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The relationship between body size and environment: The case of Late Pleistocene reindeer *(Rangifer tarandus)*

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ABSTRACT: This paper deals with the geographical variability in the size of reindeer (*Rangifer tarandus*) in western and central Europe during the Late Glacial (ca. 13-10 ka B.P.). Osteometrical data suggests that a size cline existed from NW to SE, with animals in Great Britain being smaller than those from northern Germany, which, in turn, were smaller than in Moldavia. This cline can be explained by the continentality gradient of the climate. Additionally, a difference in the mean size of reindeer from the northern European Plain and from more southern areas was detected. This difference was mostly due to a smaller size of the females in the south. We postulate that the smaller size of the females was probably caused by food-stress during the summer and early autumn periods of the year.

KEYWORDS: REINDEER, BODY SIZE, SEXUAL DIMORPHISM, CLIMATE, LATE GLACIAL

RESUMEN: Este trabajo analiza la variación en la talla del reno (*Rangifer tarandus*) en Europa occidental y central durante el Tardiglacial (ca. 13-10 ka B.P.). Datos osteométricos sugieren la existencia de una variación de tipo clinal en la talla del reno en dirección NW a SE; así, los renos en Gran Bretaña eran de menor tamaño que aquéllos del norte de Alemania, quienes, a su vez eran más pequeños que los de Moldavia. Además de esta clina, se observó una diferencia en la alzada entre los renos de la planicie norteuropea y aquéllos de regiones más meridionales. Esta diferencia parece ser debida al tamaño menor de las hembras en poblaciones del sur; a su vez, postulamos que esta menor talla de las hembras fué probablemente causada por una escasez relativa de alimentos durante el verano y comienzos del otoño en dichas regiones.

PALABRAS CLAVE: RENO, TAMAÑO, DIMORFISMO SEXUAL, CLIMA, TARDIGLACIAL

INTRODUCTION

The investigation of body size through osteometrical data is routinely carried out in archaeozoological samples for a number of different purposes: (1) to try to elucidate the process and time of domestication (e.g. Uerpmann, 1979; Davis, 1981; Meadow, 1984); (2) to differentiate closely related taxa (e.g. Eisenmann & Beckouche, 1986; Dive & Eisenmann, 1991); (3) to set apart males from females in dimorphic species (e.g. Altuna, 1978; Grigson, 1982; Mariezkurrena & Altuna, 1983; Horwitz *et al.*, 1990; Weinstock, in press) etc.

An additional task for which osteometrical data can be used is the correlation of size variability for species subjected to climatic and environmental gradients. This is a much more difficult undertaking than the previously mentioned phenomena. There exist some trends - such as the size diminution of many species at the end of the Pleistocene- which can be confidently ascribed to changes in the environment. However, proceeding beyond very general statements (i.e. trying to selet the factors or groups of factors causing size changes and the mechanisms behind them) is much more difficult. This is due to the complex nature of the variables «Body Size» and «Environment». Body size of an animal within a population depends on a series of factors, which can be divided into two categories: ontogenetical and ecological (Figure 1). Factors in the first category include «sex» and «age». It is obvious that younger animals are smaller than full-grown conspecifics and, in most mammalian species, males are larger than females, although the degree of sexual dimorphism differs among species and may even vary between populations of the same species (e.g. Skogland, 1989). Ecological factors affecting body size include climate (which, in turn, includes a number of parameters such as the amount and timing of precipitation, temperature, and seasonality), vegetation, population density, the colonisation of new habitats, and interspecific competition (see e.g. Pitelka, 1951; Scheffer, 1955; Rensch, 1960; Klein, 1964, 1985; Geist, 1971, 1987; Klein & Strandgaard, 1972; Bourliere, 1973; Boyce, 1978; Guthrie, 1984 a, b; Lindstedt & Boyce, 1985; Calzada & Aguilar, 1995). As Figure 1 shows, these variables are often interconnected, so that isolating the ultimate factor or factors responsible for a change in size is very problematic.

The relationship between environment and body size in animals has been a subject of interest and debate for a long time. In attempts to clarify this matter, some empirical generalisations were already postulated in the 19th century describing the parallelism between morphological variation and features of the physical environment (e.g. Bergmann, 1847; Allen, 1877); these are the so-called «ecogeographical rules». Probably the best known is «Bergmann's rule» which states that «races from cooler climates in species of warm blooded vertebrates tend to be larger than races of the same species living in warmer climates» (Mayr, 1970: 197). Bergmann (1847) argued that large size is an adaptation for energy conservation in cold environments, since large animals lose less heat relative to mass than smaller ones. While postulated 150 years ago, Bergmann's rule continues to be used by some palaeontologists and archaezoologists as an explanation for observed size changes in the past (e.g. Davis, 1981; Klein, 1986; Klein & Scott, 1989).

Bergmann's rule, however, is by no means devoid of problems. It has been criticised on a number of counts which will not be reviewed here (e.g. Scholander, 1955, 1956; Irving, 1957; Hayward, 1965; McNab, 1971; Geist, 1987; Dayan *et al.*, 1991). In Rensch's (1938, 1960) opinion, the applicability of Bergmann's rule depends on «all other things being equal». Given the scarcity of situations where «all other things are equal», considering that thermoregulation is but one of the many physiological constraints of an individual, and the very complex nature of both «Body Size» and «Environment», it would be indeed naive to expect a single factor such as temperature to explain size variation.

