AN EXAMPLE OF HOW A MAMMALIAN SPECIES MAY VARY BIOMETRICALLY DURING DIFFERENT CLIMATIC CONDITIONS.
— A STUDY OF TEETH OF MODERN MOOSE (*ALCES ALCES* L) TOGETHER WITH TEETH FROM DWELLING SITES IN NORTHERN SWEDEN.

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Introduction

During the Early Norrland research project the bone material from 174 dwelling sites in Northern Sweden was studied. The work was performed during the period of 1968—73 by Jan Ekman and myself. The results of the comprehensive investigation are now available (Ekman—Iregren 1984).

The moose *(Alces alces* L) was by far the dominating prey as regards both temporal and spatial distribution. But at most sites the bones had been accidentally burnt and the teeth were destroyed. In three sites however cultural layers had been formed and thus preserved the teeth and unburnt bones of moose hunted by early man. This material was used for the present study.

Investigated sites

The distribution of the sites can be seen in Figure 1.

Tåsjö 101 (Bellsås), Tåsjö parish, Ångermanland (Site A)

References: Baudou (1977 p. 29—30, 94—99, 146), Ekman—Iregren (1984 p. 74—78).

The dwelling site was discovered in 1923 and partly excavated in 1951 and 1969. The monument consists of a circular wall built up of cracked stone, animal bones, charcoal and waste. The outer diameter of the embankment is 30 m and the maximum height almost 2 m.

Among the artefacts found are points and scrapers, which clearly show the methods of hunting as well as of skin preparation. The bone material consists of 32 kg among which the moose dominates. Scanty fragments of beaver and pike also occur. This material represents a typical site of early hunters-fishers-gatherers in Northern Sweden.

Four parts of the skull of moose bulls show that these animals had shed their antlers before they were killed. The moose bulls shed their antlers during the period December—March. The new antlers begin to grow in April—May (von Essen et al., 1968 p. 17; Gardell 1958 p. 128). These bone finds demonstrate that the dwelling site was in use during the winter and early spring months.

The radio-carbon datings of the site are seen in Fig. 2. A calibration gives a result of 4500—3600 B.C. for the time when the investigated layers were formed. Later habitation too can be proved by the presence of artefacts.

Åsele 1023—24, Åsele parish, Lapland (Site B)

References: Baudou (1977 p. 30), Allard—Modig (1977), Ekman—Iregren (1984 p. 60—68).

The site was located on the beach of the river Ångermanälven. It was excavated in 1966. A total of 350 m² was investigated 54 m² of which had clearly distinguished

