Bone growth throughout the lifetime of reindeer

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bone growth, sexual dimorphism, Rangifer tarandus

Abstract
Bei Untersuchungen zum Knochenwachstum von Rentieren aus Grönland ergab sich, dass das Wachstum einiger Dimensionen männlicher Tiere zeitlebens anhält. Bei den weiblichen Rentieren stoppt das Wachstum dagegen bei den meisten Dimensionen mit ca. 3 Jahren. Beim Vergleich zwischen 4-7jährigen und über 7jährigen Männchen zeigte sich, dass bestimmte Dimensionen bis zu 18 % zunehmen. Der Grund hierfür dürfte in der Zunahme des Körpergewichts liegen, was wiederum bedingt ist durch die kontinuierliche Zunahme des Geweihgewichts bei männlichen Rentieren. Vor allem bestimmte Sehnen und Muskeln, die die größere Körperlast zu tragen haben, üben Zug auf den Knochen aus, der entsprechend durch Verdickung an diesen Stellen reagiert. Da diese Zunahme der Knochendicke nur männliche Tiere betrifft, wird die Differenz in bestimmten Längen-Breiten Verhältnissen zwischen weiblichen und männlichen Tieren größer. Mit zunehmendem Durchschnittsalter der Rentierpopulation wird dadurch der Geschlechtsdimorphismus, der sich an bestimmten Einzelmaße feststellen oder durch Indizes ausdrücken läßt, verstärkt.

An investigation into bone development of Greenland reindeer revealed that the growth of certain dimensions in males persisted throughout the whole lifetime, whereas, in females the growth of most bones stopped at approx. 3 years of age. In males, some dimensions increased by up to 18% from 4 to 7 years and above. The reason may lie in the increase of body mass caused by the increased weight of the antlers. Also the stress caused by the sinews and muscles that carry and move the greater body mass, affect the bones which react with a thickening. Due to the fact that it is mainly male animals which are affected by the growth in bone dimensions the difference in certain length-width proportions between males and females increases with age. Thus sexual dimorphism, which can be seen both in certain single dimensions and which can also be expressed by indices increases with the average age of a Rangifer population.

1. Introduction

In general, one assumes that the growth of a bone, especially the increase in length, ends with the fusion of the epiphysis (e.g., Reitz & Wing 1999, 75). For example, Herre (1955, 77) writes that reindeer growth ends at 3 years of age. Reimers (1975) and Skogland (1983) state that female reindeer continue to grow only until the 3rd year of life. Weinstock (2000, 10) argues, that the growth cessation of females can differ between populations. Skogland (1989), for example, showed that female caribou in North America cease growing at 4-5 years of age. Jacobi (1931) writes that the growth of reindeer in general continues until the 4th or 5th year of life. Skogland (1983) is of the opinion that male reindeer grow in size until the age of approx. 5-6 years, by which time they participate fully in the rut. Thus, sexual
dimorphism in body size of adult *Rangifer* is partly due to females reaching their maximum adult weight earlier than males. In the course of analysing reindeer bone development (Pasda in prep.) it was noticed that dimorphism was already evident within the first 12-18 months of life, and that the different rates of growth between males and females resulted in real morphological differences (*Wuchsformunterschiede* — no single English term exists for this German word whose meaning is approximately translated as visible differences between the proportions of the bones). Yet, more surprising was the fact that bones continue to grow long after the end of epiphyseal fusion, especially in males.

