoid are closed at about 1½ years, further growth in moose skulls is possible only by growth of the crown region of the head, i.e. along the fronto-parietal and parieto-temporal sutures, which remain open until about 3½ years of age. The occipito-parietal suture has begun to close in 2½ year old animals. (4) Mineralization of the basisphenoid cartilages proceeds more quickly in female moose than in males. We do not, as of yet, have an explanation for this sexual dimorphic characteristic.

(5) Nearly all cranial parameters examined in this study have shown much greater variation in males than females. This is in accordance with our findings in white-tailed deer, and could reflect the greater susceptibility of males to stressors of any kind, during their pre- and postnatal growth. The fact that we did not find any evidence that environmental factors could be responsible for these differences (Fig. 15 a,b), we suggest that social distress may be the cause. This hypothesis could be supported by the practice, which began in 1977, of postponement of the hunting season until after the first rutting period. (6) The PD, which is considered as an index of antler size (Bubenik 1966, Bubenik et al. 1978, Stubbe 1977) was not tightly bound to either the BCV or ML, a variation which we have mentioned in a forthcoming paper on white-tailed deer (Bubenik et al. in prep.). (7) Interesting also is the finding concerning the growing eye-angle of the woodland moose during its ontogenesis. The fact that this is not sex dimorphic leads us to the conclusion that this may be an adaptive process for improved stereoscopic perception, necessary in the dense taiga habitat. This is supported by our measurement of tundra moose from Alaska. It is a general view that ungulates of open habitat have a narrower EA than those of dense habitat. (Johnson 1901, Pfeffer 1952). (8) The delay in tooth eruption was greater in females than in males. We did not find analogous literature dealing with this phenomenon and therefore we do not know if it is a general occurrence, or only a factor of the small sample size. The only paper which we discovered regarding delayed tooth eruption was one by Passarge (1971) on roe deer (*Capreolus capreolus*) who found this phenomenon in socially disorganized populations.

There is no doubt that similar stressors exist in the Black-Sturgeon River population (Bubenik et al. 1977). Since social disorder prolongs the mating and calving seasons (Bubenik 1979, Meile and Bubenik 1979), it seems possible that this may be the reason for the high number of moose with delayed tooth eruption patterns. This, of course, is dependent on our material having been collected over a 20 day period only.

If our findings, that the BCV and other cranial parameters have begun to improve dramatically since 1978, are generally valid, then the performance of the 2½ year old moose harvested in 1980 should be much better than the same age class of 1979. The 1½ year old moose should be slightly better than their peers of 1979.

The results of this pilot study appear to be worthy of further investigation on a larger scale to find out how general they actually are. On the positive side, the BCV of calves could be a useful management tool to gather evidence concerning the overall performance of a population and the most recent generation. This in turn would enable us to make predictions about the population welfare from the harvest structure and thereby monitor selective pressure to maintain a proper social structure.

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