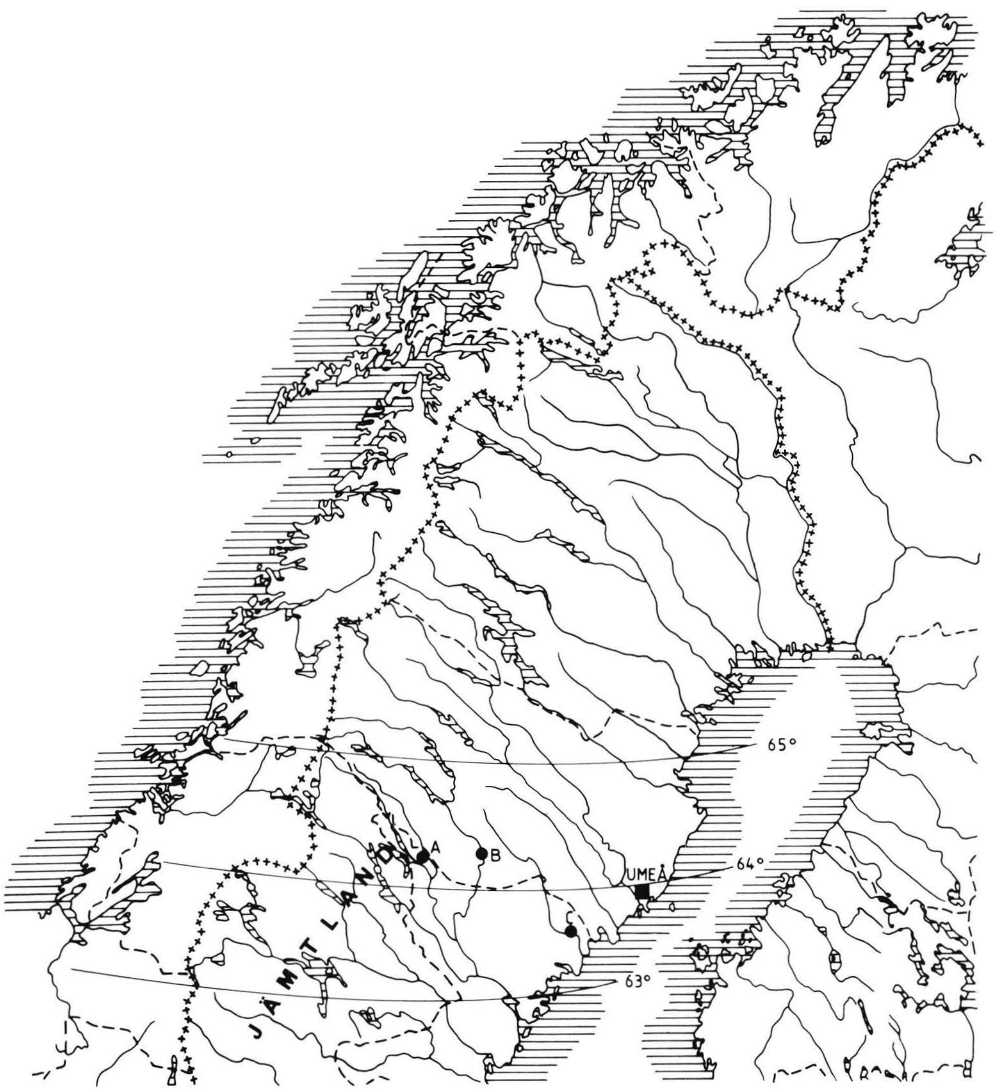

Fig. 1. The northern part of Norway, Sweden and Finland. The symbols mark the location of the three dwelling sites osteologically investigated. A; Tåsjö 101 (Andersnäset, Bellsås), B; Åsele 1023—24 (Hälla 869—70) and C; Anundsjö, Agnsjön.

strata. The cultural layer was at most 0.9 m deep. Points and arrows are proof of the economic background of the settlement.

The bone material consists of about 63 kg. A broad spectrum of birds and mammals from the taiga are represented: wolf, brown bear, pine marten, otter, beaver, arctic hare, reindeer, moose, capercaille and black grouse.

Four individuals of the moose had shed their antlers, which indicates a hunting season in the winter or early spring. Bones of the whooper swan and the bream both of which are difficult or impossible to catch in the winter show also preys of the summer in this locality.

The radio-carbon datings are seen in Fig. 2. The comprehensive layer of cultural remains (the grey cultural layer) was accumulated during a relatively short period. With calibration (T½: 5568 ± 30, Masca 1973 in McKerrell, 1975) this occupation dates from the period 2500—2000 B.C.

Agnsjön, Anundsjö parish, Ångermanland (Site C)

References: Baudou (1977 p. 61—63), Ekman—Iregren (1984 p. 95—99).

This dwelling site on the lake shore was excavated in 1960. A cultural layer 0.5 m deep was found in an area of about 40 m². Points and arrows of different types and scrapers were found as well as a large amount of bone, some 72 kg.