The animals analysed were of all ages and both sexes and died of natural causes. Skeletons were documented by a survey on foot between 1999 and 2003 in the Sisimiut- und Manitsoq-District of central west Greenland. In addition, some skeletons in the Zoological Museum of Copenhagen from the same region were also documented, making a total of 282 more or less complete skeletons. The sex, the fusion of epi- and apophyses, the dentition and certain bone measurements were recorded for each skeleton. The field work, and work in the laboratory was funded by the German Research Foundation (Deutsche Forschungsgemeinschaft, Az. Pa 527/2-1, 2-2, 3-1, 3-2; Pa 1616/1-1) and by a grant from the University of Erlangen-Nuremberg. Because the biological age of the animals was not known, thin sections for tooth cementum analyses (Pasda 2006) were prepared. The first incisors are commonly used for this technique, but in the case of the analysed Greenland reindeer, incisors were no longer present. In this region of central west Greenland, this is mostly due to polar foxes (*Alopex lagopus*) which scavenge the cadavers of reindeer. During the defleshing process, the incisors are torn away together with the soft tissue (Pasda 2001, 2005). Because of the absence of incisors, the molars were chosen instead. In seven animals, the first molar was completely missing or unusually worn making it necessary to choose the second molar for sampling. A total of sixty-three adult reindeer teeth were used. The teeth were first decalcified with nitric acid and then cut in a freezing microtome into longitudinal sections 14μm thick. For every tooth the best four to six sections were analysed. However, problems made the counting of layers difficult, the molars proving to be especially complicated (see Pasda 2006, 127-133). In many cases the layers were difficult to distinguish and owing to the sectioning method sometimes single layers or occasionally the whole secondary cementum became detached. In addition, the counting of layers was subjective, as was shown by a comparison of independent layer counts made by four different persons. In only five cases did the number of counted layers agree among all observers. In spite of these limitations, the results for young animals showed a good correlation between the dentition and the tooth cementum analysis method. The results obtained for young reindeer were also crosschecked with other information relating to the age of the animals, such as epiphyseal fusion and bone measurements (Pasda in prep.). It is well known that the accuracy and effectiveness of the cementum annulation method decreases as animals become older and tooth wear increases. In these cases, there was little possibility of testing the method or comparing it to other age related information. To illustrate the continuous growth, the measurements of the Greenland reindeer used for this analysis were divided into three age groups (table 1):

<table>
<thead>
<tr>
<th>age group</th>
<th>age in years</th>
<th>females (n)</th>
<th>males (n)</th>
<th>undet. sex (n)</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>1 to 2</td>
<td>2</td>
<td>10</td>
<td>19</td>
</tr>
</tbody>
</table>
Bones were measured whether or not the epiphyses were fused. Growth was expressed as a percentage for each measurement, in age groups (A, B, C) and for both sexes separately (see details in Pasda in prep.).

2. Bone growth

2.1. Continuous growth of male bones

Bone dimensions of fully grown males were in nearly all cases considerably larger than that of females. Female bones stopped growing in most cases with the fusion of the epiphyses (at approx. 3, or at the latest 4 years of age) and in some cases even before the fusion was complete, for example the distal tibia. No difference between males and females could be established concerning the age at which fusion of the epiphyses occurred owing to insufficient data for a detailed analysis. It was clear that many dimensions of males continued to grow after the 7th year of life, even in those bones where growth in length had ceased at an early age (e.g. scapula: less than 1 year, and phalanx proximalis. 1 year of age). Thus, the growth in length, which is finished in most cases with the fusion of epiphyses, is a different type of growth from that of the increase in width and depth dimensions after the fusion. The continuous growth of males resulted in differences in proportions between younger and older males. Continuous growth could also be seen in some dimensions of females. There was a tendency for asymmetrical growth of the scapula and of some skeletal elements that partly fuse after the 4th year of life (femur, humerus, and ulna). However, asymmetrical growth in all dimensions of the atlas, scapula, ulna, and the phalanx proximalis posterior was more striking in males. Female bones were more slender, whereas male bones were broader in relation to length in many dimensions and this relationship increased with increasing age.