While acknowledging that an investigation of the relationship between size and environment is fraught with difficulties, it is nevertheless an important task and we cannot afford to let the hardships deter us from attempting carrying it out. This paper attempts to investigate the relationship between body size of reindeer (*Rangifer tarandus*) and the environmental conditions during the Upper Pleistocene. *Rangifer* is a good choice for this purpose, since it was a common prey of Palaeolithic hunters and is represented at archaeological sites in relative large numbers.

Size variability of Pleistocene reindeer can be investigated in two ways: (i) the variability along the time-axis in a given geographical region or regions (e.g., Périgord, northern European Plain etc.) and (ii) the geographical variability of contemporaneous populations. It is this second aspect which constitutes the subject of the present paper.

During the Pleistocene, reindeer inhabited large extensions of the Eurasian continent. This fact allows for a comparison of animals living in habitats with differing climatic and environmental features. The present study concentrates on the Late Glacial (ca. 13-10 ka B.P.), the period for which most osteometrical information could be gathered and also the one with the best chronological resolution.

MATERIAL AND METHODS

The faunal material comes from northern Spain, southern France, the Paris basin, Great Britain, Belgium, northern and southern Germany, Switzerland, and Moldavia. Most of the fragments were measured by ourselves. Where this was not possible, osteometrical data was gathered from the literature. A number of scholars kindly provided unpublished data for our study (Table 2). Measurements were taken to the nearest 0.1 mm following von den Driesch (1976). In addition, some new depth-measurements were defined and recorded (Figure 2).

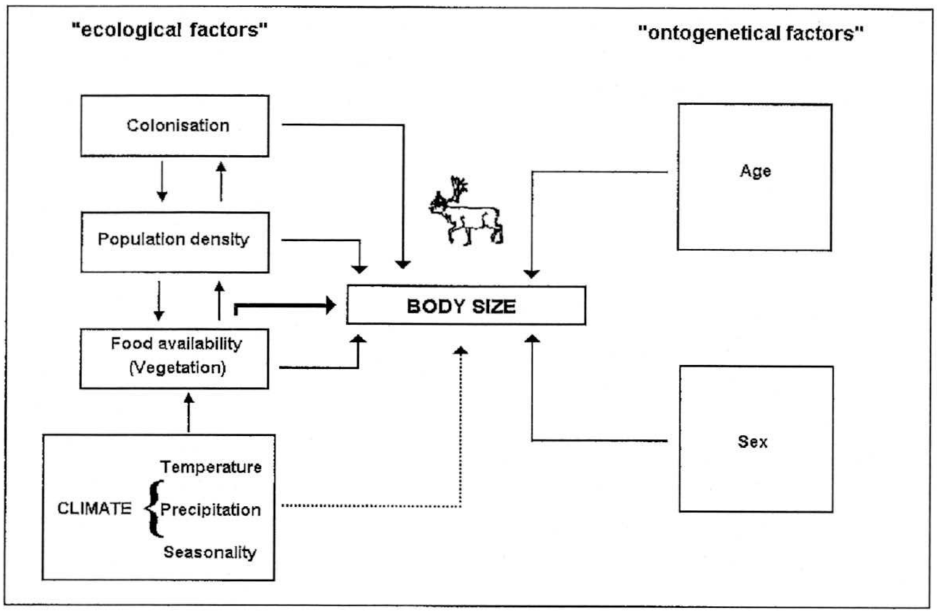

FIGURE 1
Factors influencing body size of individuals in a population.

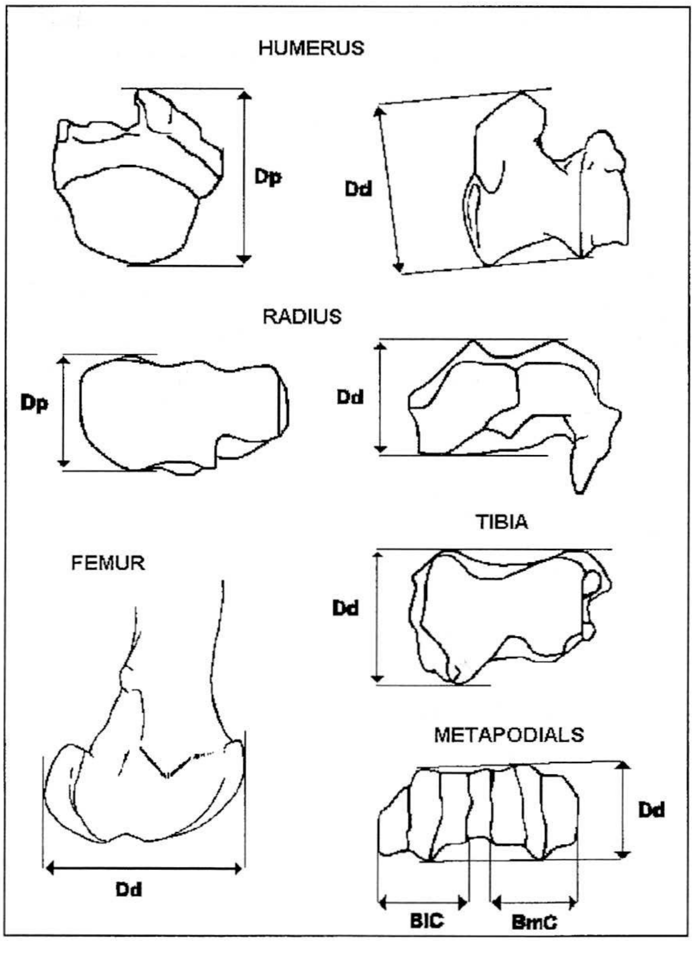

FIGURE 2
Measurements used in the present study in addition to those in von den Driesch (1976). Dp = proximal depth; Dd = distal depth; BmC = width of medial condyle; BlC = width of lateral condyle.

