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A discussion of the size of recent red deer (*Cervus elaphus* L.) compared with prehistoric[1]) specimens*)

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Red deer (*Cervus elaphus* L.) are known from many prehistoric sites in Western Europe; a number of these are usually of great size as compared with contemporary animals. This essay is an attempt to summarize the literature concerning the size of the prehistoric red deer in comparison with the recent species and to discuss the different influences of the habitat (extent and character of the biotope, food, climate) on the dimensions of red deer. It is the intention that it should attribute to a better understanding of the factors that may have caused the great size of many prehistoric red deer and to try and find out if a similarity between the variation during the course of postglacial times and the local variation in relation to the habitat exists. Most investigators agree that the prehistoric red deer belongs to the same species as the recent red deer, *Cervus elaphus* L. The red deer from Western and Central Europe (France, the Netherlands, Belgium, Luxembourg, Denmark, Switzerland, Germany, Italy, the Balkans and Western Russia) are usually considered to be all of the same subspecies *C. elaphus hippelaphus* ERXLEBEN, 1777 (e.g. HALTENORTH & TRENSE, 1956). Within this subspecies a number of varieties can certainly be distinguished according to different habitats, but, as will be clear at the end of this article, it is likely that most of their differences are only phenotypical. On the other hand some investigators distinguish quite a lot of subspecies.

The first thing to be demonstrated here is the fact that most prehistoric red deer are indeed considerably larger than the present red deer. RÜTIMEYER (1861, p. 59, 60) pointed out that remains of red deer recorded from the Swiss lake-dwellings are about one third larger than the corresponding parts of recent species of *C. elaphus* in Switzerland. RITCHIE (1920, p. 336) is also of the opinion that red deer were about one third larger in former times than a well developed animal of today. RITCHIE

[1]) When the word "prehistoric" is used in this article, prehistoric times in North-Western and Central Europe, not older than the neolithic period, are meant.

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based his conclusion on the following prehistoric finds: three antlers and one complete skeleton. VAN GIFFEN (1913, p. 135, 136) likewise reports the large dimensions of some scanty remains of red deer known from the Dutch terps (including a mandibula). According to INGEBRIGTSEN (1923, p. 204, 205) WAHLGREN holds the opinion that the size of the recent red deer and of the prehistoric ones can easily be explained by differences in environment and age. INGEBRIGTSEN himself on the other hand thinks that it is clearly demonstrated by the investigations of BRINKMANN that subfossil red deer were indeed larger than the recent ones. BRINKMANN poses the idea that measuring teeth is very useful to compare sizes of deer; when measuring a molar one is independent of the age of the animal in question and to a certain degree independent likewise of the influences of the environment. For when a molar is fully developed it will not increase in size any more, even when the animal in question has not yet stopped growing. The size of the teeth therefore are a standard for the size which the animal can attain when conditions are normal. When the teeth are larger and better developed, the deer in question will be larger and better developed too. On account of BRINKMANN's assertions that measuring teeth is the most proper method to prove that subfossil red deer were of greater size than the now living specimens, INGEBRIGTSEN has been measuring the M3 of the lower jaw of subfossil and recent red deer; it has become clear that subfossil deer were indeed larger (cf. the following table; though the animals are supposed to differ one third in lenght, the molars do not shows this difference). At the same time it should be born in mind that also smaller prehistoric remains of red deer exist. Probably there was a large variation in size in those times too, as it appears from my own observations.[2])

Lenght M3 (mandibula) of *Cervus elaphus* L.

Origin	Number	Variation of length in mm.	Average length
Recent			
Norway (BRINKMANN)	53	21——30	26.5[3])
Norway (INGEBRIGTSEN)	179	21——32	27.0
Prehistoric			
Norway, neolithic (BRINKMANN)	13	30——34	32.1
Denmark, neolithic (BRINKMANN)	124	28——40	32.5
Lake-dwellings, Bodensee, mainly neolithic (VOGEL)	13	31.5—37	31.7

[2]) E.g. The remains of C. *elaphus* recorded in the neolithic settlements of *Vlaardingen* and *Hekelingen* in the South-Western part of the Netherlands are almost of the same size as recent Dutch specimens. (Hekelingen excavation Rijksdienst Oudheidkundig Bodemonderzoek at Amersfoort under the management of Dr. P. J. MODDERMAN; Vlaardingen excavation Instituut voor Prae- en Protohistorie at Amsterdam under the management of Prof. Dr. W. GLASBERGEN). The results of the excavation of Vlaardingen will be published later on.

