

Body Size Trends of Roe Deer (*Capreolus capreolus*) from Danish Mesolithic Sites

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INTRODUCTION

During the climatic amelioration following the last glaciation, numerous mammalian species underwent marked reduction in mean body size as reflected in bone dimensions (*e.g.*, Kurtén 1959, 1965, 1968; Davis 1977, 1981; Boessneck & von den Driesch 1978; Uerpmann 1978; Guthrie 1984; Klein & Cruz-Urbe 1984).

Davis (1981) pointed out that the Late Pleistocene – Holocene size diminution seen in most mammalian lineages was probably world-wide. Examples of this kind of body size change have been termed "post-Pleistocene dwarfing" (Marshall & Corruccini 1978).

Kurtén (1959) emphasized that there is no need to invoke genetic change as a factor underlying dwarfing of Late Quaternary mammals and that size changes may be "a characteristic of the environment rather than of the animals themselves".

Although the reasons for the initiation of size reduction are still not fully understood, it is generally assumed that adverse environmental conditions were responsible for the Late Pleistocene-Holocene trend of size decline of mammals. In this context, mammalian remains recovered from dated archaeological sites have proved valuable in monitoring body size changes within a chronological framework.

Skeletal remains of roe deer (*Capreolus capreolus*) have been found in substantial numbers associated with Danish Mesolithic sites covering the period 9000 to 5000 radiocarbon years b.p. (before present), indicating that this species formed an important part of the diet of the Mesolithic hunter-gatherers. With the advent of agriculture and animal husbandry, hunting became less important and thus from the Neolithic period onwards, roe deer remains are either absent, or present only in insignificant numbers, in archaeological context.

Møhl (1971, 1987) and Aaris-Sørensen (1976), working

on faunal remains from selected Danish Mesolithic sites, noted a size discrepancy between subfossil and recent roe deer.

These findings are in accordance with similar studies from other parts of Europe. Boessneck (1958), in an analysis of roe deer remains from archaeological sites throughout central Europe in comparison with recent material, showed that Mesolithic and Neolithic specimens grew to a larger size than their present-day conspecifics. Likewise, Requate (1957) reported on roe deer of considerable size from Mesolithic sites in Schleswig-Holstein.

Although temporal variation of roe deer has been established, the timing of the size reduction has not been documented in detail. Thus, the purpose of the present paper is to investigate whether significant changes in mean body size of Danish roe deer occurred during the Mesolithic period in relation to changing environmental conditions. Recent data have been included for control purposes.

MATERIAL AND METHODS

Mesolithic sites from which subfossil material has been examined are shown in Table 1. The chronology of the sites mentioned is given in relation to chronozones and cultures.

According to Mangerud *et al.* (1974), the Boreal chronozone covers the period 9000 to 8000 radiocarbon years b.p., whereas the Atlantic chronozone covers the period 8000 to 5000 radiocarbon years b.p.

The Danish Mesolithic period is divided into three archaeo-cultural stages (Maglemose, Kongemose and Ertebølle) named after their archaeological type-sites. Cultural assignment follows Brinch Petersen (1973).

The subfossil material mentioned in Table 1 is kept at the Zoological Museum, University of Copenhagen

(ZMUC) with the exception of the bone material from Tybrind Vig, which is deposited at the Institute of Prehistoric Archaeology, University of Aarhus.

Mensural data from published faunal lists include Lundby-II (Rosenlund 1980), Sværdborg I-1943 (Aaris-Sørensen 1976) and Ulkestrup Lyng Øst (Richter 1982).

Mensural data from unpublished faunal lists include Vedbæk Boldbaner, Maglemosegårds Vænge, Henriks-holm-Bøgebakken, Maglemosegård (Aaris-Sørensen *in litt.*) and Tybrind Vig (Trolle-Lassen *in litt.*).

Due to the fragmented state of the archaeo-zoological material, only measurements of frequently-occurring skeletal elements have been included in the present study. The measurements defined below were taken on subfossil and recent material. The following six parameters have been measured according to definitions given by von den Driesch (1976):

- Parameter 1: length of the lower third molar (M3)
- Parameter 2: greatest length of the glenoid process of the scapula
- Parameter 3: greatest breadth of the distal humerus
- Parameter 4: greatest length of the astragalus
- Parameter 5: greatest breadth of the astragalus
- Parameter 6: greatest length of the fused calcaneus

The number assigned to each parameter is referred to in Table 1.

In order to achieve comparable results, only measurements of skeletal elements from adult roe deer should be included. Age analyses of archaeo-zoological material are generally based on eruption and wear of teeth and epiphyseal fusion (Payne 1972).

The length of the lower third molar (parameter 1) and the greatest length of the fused calcaneus (parameter 6) are considered to be age-independent since these measurements can only be taken on adult specimens (Payne 1972; von den Driesch 1976). Referring to recent roe deer, Noe-Nyegaard (1988) points out that the epiphyseal union of the proximal and distal ends of various bone elements takes place at different ages and that the same skeletal element may fuse at different times in the two sexes. As to the measurements of the scapula (parameter 2) and humerus (parameter 3) only ossified epiphyses have been measured. According to Davis (1981), increase in epiphyseal widths following ossification of the embryonic cartilaginous model is assumed to be minimal. Payne (1972) argues that it is unwise to use a measure-

ment such as the length of the astragalus in investigating body size changes, as this bone is measurable from birth and grows substantially thereafter. Nevertheless, astragalus measurements have proved valuable in demonstrating temporal variation in roe deer (Boessneck 1956; Aaris-Sørensen 1976). As the astragalus lacks epiphyseal sutures, von den Driesch (1976) has suggested using the degree of compactness of this bone as a criterion of age. In the present study, measurements (parameters 4 & 5) were taken on astragali with hard shining surfaces. However, as von den Driesch (1976) points out, measurements of astragali of young specimens cannot be avoided altogether.