In order to compare the size of reindeer from different regions, the «Variability Size Index», or VSI, (Uerpmann, 1982, 1990) was used. This method enables the comparison of breath and width measurements of the different postcranial skeletal elements to be pooled together, thus considerably enlarging the sample size of the assemblages under comparison. The method is based on the confrontation of archaeological specimens to a standard. The standard is not an individual as in the case of the «Logarithmic Size Index» (Uerpmann, 1979, 1990) but, rather, a population; this means that the differing variabilities of the various dimensions are taken into account. For each measurement taken on a bone an index is calculated according to the formula:

$$\mathrm{VSI} = \frac{x - m}{2s} * 50$$

where «x» is the value of the fragment in question for a given parameter (e.g. distal width of the tibia), «m» is the arithmetic mean of the same parameter in the standard population, and «s» is the standard deviation of the standard population. If a number of measurements are taken from the same fragment, then a «mean VSI» for this piece is provided by the arithmetic mean of the various indexes . Thus, the size of each bone is represented by a single VSI index which can take either a positive value (in case the fragment in question is larger than the standard) or negative values in case it is smaller.

In the case of Moldavia, the mean value and range for a number of measurements was available but the osteometrical data for the isolated bones was lacking (data after Belan, n.d.). The mean VSI for this area was therefore built in the following manner: for each of the available mean values (i.e. distal width of humerus, radius, tibia, metacarpus, and metatarsus plus the proximal width of the metatarsus) a VSI was calculated; from these, the arithmetic mean was calculated to obtain the final VSI value. The standard deviation was likewise estimated using the means, while the maximum and minimum values were based on the single largest and smallest value from the ranges of all of the skeletal parts mentioned above.

For our study, the abundant material from the Ahrensburgian layer of Stellmoor, near Hamburg in northern Germany, was selected as the standard population.

This open-air site dating to the Younger Dryas period –ca. 10 ka B.P.– was excavated by A. Rust during the 1930s (Rust, 1943). The preservation is extraordinary; not only were stone implements animal bones and coprolites preserved but also wood remains, including pinewood arrows (Rust, 1943). While the remains at the site do not represent a single event, chronological, geological, and palynological data show that the assemblage can be treated as a meaningful archaeological unit (Grønnow, 1987).

More than 18,000 reindeer fragments (>90% of the faunal assemblage) were recovered. They can be regarded as being the product of an non-selective mass-kill (Grønnow, 1987; Bratlund, 1991; Weinstock, in preparation) and as having been accumulated within a relatively short timespan. This material is almost ideal as a «standard population». The values for the calculation of the variability size indices are shown in Table 1.

RESULTS AND DISCUSSION

Geographical Variability of Reindeer during the Late Glacial

The mean VSI values for the sites examined in the present study are listed in Table 2 and plotted in Figure 3. Two trends are readily apparent: i) a size cline from north-west (NW) to south-east (SE) and ii) a considerable size difference between reindeer of the northern European Plain and their southern conspecifics from southern regions in western and central Europe.

Size cline from NW to SE

A size gradient existed from NW to SE with reindeer in Great Britain being somewhat smaller than those in northern Germany and Belgium which, in turn, were somewhat smaller than those in Moldavia. It must be mentioned that for this last area, no raw measurements were available and the VSI was calculated in a somewhat different way (see above); if osteometrical data for each fragment were to be used, the value of the VSI may not be identical to the one reported here. In any case, the plot of the mean values for different measurements for Moldavia and Stellmoor (Figure 4) makes it clear that reindeer in the former region were considerably larger than in the latter.

Element	**Dimension**	**mean (m)**	**standard deviation (s)**	**n**
Atlas	GB	110.76	18.47	78
	BFcr	67.80	3.51	123
	BFcd	63.00	5.50	118
	GL	77.68	9.65	82
	GLF	66.03	4.42	124
Axis	BFcr	63.83	4.90	72
	SBV	41.86	4.62	72
	BPacd	42.01	5.70	62
	LCDe	80.90	5.22	71
	LAPa	78.14	7.36	30
Scapula	SLC	33.63	4.04	231
	GLP	46.32	3.21	215
	LG	35.48	2.35	198
	BG	30.60	2.72	224
Humerus	Bd	47.04	2.63	228
	BT	43.47	2.37	228
	SD	21.89	2.34	50
	Dd	48.57	2.64	228
	Bp	59.98	4.41	42
	Dp	70.27	3.83	43
Radius	Bp	45.41	2.69	176
	SD	23.60	3.13	84
	Bd	43.04	2.82	128
	BFp	42.76	2.15	174
	Dp	25.98	1.42	163
	Dd	28.77	1.99	85
Ulna	BPC	25.57	1.67	57
	DPA	42.55	3.27	58
	SDO	37.60	2.38	57
Metacarpus	Bp	34.97	2.03	85
	Dp	25.57	1.38	85
	SD	19.85	2.35	75
	Bd	42.97	1.95	165
	Dd	22.53	1.02	165
	Depth Diaphysis	14.82	1.21	91
	B. medial Condyle	19.52	1.07	164
	B. lateral Condyle	19.55	1.07	164
Pelvis	LA	40.41	1.84	119
Femur	Bp	69.51	2.60	38
	DC	29.96	1.22	74
	SD	21.99	0.96	21
	Bd	57.61	2.76	31
	Breadth Trochlea pat.	28.14	1.46	32
	Dd	73.06	2.64	29
Tibia	Bp	62.23	2.70	49
	SD	22.79	0.88	24
	Bd	40.09	1.89	133
	Dd	33.16	1.61	133
Talus	GLl	45.92	1.88	138
	GLm	43.43	1.66	138
	Depth lateral	25.52	I .07	138
	Depth medial	26.92	I .47	137
	Bd	28.47	1.42	138
Calcaneus	GL	95.72	4.50	113
	GB	30.64	1.79	111
	Dl	34.86	1.51	113
	smallest depth Tuber	23.35	1.46	111
Centrotarsale	Breadth	35.64	1.89	79
	Depth	32.03	1.62	79
Metatarsus	Bp	30.68	1.27	40
	Dp	33.76	1.43	38
	SD	17.95	1.05	15
	Bd	41.63	1.50	26
	Dd	23.31	0.81	26
	Depth Diaphysis	16.77	0.85	25
	Breadth med. Condyle	19.17	0.78	26
	Breadth lat. Condyle	18.54	0.75	26