The moose bones dominated the butchering refuse. Bones from beaver, pine marten, capercaille and pike are also present. Shed antlers and a cranial part from which the

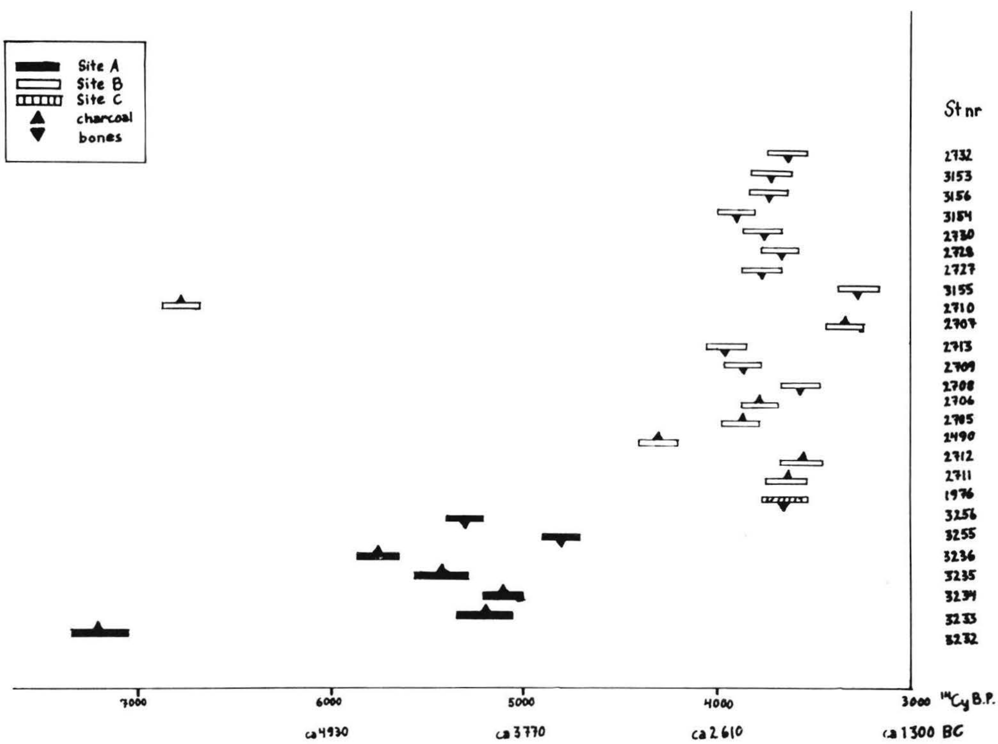

Fig. 2. Radiocarbon datings from the three dwelling sites. The datings are made both on bone and charcoal. All datings are made in the Stockholm laboratory; their file numbers are designated St 0000. The ^{14}C-halftime used in calibration is 5568 ± 30 (Masca 1973 in McKerrell, 1975).

antlers have been shed make it clear that the site was used during the winter or early spring months. Habitation during other seasons of the year could not be proved with the help of the bone material.

The dwelling site was occupied during the Mesolithic, the Neolithic and later. Baudou (1977 p. 6) judges the longest occupation to have taken place during the 3rd millenium B.C. Only one radio-carbon dating has been made (Fig. 2).

Favourable biotopes and the diet of the moose

The moose is a typical browsing species of the taiga. The diet of the moose varies through the year. In the summer it consists preferably of leaves and twings of *Salix, Sorbus, Populus* and of herbs and grasses. Aquatic herbs are also eaten. *Betula* is browsed but not favoured. In the autumn after defoliation and in the spring dwarf shrubs are very important. During the winter buds and sprouts of many trees are major components of the intake. But the principal food resource in the winter is *Pinus* (Bergström—Hjeljord, in press).

History of vegetation in the area concerned

During the last decade a great many sites (lakes and mires) from Northern Sweden have been biostratigraphically investigated. This has partly been done within the Early Norr-

Table 1. Length of the last molar of the mandible of moose *(Alces alces* L). Dwelling site materials from Northern Sweden.