[3]) The recent red deer in Norway is very small. According to the author's measurements recent red deer in the Netherlands proved to be larger than the Norwegian deer; five specimens were measured (mainly of Dutch origin, Veluwe, to be found in the collection of the Zoölogisch Museum at Amsterdam). The average length of the M3 (mandibula) was 29.4 mm, the variation in length 22—34 mm.

Many investigators have already tried to analyse the nature of the factors that have caused the reduction of red deer since prehistoric times. Is it correct to explain this reduction in size by a change in the environment and the climate only? In addition the question arises if it is correct to consider the large prehistoric red deer as belonging to the same species as the recent ones; in considering those questions we have to know what influence the environment can have on the size of the animals. Most naturalists are of the opinion that the reduction of the forest is to blame for the "degeneration" of red deer, and also of course human activity viz. the clearance of the forest. RITCHIE (1920, p. 337, 350) for example remarks that on the one hand human beings will always have slain the animals that were easiest to catch and not the best, so that man cannot directly have caused this reduction in size. In this connection he points to the fact that there is always a large number of juvenile animal remains in prehistoric sites. Man on the other hand is to blame for the clearance of the forest, and of course it was always the forest on the most fertile soils that were subject to this clearance. Through this activity the space available for the wild animals will have constantly declined. As to the red deer RITCHIE puts forward the opinion that red deer are pre-eminently forest animals; this fact is to be demonstrated by their distribution in those parts of the *Coniferae*-zone that still exist today. Many other species have suffered by the reduction of their area as a result of human interference. For that reason many species are now extinct in these regions. However, such a reduction in size is not known in any other animal. RÜTIMEYER (1861) e.g. mentions a large number of animal species, not more known in Switzerland today, and he also noticed that the size of almost all other species of animals (except the boar) corresponds with the dimensions of the recent species.

In literature one may often find that considering the different influences of the environment no clear distinction has been made between the size of the antlers and the other dimensions (the investigation of BRINKMANN, i.e. the measuring of teeth, greatly contrasts with this view). This presents difficulties, since especially the antlers react very strongly to different conditions. VOGT (cf. VAN MAASDIJK 1948 p. 87—92) was able to breed red deer in a preserve with antlers similar to those of the prehistoric deer; he obtained these results by giving feed supplements viz. the so-called "sesamcakes" containing 50 parts calcium phosphate, 25 parts salt, 25 parts loam and 1 to 2 parts fennel-, caraway- or anise-seeds. In spite of the above mentioned objections it will appear that the size of the entire animal can be influenced likewise by the environment. BOTEZAT (1935 p. 186) and many other naturalists are of the opinion that the size of the biotope is very important for the size of many large animals, amongst others red deer. A reduction of the biotope causes a decrease in the size of these animals. DIERICH (1910 p. 31) remarks that recent red deer can attain the same size as prehistoric ones when conditions are good (food, unlimited area etc.). As to the prehistoric antlers DIERICH examined only a small number of them in which he noticed an enormous variation; he presumed that influence of the environment had caused

this variation. BIEGER quoted by BENINDE (1937 p. 162) measured the average weight of red deer from sandy soils and loam soils in Vorpommern, Mecklenburg and Brandenburg; it appeared that the red deer from the sandy areas weighed 8,8% less than the red deer from the loam areas and the roe deer 7% less. HESSE (1921 p. 211) has demonstrated that the size of red deer as well as roe deer clearly depends on the soil and the climate. According to HESSE there seems to be an enormous variation in size for both species; in Eurasia the dimensions increase from west to east, while futher eastwards they decrease again. The direction of this increase corresponds with the decline of the minimum temperature, and this direction is perpendicular to that of the January isotherms. LINKE (1957 p. 48) is of the opinion that red deer cannot bear an oceanic climate very well. It becomes clear from the literature mentioned above that presumably the size of red deer is dependent on the extent of the biotope, on the food and on the climate. Very probably "degeneration" symptoms have caused this decrease in size since prehistoric times because man has restricted their biotope more and more and also because he has always taken the most fertile soils.