TABLE 1

Values for the calculation of Variability Size Indices obtained from material from Stellmoor, Ahrensburgian layer (abbreviations as in von den Driesch, 1976).

Site	mean	st. dev.	min.	max.	n
Spain and southern France					
Northern Spain*	-14.17	30.92	-55.72	31.15	9
Dufaure 4[1]	-15.38	25.23	-101.05	53.91	116
Gare de Couze H*	-22.70	23.47	-66.2	49.43	60
La Madeleine (Excav. 1865)*	-18.69	21.14	-68.51	31.95	205
Gare de Couze G*	-18.00	23.8	-99.84	52.58	238
Veyrier[2]	-14.62	26.99	-114.22	33.53	74
Paris Basin					
Pincevent[3]	-19.51	35.18	-130.74	88.11	606
Southern Germany and Switzerland					
Schussenquelle*	-17.51	27.27	-89.2	48.35	209
Petersfels*	-22.41	28.31	-103.21	63.29	158
Kesslerloch*	-19.33	25.89	-113.69	62.24	1384
Lower Rhine valley (Germany)					
Andernach[4]	-13.73	43.18	-57.41	62.3	6
Great Britain					
Kent`s Cavern*	-7.78	21.73	-41.94	29.32	23
Ossom's Cave*	-6.21	33.78	-74.47	62.5	28
Northern Germany and Belgium					
Hamburgian (Stellmoor HL + Meiendorf)*	-4.11	25.42	-58.6	77.81	330
Stellmoor AL*	0.51	23.29	-53.21	70.49	1803
Hohler Stein[5]	-2.84	22.64	-36.06	49.92	25
Remouchamps[5]	1.97	27.04	-60.5	50.39	27
Moldavia[6]	16.68	17.17	-76.53	96.85	206

TABLE 2

Statistical values of VSIs from Late Glacial sites. Sources for osteometrical data: * measured by author; 1: Altuna *et al.*, 1991; 2: Koenig & Studer, 1981; 3: J. Enloe, pers.comm.; 4: M. Street, pers. comm.; 5: Baales, 1996; 6: Belan n.d. (see above for explanation of how the values for this group were calculated).

SITE	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1 Stellmoor		*	-	-	+	+	*	*	*	*	*	*	*	*	*
2 Hamburgian	*		-	-	-	-	*	*	*	*	*	*	*	*	*
3 Remouchamps	-	-		-	+	-	*	*	*	*	*	*	*	*	*
4 Hohler Stein	-	-	-		-	-	*	*	*	*	*	*	*	*	*
5 Kent's Cavern	+	-	+	-		-	*	*	*	-	*	*	*	*	-
6 Ossom's Cave	+	-	-	-	-		*	*	*	-	*	*	*	*	-
7 Schussenquelle	*	*	*	*	*	*		-	+	-	-	-	-	+	-
8 Kesslerloch	*	*	*	*	*	*	-		-	*	-	-	-	-	-
9 Petersfels	*	*	*	*	*	*	+	-		*	+	-	+	-	*
10 Veyrier	*	*	*	*	-	-	-	*	*		*	+	+	*	-
11 La Madeleine	*	*	*	*	*	*	-	-	+	*		-	-	+	-
12 Pincevent	*	*	*	*	*	*	-	-	-	+	-		-	-	-
13 Couze G-G1	*	*	*	*	*	*	-	-	+	+	-	-		+	-
14 Couze H	*	*	*	*	*	*	+	-	-	*	+	-	+		*
15 Dufaure 4	*	*	*	*	-	-	-	-	*	-	-	-	-	*	

TABLE 3

Wilcoxon significance-test for arithmetical means of VSIs, Late Glacial sites. Sites or groups of sites with n<10 and Moldavia not included. *= highly significant (α=0.05); + significant (α=0.1); - not significant.