Sin/dx	Length (mm)	Sin/dx	Length (mm)	Sin/dx	Length (mm)
Site A: Tåsjö 101					
dx	(39.0)	dx	38.0	dx	41.0
sin	40.5	dx	39.0	dx	42.5
dx	41.5	sin	40.5	sin	43.0
sin	40.5	sin	43.5	sin	40.0
sin	(42.5)	dx	40.0	sin	42.5
sin	42.5	sin	41.5		
Mean: 41.06 mm		No. 17	Range: 38.00—43.50 mm		S.D. 1.52
Site B: Åsele 1023—24					
dx	42.0	sin	40.0	dx	40.5
sin	(42.5)	sin	41.0	dx	39.5
sin	41.5	sin	(40.5)	dx	39.0
sin	(40.5)	sin	(38.5)	dx	42.0
sin	39.5	sin	(39.5)	dx	42.5
sin	44.5	dx	40.5	dx	43.0
sin	41.0	dx	39.5	dx	43.0
sin	(39.5)				
Mean: 49.91 mm		No. 22	Range: 38.50—44.50 mm		S.D. 1.51
Site C: Anundsjö, Agnsjön					
sin	39.0	dx	43.0	dx	41.0
sin	43.0	dx	42.5	dx	38.5
dx	41.0	dx	41.5	dx	(37.5)
Mean: 40.78 mm		No. 9	Range: 37.50—43.00 mm		S.D. 1.90

land research project. These results convey a fairly accurate picture of how the landscape was formed in some areas. According to Modig (1979 p. 96) the ice receded from the Anundsjö region *c.* 9100 years ago. Further more the Åsele and Tåsjö-regions were deglaciated *c.* 2—300 years later — calculated on an ice retreat of about 300 m per year. Another 4000 years later the Anundsjö-region was suitable for settlers (Modig, 1979 p. 105). The Litorina Sea had been formed.

From a work by Huttunen—Tolonen (1972 p. 15), regarding the vegetation of a site in the vicinity of my site B, I quote: »During the AT 1 zone, *Pinus* is dominant. During the AT 2 zone, on the other hand, *Betula* predominates, while *Ulmus* also reaches its maximum though it remains less than 2 %. ...In the SB period, *Pinus* once more predominates, while *Betula* decreases. ...The low proportion of NAP (excluding *Cyperaceae)* shows that the forests around the bog were dense up to the SA period.»

The vegetational history of the Tåsjö-area has not been investigated recently. But it is clear however that the biotopes around the dwelling sites, at the time of settling, were suitable to the moose. These settlements have preserved bones and teeth of individuals that should reflect the good possibilities of browsing during the climate optimum in Scandinavia.

Size of the moose's teeth in comparison with modern moose

Site materials

In the present investigation only adult animals are studied. The third molar of moose erupts at the age of 16 months (Bromée—Skuncke, 1952 p. 7). The measurements were taken as follows. A sliding caliper was used and the measurements were shortened to the nearest 0.5 mm. The maximum length was measured from the lingual side as if the tooth was in its natural position in the mandible. I have chosen to measure at the base of the crown (Fig. 3) as these measurements show greater homogeneity than such as are taken close to the surface of the tooth. The breadth was taken at right angles to the first measurement but is not discussed in this context.

A parenthesis shows a small uncertainty in the value, which — despite minor damage — was calculated to be the original value. If the tooth showed a greater damage it was