The growth of all reindeer reached maximum values of 40% from age group A compared to age group B (figure 1). The average growth of age group A compared to B was 13.5%. This strong growth was not surprising since many bones were still not completely ossified. After ossification of most bones in age group B compared to C bone growth reached maximum values of 18% with an average growth of 2.9%. When split into male and female animals the male reindeer had an average growth of 3.6%. Exclusion of measurements of skeletal elements that ossify in age group B (fusion of epi- and apophyses see Pasda in prep. tab. 13; late ossifying elements: ulna all measurements, humerus Bp, Dp, GL, GLC and femur Bp and GL - measurements and abbreviations according to von den Driesch 1976, and Weinstock 2000) gave an average growth of 3.8%. Bones of female reindeer showed an average growth of 1.7% without the above mentioned measurements of ulna, humerus and femur and of 1.8% including those measurements.
Figure 1: Percentage growth of bones of both sexes from age group A to B, and from B to C.

Distinct changes of dimensions were observed for most bone segments from male animals (figure 2; see details in Pasda in prep.), compared with smaller changes in the females.

Figure 2: Average percentage growth from age group B compared to C (abbreviations according to Weinstock 2000).
2.2. Statistics of the bone growth

A bivariate statistics was carried out using the EDV-program DIVA (Plogmann 1990) at the Institute of Palaeoanatomy, and History of Veterinary Medicine of the University of Munich. The tests were carried out using logarithmic data, derived from bones with fused epiphyses only. Two different tests were carried out. Test A was a test of the position and gradient of the two straight lines (or allometric lines) whether or not they were different in position or gradient or both, and if both straight lines were different whether or not the difference was significant (last but one column). Test B was a test of differences of the gradient and to evaluate in which way the straight lines were different. Three differences in the gradient and position of the allometric lines and of the appearance of an ellipse of distribution were possible:

1. The case of equal position and equal gradient of the straight lines implies the result ‘no significant difference’ (test A and B show no significant difference, figure 3, left; Plogmann 1990). A single ellipse of distribution appears resulting in only one straight line. Statistically both groups belong to a single group. This means that male reindeer may have greater dimensions than females, or older males greater than younger males, nevertheless the dimensions are greater symmetrically, and the morphological differences (Wuchsform, see chapter Introduction) remains the same.

2. The case of different position but same gradient of the straight lines (test A with, test B without significant difference, see figure 3, centre) give rise to two separate ellipses of distribution. The gradient of the straight line is equal in both cases. This means that the bones of both groups have different proportions. According to Reichstein (1991, 20) if differences in proportions (excluding the length of the bone) are present, then they can be referred to as real morphological differences (Wuchsformunterschiede, see chapter Introduction).

3. The case of different position and different gradient of the allometric lines (test A and B with significant difference) implies no similarity between the two straight lines and two separate ellipses of distribution appear (see figure 3, right). Because the allometric lines are different in position and gradient according to Reichstein (1991, 20) there are other influences on the proportions of the bones.

For all bones length vs. width dimensions were tested to investigate whether or not allometric relations existed. Dimensions were tested for females vs. males (which are not shown here) and for younger vs. older for both females and males (for significant results see table 2). Only skeletal elements with completely fused epiphyses (proximally and distally) were used. Because of the variation in the development of skeletal elements, bones of different biological ages were analysed. For example, the metatarsus and phalanx proximalis posterior were taken from animals at least 3 years old but since a complete conjunction of the epiphyses at the ulna only takes place at 6 years of age elements of considerably older animals had to be used.
Figure 3: Epistropheus and scapula: comparison of younger (squares: 4-7 years) and older (crosses: > 7 years) male reindeer. Tibia: comparison of adult males (squares) and females (crosses). Left: epistropheus, SBV-LCDe, Double log function plotting. Allometric line and 95 %-variance ellipse (Streuungsellipse). Allometric line formula LCDe = 0.8275 x log SBV + 46.402. Centre: tibia, GL-Dd, allometric line formula for males Dd = 0.021 x log GL + 26.388; for females females Dd=0.0354 x log GL + 20.588; Right: scapula, BG-SLC. Allometric line formula for younger males Bg = 0.3803 x log SLC + 19.156; for older males Bg = 0.4957 x log SLC + 15.046. The plots were drawn using DIVA (Plogmann 1990).