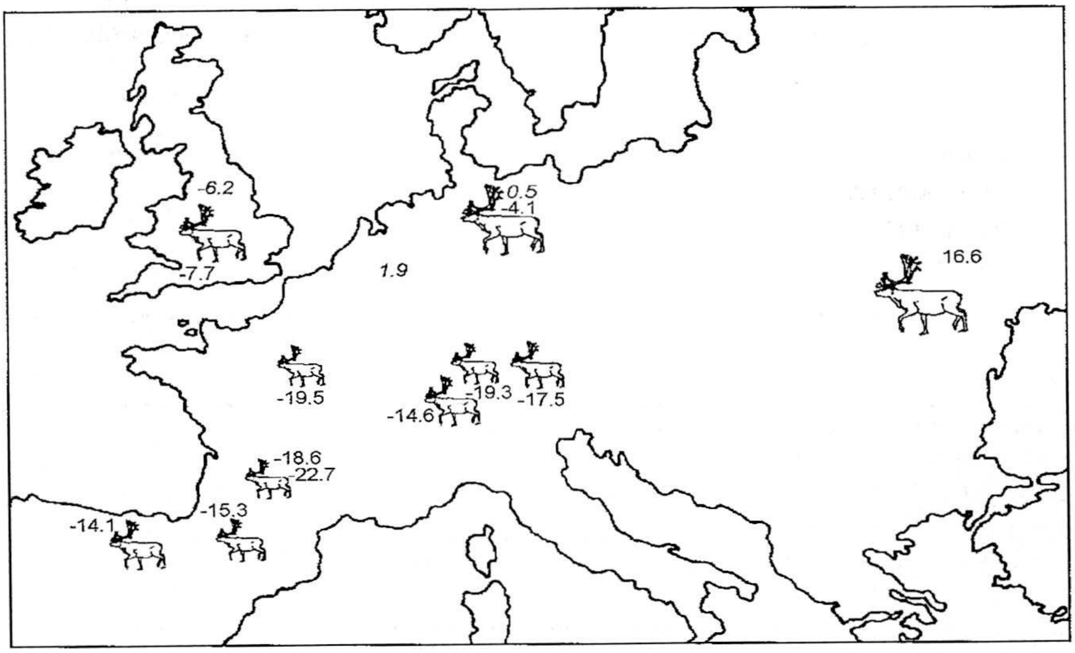

FIGURE 3

Schematic representation of reindeer size and mean VSIs from Late Glacial sites. Numbers in standard form = sites from the Bölling/Allerod period (ca. 13-11 ka BP); numbers in italics = sites from the Younger Dryas (ca. 10 ka BP). Size of depicted reindeer are only meant to convey a visual impression of size differences; they are not drawn in exact scale.

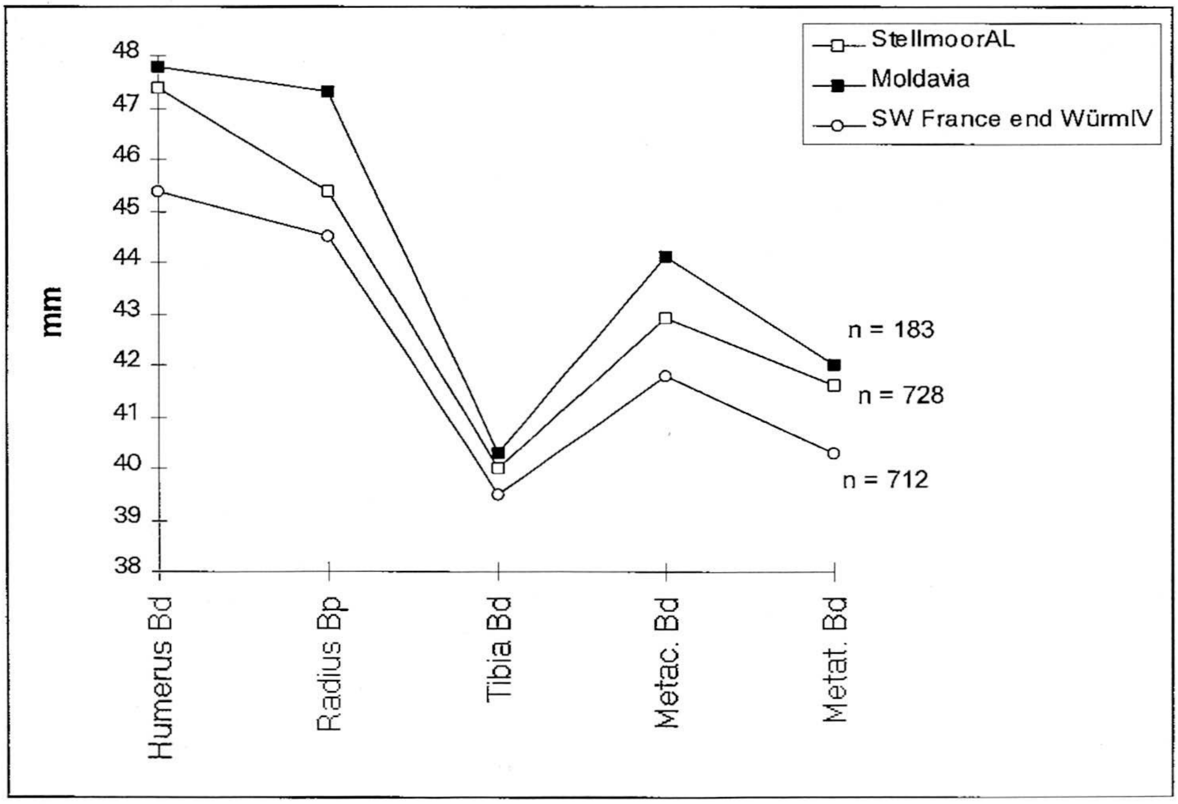

FIGURE 4

Mean values of selected measurements in Stellmoor Ahrensburgian layer (material measured by author), Moldavia (after Belan, unpublished manuscript), and the Périgord (after Delpech, 1983).