However, a very important factor is often neglected, namely the character of the environment. It is not correct to consider red deer as inhabiting dry areas only, but naturalists in general seem to agree in looking upon the red deer as an animal of the dry forest (e.g. RITCHIE 1920, FRASER DARLING 1937). Until recently there was a population of very strongly developed red deer which live(d) in the damp "Auenwälder" along the river Danube, the so-called "Auehirsche". A collection of antlers of these "Auehirsche" is to be found in Schloss Petronell in lower Austria (P. J. VAN DER FEEN, oral communication). Other investigators have mentioned these extraordinary red deer as living in the „Donau-Auen" of lower Austria. According to LINKE (1957 p. 40) the best developed red deer are found in the Carpathians and the area of the river Drau. In passing, LINKE's opinion may be quoted that these "Drauhirsche" are characterized by their strikingly flattened antlers. As areas with the best developed red deer BENINDE (1937 p. 90, 91) mentions the "Auenwälder" along the rivers Danube, Drau and Save, especially the districts between the Danube and the Drau (e.g. the Darda district near the junction of the Drau and the Danube). The size of the red deer of these damp „Auenwälder" is reported to be comparable with that of prehistoric animals. BLYTH (1841 p. 748) also noticed how large the red deer in Hungary were and compared the size of these animals with the prehistoric specimens. In regard to these large Hungarian deer BLYTH wrote, that he did not know if they were still to be found. FITZINGER (1874 p. 547) did not agree with BLYTH; according to FITZINGER those specimens of large Hungarian red deer could only be animals of great age and it would therefore not be correct to consider these large red deer as a variety of *C. elaphus*. V. MOJSISOVICS (1884 p. 122) demonstrated that a stock of very strong red deer really existed in the "Auenwälder" and that their size could not be a question of old age only; he too compared the red deer of the "Auenwälder" with the prehistoric ones ("eines dem Aussterben nahen "Geschlechtes" der Edelhirsche, dem der Urhirsche

der Jetztzeit"). As to the environment of these "Auehirsche" V. MOJSISOVICS can be quoted. "Man hat wiederholt als "wichtigsten Factor" des successiven "Geringerwerden" des Hochwildes die Verminderung der Eichen- und Buchenbestände bezeichnet, — in wie weit dies anderen Ortes seine Begründung hat, ist nicht meine Sache hier zu erörtern; für "Bellye" und "Darda" und für das unmittelbare Nachbargebiet scheint dieser Factor im Ganzen weniger in Betracht zu kommen, indem der "Kern" des Standwildes hier vorwiegend in den wilden, von Rohr- und Sumpfplatten durchzogenen Riedwäldern zu suchen ist, während die mehr isolirt stehenden monotoneren Landwälder ..... in der Regel nur temporär (hauptsächlich von Wechselwild) bezogen werden, wozu unter Anderem auch anhaltende Hochwässer eine veranlassende Ursache abgeben können. Die abwechslungsreichen, überaus günstigen Bodenverhältnisse des Riedes, die reichliche und fette Aesung ...., konnten bedingen, dass sich hier ein Hochwildschlag bis zum heutigen Tage erhielt, wie ein ähnlicher in Centraleuropa sich kaum wieder finden dürfte." V. MOJSISOVICS made it clear in this section that the "Auenwälder" are very suited for the development of red deer. According to him it is a well-known fact that red deer prosper better near brooks, on loamy sandy soils, etc. (in short, soils that often have a reed-flora) than on stony and purely sandy soils. It is therefore obvious that "Auehirsche" are generally "better" than deer in the mountains. It may be added that in the opinion of V. MOJSISOVICS the roe deer are also of a larger size in brookforests. Large red deer are not only known in Danube areas; they are also found in brook-forests elsewhere. HESSE (1921 p. 217) mentions two types of red deer in Brandenburg, a smaller type in the heath-lands and a larger one in the "Oderbruch" and in the "Spreewald". LINKE (1957 p. 40) is of the opinion that deer in the mountains are smaller than red deer in the plains. Moreover, the size of the red deer increases from west to east.

The question remains if it is necessary to make a rigid distinction between the different local forms. According to BENINDE (1937 p. 104, 106) it turned out in Germany that importation of red deer from the famous Darda district could not improve the stock of German red deer; on the contrary, within just a generation there was no longer much difference to be noticed. BENINDE has the idea that "auf märkischem Heidesand die Erbmasse der ungarischen Auehirsche sich nicht hat behaupten können sondern im Phänotyp verschwunden ist." BOTEZAT (1935 p. 187) puts forward the opinion that the red deer display such a great variability that specimens of this species transferred to another habitat usually become similar to the local specimens in that habitat (presumably phenotypical variability is meant). BOTEZAT points out that this fact has already been known for a long time in connection with red deer of Carpathian origin which have been imported into Germany. Even imported Wapiti deer have become similar to the German red deer, with the exception of their call in the rutting period. However, in spite of this great "phenotypical" variability, BOTEZAT (p. 209) still has the idea that certain differences exist within the group of European red deer and that making a division into races and varieties — perhaps he includes subspecies too — cannot