Table 2: Significant difference between the dimensions of 3 to 7 year old and >7 year old male and female reindeer (level of significance: 95 %). The increasing dimensions are underlined.

<table>
<thead>
<tr>
<th>sex</th>
<th>minimum age of the analysed skeletal elements</th>
<th>skeletal element</th>
<th>significant difference of dimensions in the test A</th>
<th>test B</th>
</tr>
</thead>
<tbody>
<tr>
<td>♂♂</td>
<td>3 years</td>
<td>scapula</td>
<td>SLC-BG; GLP-BG</td>
<td></td>
</tr>
<tr>
<td>♂♂</td>
<td>3 years</td>
<td>phalanx prox. post.</td>
<td>Gpl-Dd</td>
<td></td>
</tr>
<tr>
<td>♂♂</td>
<td>4 years</td>
<td>atlas</td>
<td>GL-GB</td>
<td></td>
</tr>
<tr>
<td>♂♂</td>
<td>6 years</td>
<td>ulna</td>
<td>GL-BPC, GL-SDO, GL-DPA</td>
<td>GL-BPC, GL-SDO, GL-DPA</td>
</tr>
<tr>
<td>♀♀</td>
<td>3 years</td>
<td>scapula</td>
<td>SLC-BG</td>
<td></td>
</tr>
</tbody>
</table>

Some bones showed considerable growth in all dimensions with increasing age, e.g. the epistropheus (SBV-LCDe, figure 3, left). However, significant asymmetrical growth could be seen between younger and older male reindeer at the atlas, scapula (figure 3, right), ulna, and phalanx proximalis posterior (table 2). In the case of the scapula the Collum scapulae (SLC) showed more growth compared with the width of the Cavitas glenoidalis (BG). The SLC was the only dimension of females where significant growth was visible. On the other hand, the length of the Cavitas glenoidalis (GLP) showed a marked contrast to the width (BG). At the atlas width (GB) especially showed a marked contrast to the length (GL). At the phalanx proximalis posterior, it was mainly the distal depth (Dd) that increased in relation to the length (Gpl). At the ulna, several dimensions increased, although only ulnae of animals older than 6 years of age were used for this analysis. The dimensions of the articular surface, especially the greatest width of the proximal articular surface grew markedly in relation to the length. The results show that the morphological differences (Wuchsformunterschiede, see chapter Introduction) developed with increasing age in certain skeletal elements especially of male reindeer.
2.3. Comparison of male and female bone growth using the
Variability Size Index method

The Variability Size Index (VSI) is one way of comparison of the size of individuals represented in archaeological bone samples, for example from different time periods, or different geographical areas (Weinstock 2000, 23). The VSI (Uerpmann 1982) allows the simultaneous use of diverse skeletal elements in biometrical evaluations. Some factors such as the variability of different dimensions or the number of females compared to males in the archaeological bone material create problems (Meadow 1984; Uerpmann 1982; Weinstock 2000, 26). Furthermore, it is possible that the bone growth and thus the age of males may influence the results. To examine this possible influence, a VSI was calculated for females and males separately.

The method requires a standard population. As a standard the reindeer bones of the Ahrensburgian layer of Stellmoor, northern Germany, published by Weinstock (2000, 28-29) and already applied by him for this method were chosen. Comparison of the VSI for the sexes separately showed that for females no growth was apparent in age group B compared to C (table 3, figure 4). The small number of females possibly influenced the result but this seemed not to be the case. In contrast, for male animals the VSI (containing width and depth dimensions) showed a clear growth with increasing age. Because of some differences in the measuring method and difficulties in defining the measurements, some of the data published by Weinstock were omitted. Axis and atlas which are highly dimorphic and which showed the strongest growth (figure 2) had to be excluded because of the strongly aberrant values in the VSI statistics. Had these bones been included they would have further enhanced the conclusion.