Whether a NW-SE size cline - or in fact any size cline at all - exists in modern wild reindeer is unknown, since precise comparative data is lacking (Syroechkovskii, 1995). Moreover, one should be reminded that interbreeding with domestic animals has occurred to a smaller or larger degree in most wild reindeer populations. However, equivalent W-SE or SW-NE size gradients have been reported in recent populations of red deer *Cervus elaphus* (Beninde, 1937; Pietschmann, 1977), wild boar *Sus scrofa* (Herre 1986; Briedermann, 1990), and brown bear *Ursus arctos* (Jakubiec, 1993). Despite this, there have been very few serious attempts to explain such clinal variation. This must not come as a surprise since, as mentioned above, the many interrelated factors involved in the determination of body size makes such an endeavour very complicated. A brave attempt to explain observed size differences is the study by J. Beninde (1937) on *Cervus elaphus*. Beninde showed that the observed NW-SE size gradient could not be explained by differences in the mean values of either summer or winter temperatures but by the difference between them thus meaning -roughly speaking- the difference in the continentality gradient of the climate. He, nevertheless, made the climatic factors directly responsible for this difference in size by extrapolating from human experience. Thus, he argued that since cloudy and humid weather makes many people feel depressed this will of course affect the growth of deer as well!. Conversely, the dry continental climate of eastern Europe would be invigorating for the animals.

Beninde ignored the important effects of climate on the vegetation - i.e. on the food supply of the animals -as well as the demographic effects which climatic conditions can produce- e.g., a narrow or broad «Winter Bottleneck». While the precise reasons for the size cline remains to be clarified, more severe winters -i.e., a higher mortality rate- in the SE could prove to be an important factor by reducing intraspecific competition during the following growth season (Guthrie, 1984 a, b). As a side effect of reduced competition, the quality and quantity of available growth herbage per individual would increase, allowing for the development of a larger body size. In fact, it is a well known principle among wildlife managers that the individual deer quality in a herd can be increased by increasing the hunting bag during the non-growth season (Klein, 1965; Guthrie, 1984 b).

Size difference between «northern» and «southern» reindeer in western and central Europe

A clear and statistically significant difference has been evidenced between reindeer in the North European Plain (Great Britain, northern Germany, Belgium) and those from northern Spain, France (Périgord, Paris Basin), southern Germany, and Switzerland. While some variability exists in both groups, the former show considerably larger VSI mean values than the latter (Tables 2 & 3 and Figure 3).

To grasp the nature of this size difference it is more useful to consider the distribution and relative frequencies of the Variability Size Indices than their arithmetic mean. Thus, the distribution of the VSI values for sites with n>100 is plotted in Figure 5. It is readily apparent that the most obvious difference between both groups is in the smaller range, i.e. in their *minima*. [It is striking, for example, that among the ca. 1800 bones measured from Stellmoor in northern Germany none reaches a VSI minimum near that of the Swiss site of Kesslerloch (n = 1384)].

By plotting the relative VSI frequencies from contemporaneous sites (= Bölling, ca. 13-12 ka B.P.) in northern and southern Germany, it can be shown that the very low minima of the southern sites are not due to isolated anomalous values (Figure 6). Both assemblages show a bimodal distribution. The shape of the VSI curve is influenced by the sex structure of the thanatocoenoses and only to a lesser extent by its age structure since bones of young animals were not measured whenever recognised as such. Therefore one can safely assume that the left peak in a curve represents the females while the right peak should represent the males. It is clear that while the male peaks of both curves do not differ much, the female peak of the Schussenquelle is displaced to the left in relation to that of the north German sites, pointing to the smaller size of the females in southern Germany.

This same pattern emerges when using measurements of isolated skeletal elements rather than VSIs. Figures 7 and 8 show that while in Switzerland and southern Germany some individuals were as large as in northern Germany, the smallest reindeer in the north never reached a size as small as that found in the south.

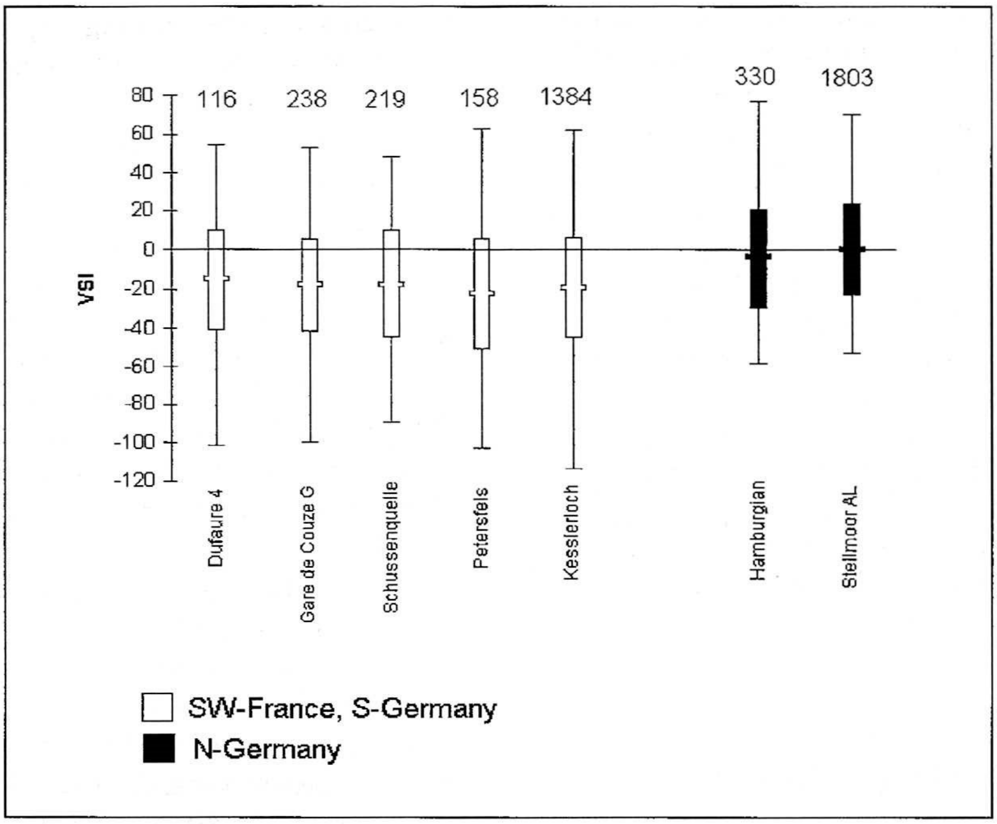

FIGURE 5

VSI distribution in Late Glacial sites in central and western Europe
y sites with n>100 plotted).