be avoided [4]). In his opinion these differences are the different living conditions in their enormous area and also the size of the animals, their colour, etc., which correspond with these conditions. On the other hand these differences are not very important and therefore BOTEZAT considers the whole group of European and West Russian red deer as one single species (LYDEKKER, 1898). Thus it may be correct to consider this whole group of Western, Central and Eastern European red deer as one single species, as has been put forward at the beginning of this article. BOTEZAT's treatise is mainly based on ecological views, a fact which BOTEZAT himself admits in his title. One gets the impression that the systematic points are somewhat neglected. In any event the author has the idea that BOTEZAT does not strictly distinguish between subspecies and variety. For when we make a distinction between two different subspecies we expect to find genotypical differences; if we make a distinction between two different varieties the differences may be only phenotypical. In the case of the European and West Russian red deer there are strong indications, as I just pointed out, that the differences are chiefly phenotypical. We therefore do not agree with BOTEZAT (p. 210) when he mentions in Europe and West Russia three series of subspecies of *Cervus elaphus* namely a Southern, an Eastern and a Western one. On the contrary, the opinion is that we had better call the last two series of subspecies varieties or ecological forms. Besides the European subspecies C. *elaphus hippelaphus* ERXLEBEN, 1777, soms other subspecies (cf. ELLERMAN & MORRISON-SCOTT 1951) are recognized today in Southern and Northern Europe (real subspecies or varieties?), but on the question of the number of subspecies we are rather in the dark still. In this article we will not consider the (smaller) subspecies of Southern Europe and only describe BOTEZAT's Eastern and Western series since this author mentions the red deer of the "Donau-Auen" in the Eastern series. According to BOTEZAT the red deer of the Eastern series are rather large, they have got long heads, their colouring is a light yellow-brown, while their antlers are large, long and graceful with high crown-antlers; the type of these Eastern red deer is in between the Persian-Caspian deer on the one hand and the Western ones on the other. The red deer if his Western series and especially the Swedish ones are the most typical red deer; they are smaller with relatively short heads, their colouring is dark brownish and their antlers are relatively short with low crown-antlers. BOTEZAT (p. 212, 213) calls the red deer of the Carpathians and the "Donau-Auen" C. *elaphus carpaticus* and he distinguishes in this "subspecies" two "varieties" C. *elaphus carpaticus var. campestris* of the plain and C. *elaphus carpaticus var. montanus* of the mountain. (The nomenclatorial status of these names of BOTEZAT is rather uncertain and doubtful, many of them will have to be considered as nomina nuda.) These two varieties are said to differ in stature, colouring, shape of the head, hoofs and in the shape of the antlers. The

[4]) The above mentioned differences, strangely enough, at the same time lead BOTEZAT to distinguish many subspecies and even varieties in them. Presumably BOTEZAT considers the subspecies as a much lower systematical unit than we do now, perhaps as a variety, and the variety as a form. It is my opinion that owing to this difference in valuation of the taxonomical hierachical units, a contradiction seems to exist between his views and ours.

variety of the plain (and also the red deer of the "Donau-Auen") would be more similar to the Eastern series, whereas the mountain variety would come nearer to the Western type. So, although we can no longer hold the view that there are so many subspecies, we must admit that BOTEZAT has correctly noticed the enormous variability of the red deer.

Recapitulating, there are the following points to be noticed. The character of the red deer is strongly influenced by the conditions of the environment; in particular the size of the animal and the shape of the antlers are rather closely bound up with these conditions. The dimensions of the red deer probably show more clearly the influences of the environment than those of many other animals (cf. the report of RÜTIMEYER concerning the size of animal species of the Swiss lake-dwellings). It is very likely that the characters of the red deer are largely phenotypically determined, so that on this base a division into a number of subspecies does not seem justified. It is generally accepted that human activity, especially in regard to the clearance of the forest, is to blame for the reduction, since prehistoric times, of the size of the red deer. Probably the variation in size of red deer during the course of postglacial times is identical with the local variation in relation to the habitat. Even in neolithic times there existed a large variation in size, presumably in connection with the habitat. As to the forest, not only the forest of dry regions is to be considered as a proper habitat for red deer but areas with a high water-table can also be very suitable when rich in food. It is not unlikely that biotopes like the Austrian "Auenwälder" existed in the neighbourhood of the Swiss lake-dwellings and in other parts of Europe, in which red deer can therefore have prospered very well. Conditions in former days, more proper for red deer, may have caused the largeness of many prehistoric red deer compared with the size of recent ones, and we should not forget with regard to those conditions, that brook-forests with a varying water-table like the "Auenwälder" may have been very suitable too.

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