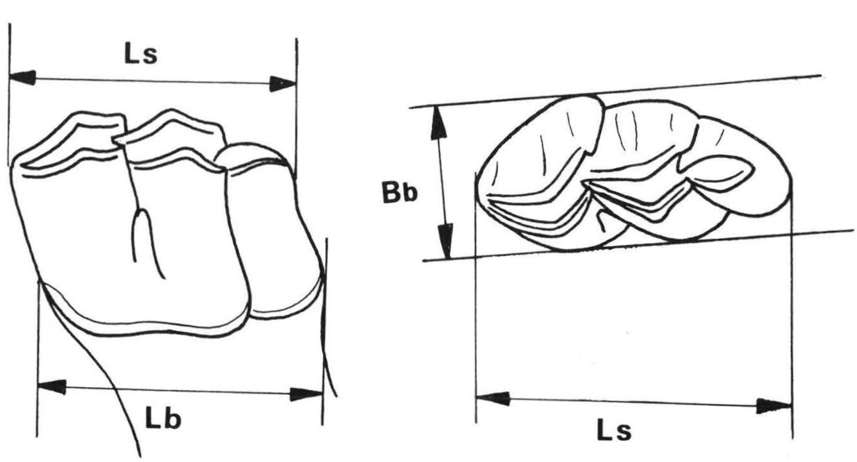

Fig. 3. Drawing of a third molar of the mandible of moose. Ls, tooth length at the biting surface, Lb, tooth length at the base of the crown, Bb, tooth breadth at the base of the crown.

Table 2. Length of the last molar of the mandible of recent moose (*Alces alces* L) killed in traffic accidents in Jämtland county.

Sin/dx	Length (mm)	Sin/dx	Length (mm)	Sin/dx	Length (mm)
sin	38.5	sin	35.0	dx	35.0
dx	39.0	dx	35.0	dx	38.5
sin	37.5	sin	39.0	sin	37.5
dx	37.0	dx	39.5	sin	38.0
sin	38.5				
Mean: 37.54 mm		No. 13	Range: 35.0—39.0 mm		S.D. 1.54

left out of the investigation. Table 1 includes the values of all mensurable M_3:s distributed according to locality.

Modern materials

In this investigation I have used a small sample of moose killed in traffic accidents (material D) in the county of Jämtland (Table 2). This material has been discussed earlier (Iregren, 1984). The present work was enlarged as Dr. Finn Stålfelt from the Swedish Sportsmen's Association made his vast material of mandibles available for my study. I am very grateful to him for his courtesy.

These moose individuals were shot in Jämtland during the regular autumn hunting season. The variances of the tooth row measurements were found to be equal in animals of the north (material E 1), the east (E 2) and the south (E 3) of the area. The values of the three sub-populations were tested to see if there were obvious divergences within the materials (Table 4). The Student's t-test showed that the three sub-populations could be regared as parts of one population in common in this county. Later these values were treated as one statistical unit in this work.

Comparisons

From Tables 1—3 it is seen that the mean values of tooth length of the site materials are greater than those of modern moose. Table 5 presents the results of the tests (Student's t-test). When the site materials were tested against the modern materials it proved to be most unlikely that the populations would have equal tooth size (p-values < 0.005). The teeth of todays moose have evidently become smaller.

Discussion

The evolutionary trend of »postglacial dwarfing» (Kurtén, 1959 p. 207) seem to vary from species to species (Kurtén, 1953, 1965; Degerbøl, 1933) so it is hard to discern a general trend. It may well be that not only climate but also biotope and e.g. winter habits of the species may influence size (cf the badger (Degerbøl, 1933 p. 554—576). So it is difficult to use the explanations valid in carnivore evolution when discussing the moose. Ungulates have not so far been studied in this respect.

To conclude: A milder climate, such as that of the Atlantic Period, would increase the number of broad-leaved trees and thus the nutrition available to moose. The most important factor for size, however, is the genetic composition of the population and how genetic processes influenced the different populations of moose during this period.

Table 3. Length of the last molar (M_3) of the mandible of recent moose *(Alces alces* L) from the county of Jämtland. The individuals are legally hunted during the 1960's.