![Figure 4: Comparison of younger (age group B) and older (age group C) females and males; n is the number of measurements (not number of individuals).](image)

<table>
<thead>
<tr>
<th>sex and age</th>
<th>number</th>
<th>median</th>
<th>mean</th>
<th>standard deviation of mean</th>
<th>min</th>
<th>max</th>
</tr>
</thead>
<tbody>
<tr>
<td>female 4-7 years</td>
<td>53</td>
<td>-4.080</td>
<td>4.023</td>
<td>2.8692</td>
<td>-34.7</td>
<td>34.0</td>
</tr>
<tr>
<td>male 4-7 years</td>
<td>134</td>
<td>8.313</td>
<td>13.315</td>
<td>1.4557</td>
<td>-20.2</td>
<td>40.0</td>
</tr>
<tr>
<td>female &gt; 7 years</td>
<td>302</td>
<td>-2.728</td>
<td>3.759</td>
<td>1.1145</td>
<td>-31.3</td>
<td>34.5</td>
</tr>
<tr>
<td>male &gt; 7 years</td>
<td>194</td>
<td>16.320</td>
<td>19.404</td>
<td>1.3629</td>
<td>-16.5</td>
<td>70.7</td>
</tr>
<tr>
<td>total</td>
<td>683</td>
<td>3.657</td>
<td>10.098</td>
<td>0.7686</td>
<td>-34.7</td>
<td>70.7</td>
</tr>
</tbody>
</table>
This analysis shows that the growth of certain dimensions (see table 2) indeed influences the values of the VSI (see figure 4, table 3). Width and depth are apparently dependent upon the weight of the animals, and as the weight of males increases with age, so does the size of their bones. Length dimensions are not so depended on the weight of the animals; therefore, length measurements would be more appropriate than width and depth for the VSI calculation. Unfortunately, length dimensions are rare in archaeological bone material and it is necessary to use width and depth dimensions instead. Since length dimensions are not used for the calculation of VSI, Uerpmann (1990, 118-120) stresses that the VSI should not be misinterpreted as being equal to body height. This point was made by him in his description of the LSI calculation (for the LSI a single standard individual is used instead of a standard population as for the VSI).

### 3. Possible reasons for the bone growth

The main cause of growth and the allometric change of physical proportions is due to the distinct gain in weight with increasing age of male animals, which may possibly be caused by the increased size of the antlers. No data concerning the gain in weight of antlers was found. Various statements about gain in body weight have been published. Based on a few data, Baskin & Danell (2003, 131, fig. 8.3; after Pavlov et al. 1989) showed that from the 40th month of life in a Tamyr population of wild reindeer a clear difference in weight gain existed between the sexes. While females gained next to nothing, the increase of weight in males was considerable. Reimers (1975, 184) showed similar results for wild Norwegian reindeer. He demonstrated a clear difference in weight of animals as young as 1 year old. Likewise, in wild reindeer of South Georgia (Leader-Williams 1988, 135-136) males are heavier than females by 12 months of age. However, males achieve heavier body and organ weights than females (Leader-Williams 1988, fig. 6.9, 6.10, tab. 6.2), and continue to gain weight for longer than females (Leader-Williams 1988, fig. 6.8). Concerning Figure 6.9 in Leader-Williams (1988, 136) females at approx. 50 months of age reach a maximum weight of 85 kg, whilst males reach 140 kg. Herre (1955) published an average weight for wild reindeer of 100 kg for males and 75 kg for females. Meunier (1964 in Niethammer & Krapp 1986, 206) reports that strong males in good condition weigh 175-250 kg.