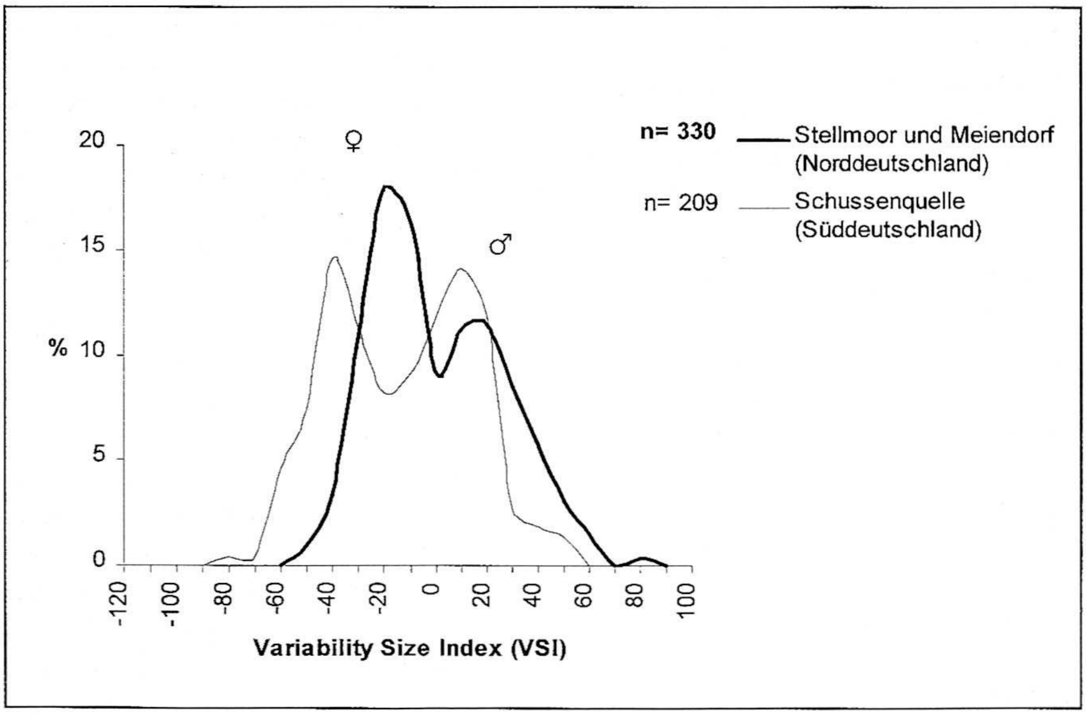

FIGURE 6

VSI frequencies of Hamburgian sites (Stellmoor + Meiendorf) in northern Germany and Schussenquelle in southern Germany. The sites are contemporaneous and date to the Bölling chronozone.

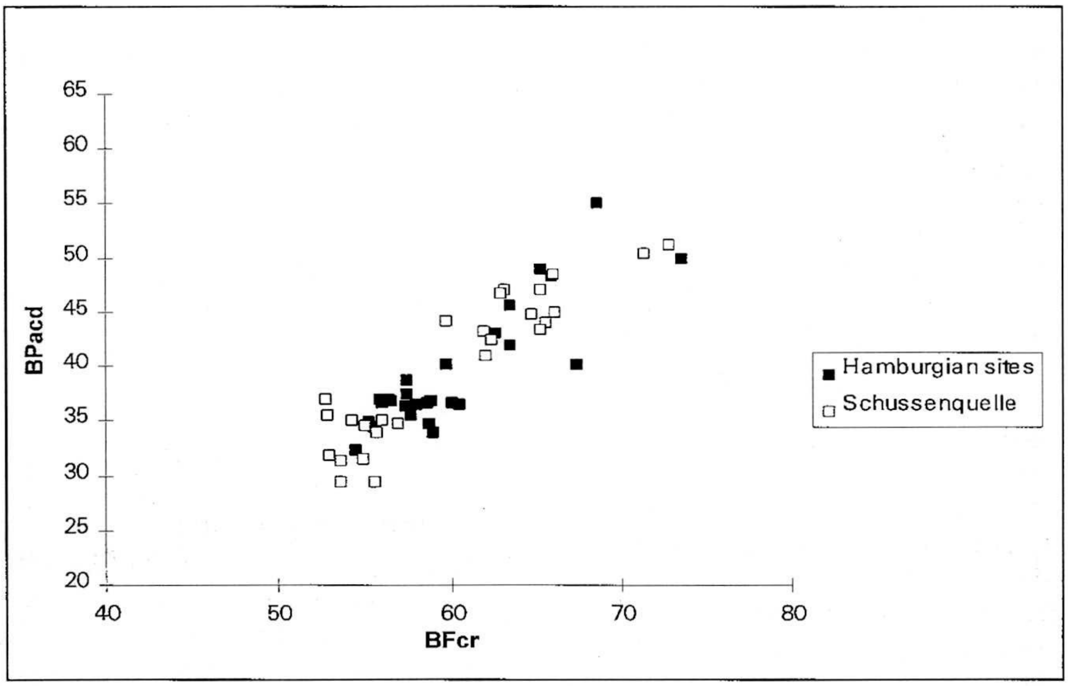

FIGURE 7

Plot of axis (BFcr/BPacd) from the Hamburgian sites of Meiendorf & Stellmoor (northern Germany) and Schussenquelle (southern Germany).