Individual	Length (mm)	Individual	Length (mm)	Individual	Length (mm)
Northern sub-population (E 1)					
41	36.5	338	39.0	452	41.5
49	39.5	342	39.5	461	36.0
59	40.5	372	40.0	462	41.5
60	40.0	373	36.5	463	42.0
61	39.5	374	39.0	464	40.5
62	41.0	375	38.5	467	44.5
66	39.0	376	41.0	468	39.5
71	41.5	379	40.0	469	40.0
76	42.5	380	38.0	490	38.5
77	44.5	381	38.5	491	40.0
80	38.0	383	40.5	493	41.0
84	40.5	388	40.5	500	41.5
320	41.5	396	41.0	504	40.0
321	36.0	401	43.0	Sj 1	45.0
322	39.5	432	39.0	Sj 2	39.0
328	41.5	450	37.0	Sj 10	40.5
Mean value: 40.07 mm		No. 48		Range: 36.0—44.5 mm	
Eastern sub-population (E 2)					
3	39.0	333	37.5	443	40.5
204	39.0	334	39.0	451	39.0
301	40.0	336	40.0	458	40.5
304	37.0	347	40.0	459	40.0
306	40.0	348	37.5	489	38.5
307	35.5	356	36.0	495	40.5
308	40.0	384	39.5	512	41.0
318	40.0				
Mean value: 39.09 mm		No. 22		Range: 36.0—41.0 mm	
Southern sub-population (E 3)					
118	40.0	201	38.5	364	38.5
120	38.5	206	39.0	366	38.0
122	38.5	309	38.5	367	41.5
133	38.5	310	37.0	368	40.0
153	40.5	315	36.0	369	38.5
154	38.5	329	39.5	370	39.0
157	38.5	337	40.0	371	39.5
158	40.5	340	37.0	390	38.5
163	41.0	345	36.5	407	36.5
167	40.0	350	39.5	425	39.5
168	37.5	351	38.0	471	39.5
176	41.0	358	40.0	478	39.0
188	37.5	363	38.5	481	39.0
Mean value: 38.86 mm		No. 39		Range: 36.0—41.5 mm	
Individuals not divided into sub-population					
13	40.0	92	38.5	354	37.0
26	41.5	94	40.0	382	41.5
28	37.5	325	37.5	484	37.0
35	40.5	327	37.5	485	38.0
36	38.0	331	39.5	501	40.0
37	38.5	352	42.5	509	41.0
91	40.0				
E total: Mean value: 39.41 mm		No. 128		Range: 36.0—44.5 mm	

Table 4. Tooth row measurements (P_2—M_3) of the moose *(Alces alces* L) of three geographical sub-populations. The mean and the standard deviation are given together with the t-values from Student's test from the comparison between the sub-populations.

Populations	*Northern* (E 1)	*Eastern* (E 2)	*Southern* (E 3)
N	34	20	25
M	166.53	164.80	163.88
S.D.	5.17	4.47	4.75
Populations	E 1×E 2	E 2×E 3	E 1×E 3
t	1.24	0.66	2.01
DF	52	43	57
P	p>0.05	p>0.05	p<0.05

Table 5. Comparison (Tooth Length) between Atlantic (A), Sub-boreal (B, C), recent moose *(Alces alces* L) killed in traffic accidents (D) and legally hunted moose (E).

Populations	*t*	DF	*P*
D×A	6.25	28	<0.005
D×B	6.33	33	<0.005
D×C	4.41	20	<0.005
E×A	3.85	133	<0.005
E×B	3.98	138	<0.005
E×C	3.39	125	<0.05

On the other hand, there might be adverse effects e.g. larger individuals could be favoured in a colder climate due to diminished heat-loss (Bergmann's rule). As the moose of today in a colder climate is smaller may talk against the importance of Bergmann's rule to moose. Another fact to stress is the presence of over-crowded populations as the main predator, the wolf, is extinct. Thus follows a strong intra-species competition which also may influence the individual size in todays Sweden.

It is evident that changes in tooth size over the time have occurred. The teeth of todays moose have become smaller. My hypothesis (Iregren 1984) of a decline in tooth size of the moose since the climate optimum is supported by this investigation. One point which I am not able to discuss now concerns whether the decline had appeared before Man's ecological disturbances in historical times and before the eradication of the moose during earlier centuries (cf Ekman, 1918 p. 259—269).

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