The marked growth of the first two vertebrae in males was probably a direct result of the increased weight of antlers. The epistropheus grows in all dimensions without apparent allometric growth (Figure 2), this is not true of the atlas, which grows mainly in width. Work on white-tailed deer (French et a. 1955; Johnson 1937; Severinghaus et al. 1950; Kelsall 1968, 39) demonstrated a direct relationship between nutrition and antler development in that species. Their conclusions showed that animals on heavily populated ranges, or individuals with inadequate nutrition had shorter, narrower, and more simply developed antlers than deer in less crowded conditions with a more adequate food supply. It is also likely that the size of the atlas and the epistropheus varied in the same way as the size of the antlers. The reason for the asymmetric growth of certain postcranial dimensions may lie in the action of muscles and sinews which was probably influenced by the body mass. The high correlation between postcranial dimensions and body-mass has been reported for many ungulate groups (e.g. Alexander 1977; Scott 1985; Scott 1987; Karp 1987). The explanation for this high correlation lay in biomechanical necessities: bones must be of sufficient thickness to withstand the compressive bending forces generated in weight-bearing
elements (Scott 1990, 301; Weinstock 2000, 23). In a series of animals of increasing size and similar shape, skeletal dimensions would be expected to increase in a regular way to accommodate increasing body-mass. While all postcranial skeletal dimensions show a significant correlation with body mass, length dimensions are not as highly correlated as non-length measurements. This is not surprising, since weight-bearing bones must withstand mainly compressive and bending forces, for which purpose the width and depth, and to a lesser extent the length of a bone, are more relevant (Weinstock 2000, 23).

The significant difference between certain dimensions of male and female reindeer was striking (Pasda in prep.). Analysis of the measurements revealed a marked sexual dimorphism. Fully grown male reindeer are usually considerably heavier than females, one factor among others being the much greater weight of male antlers. It is known that the increase in dimensions of antlers stops in very old male deer (Drechsler 1977, Huxley 1931) and possibly also in reindeer. However, it was impossible to check for a cessation of the increase in bone thickness for older males in this analysis.

When considering only males, which was primarily done in this presentation, it is striking that it is the dimensions of the anterior extremity which grows with increasing age, whose main task is to support the body weight, whereas the task of the posterior extremity is mainly locomotion. Consequently, as the weight increases, the anterior extremity has to carry more weight. Admittedly, the same applies to the posterior extremity, because the increased body mass requires a greater effort, however, it seems that locomotion is not such a significant factor as the carrying of weight. The muscles and sinews become stronger and thicker, thereby requiring greater support from the bony skeleton. The bone correspondingly reacts by an increase in mass, in nearly all cases at the shafts, but sometimes at the joints, rather than by an increase in length which ceased at a certain age. However in some bones, an increase in length could be seen after the fusion of the epiphyses (e.g. humerus, ulna, metatarsus, and phalanx proximalis posterior), but, in all cases increase in width and depth were greater.

4. **Summary**

An investigation into bone development of Greenland reindeer revealed that the growth of certain dimensions in males persisted throughout the whole lifetime, whereas, in females the growth of most bones stopped at approx. 3 years of age. In males, some dimensions increased by up to 18% from 4 to 7 year old and above, long after the fusion of the epiphyses was complete. Thus, in males the growth in length of bones, which stops in most cases with the fusion of epiphysis, is a different type of bone growth from that of the increase of width and depth dimensions. Some bones showed considerable growth in all directions while others increased only at certain sections which caused an asymmetrical growth. This resulted in statistically significant morphological differences (*Wuchsformunterschiede*) between younger and older reindeer. Also, this asymmetrical growth caused a progressive sexual dimorphism of *Rangifer* population as its average age increased. Reasons may lie in the increased body weight caused by the increasing weight of the male antlers and the difference in the accumulation of body mass between females and males caused the difference in growth of certain bone dimensions especially in males.
Asymmetrical growth at certain joints is probably directly caused by the action of muscles and sinews which have to provide a greater stress in order to carry and move a heavier body.

5. References


Weinstock 2000: Weinstock, J., Late Pleistocene reindeer populations in Middle and Western Europe. An osteometrical study of Rangifer tarandus. (Tübingen 2000).

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