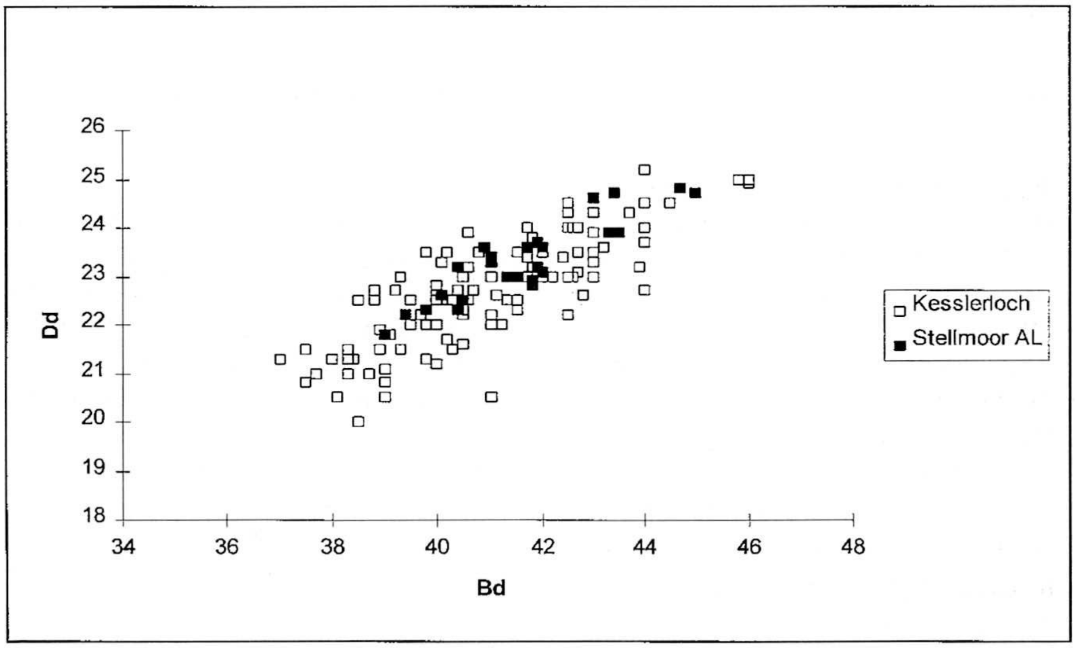

FIGURE 8

Plot of metatarsus (distal width/distal depth) from Stellmoor Ahrensburgian layer (northern Germany) and Kesslerloch (Switzerland).

How can this phenomenon be accounted for? The answer probably lies in the fact that selective forces acting upon the males from most species of polyginous ungulates, *Rangifer* among them, are not exactly the same as those acting upon the females. This is a result of the different reproductive strategies and investment of both sexes (Clutton-Brock *et al.*, 1982). Males have to compete among themselves for access to females and in this struggle large body size and large antlers are advantageous. Thus, a selection for heavier, large-antlered males is to be expected (Clutton-Brock *et al.*, 1982). Obviously, environmental constraints still impose limits to maximal male adult body size. On the other hand, adult body size in females depends on whether growth is continued after maturity. Skogland (1983, 1989), in his study of wild Norwegian reindeer, has shown that under conditions of food abundance females continued to grow after maturity. Under food limitation, however, females increased their reproductive effort by having their own body growth arrested. Thus, it can be expected that «...*the degree of sexual dimorphism* [will] *be enhanced by food limitation, given that males put a premium on developing large size to be a successful breeder, while female success is measured in terms of lactation*» (Skogland, 1989: 10).

CONCLUSIONS

To conclude, I would now like to put forward the hypothesis that the larger degree of sexual dimorphism evidenced by reindeer living in more southerly regions of western and central Europe during tardiglacial times was a product of their living under conditions of relative food limitation in particular during summer, the season in which animals obtain the protein necessary for somatic growth.

Going a step further in this analysis -i.e. getting at the specific factors causing a more pronounced food stress in southern latitudes- is much more difficult, and will necessarily involve much more sophisticated palaeoclimatic data than that available at present.

Having established that a difference in the size of females and - to a lesser extent - of males existed between northern and southern *Rangifer* population the question remains: should this difference be regarded as part of a more general size gradient (i.e. a cline) or were these two groups separated by a more or less sharply defined boundary? And if such a sharp boundary did exist, what was its shape and extension? Regrettably, very few remains of reindeer at our disposal could help us solve this question. If we look as far north as the Paris basin, reindeer at the site of Pincevent seem to be no larger than those in south-western France. A second Late Glacial site located between the northern and southern groups is Andernach, in the lower Rhineland. Unfortunately, only six reindeer bones from this location were measured (a mean VSI of -13.73 suggests a size somewhat larger than the «typical» southern animals, although much smaller than the northern ones. However, sample size is so small that further speculation based on this material is unwarranted). Thus, the question of whether a North-South cline for reindeer body size existed during the European Late Glacial cannot be answered with the data available at present. It is hoped that further work in the relevant geographical areas will someday allow us to solve this problem. For the moment, based on the data from Pincevent, it would seem that the possibility of a conjunction, that is, of two groups of populations separated by a well defined boundary without a gradation in between them is to be taken as the most parsimonious explanation.

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