Skeletons of recent Danish roe deer were examined in the collections of ZMUC and the Game Biology Station, Kalø. In total, 31 female and 23 male adult roe deer were measured. The majority of these specimens were shot in Jutland. In the following, the sexes have been pooled as the degree of sexual dimorphism was found to be negligible (see Appendix).

The subfossil material cannot be sexed on the present available evidence.

A Mauser digital sliding calliper was used throughout the present study.

The molar measurement was taken to the nearest 0.5 mm whereas the measurements of the post-cranial elements were taken to the nearest 0.1 mm.

The subfossil and recent material were subjected to statistical analysis. The arithmetic mean (\bar{x}), standard deviation (s.d.), and 95% confidence limits of the mean (95%) have been computed as a means of estimating differences between samples. In addition, Dice-Leraas diagrams were constructed for all six parameters. These diagrams facilitate graphic comparison between samples derived from normally distributed populations and are useful for demonstrating temporal clines. Sample means whose 95% confidence limits do not overlap may be considered different at the 0.05 level of probability or below. In this way 95% confidence limits may be used as a partial replacement of Student's t-test. In cases of overlap, however, it is necessary to apply Student's t-test in order to establish whether differences between sample means are statistically significant. The statistical methods employed in this study follow Simpson *et al.* (1960) and Klein & Cruz-Urbe (1984).

	1.	2.	3.	4.	5.	6.	Chronoz.	Culture
Lundby I	4	17	12	11	11	4	Boreal	Maglemose
Lundby II (Rosenlund 1980)	0	6	6	0	0	0	Boreal	Maglemose
Maglemose	7	10	7	3	3	4	Boreal	Maglemose
Holmegaard V	1	2	6	1	1	2	Boreal	Maglemose
Sværdborg I-1917	4	18	35	21	21	10	Boreal	Maglemose
Holmegaard IV	2	10	10	6	6	5	Boreal	Maglemose
Holmegaard I-1922	7	15	17	7	7	2	Boreal	Maglemose
Holmegaard I-1923	1	2	1	2	2	1	Boreal	Maglemose
Sværdborg I-1923	3	51	36	28	28	11	Boreal	Maglemose
Sværdborg I-1943 (Aaris-Sørensen 1976)	0	0	0	26	24	0	Boreal	Maglemose
Sværdborg II-1946	2	0	1	1	1	2	Boreal	Maglemose
Ulkestrup Lyng Øst (Richter 1982)	0	1	4	5	5	1	Boreal	Maglemose
Villingebæk	0	4	3	0	0	2	Atlantic	Kongemose
Gislinge Lammefjord	1	2	3	0	0	1	Atlantic	Kongemose
Argusgrunden	0	0	0	0	0	2	Atlantic	Kongemose
Vedbæk Boldbaner (Aaris-Sørensen in litt.)	0	11	17	1	1	1	Atlantic	Kongemose
Maglemosegårds Vænge (Aaris-Sørensen in litt.)	2	1	1	2	2	4	Atlantic	Kongem./Erteb.
Henriksholm-Bøgebakken (Aaris-Sørensen in litt.)	1	5	3	1	1	1	Atlantic	Kongem./Erteb.
Maglemosegård (Aaris-Sørensen in litt.)	18	6	18	11	11	7	Atlantic	Kongem./Erteb.
Nivå	20	19	36	26	26	13	Atlantic	Kongem./Erteb.
Bloksbjerg*	5	28	14	17	17	14	Atlantic	Kongem./Erteb.
Godsted	3	11	3	15	15	15	Atlantic	Ertebølle
Bergmandsdal	1	0	1	0	0	1	Atlantic	Ertebølle
Salpetermosen	22	46	45	40	40	26	Atlantic	Ertebølle
Ølby Lyng*	0	5	1	8	8	1	Atlantic	Ertebølle
Flynderhøge	0	12	2	0	0	3	Atlantic	Ertebølle
Dyrholmen	0	11	16	6	6	10	Atlantic	Ertebølle
Ertebølle 1893-97*	12	28	14	34	34	21	Atlantic	Ertebølle
Krabbesholm	1	0	0	1	1	0	Atlantic	Ertebølle
Bjørnsholm	8	5	8	4	4	5	Atlantic	Ertebølle
Sebber	1	0	1	0	0	1	Atlantic	Ertebølle
Aamølle	0	0	1	6	6	2	Atlantic	Ertebølle
Fannerup*	1	1	0	1	1	0	Atlantic	Ertebølle
Kolind*	0	1	1	0	0	1	Atlantic	Ertebølle
Mejlgaard*	7	2	6	8	8	6	Atlantic	Ertebølle
Brabrand	0	0	0	0	0	1	Atlantic	Ertebølle
Ordrup Næs	0	0	0	1	1	0	Atlantic	Ertebølle
Klintesø*	6	16	8	7	7	6	Atlantic	Ertebølle
Faarevejle*	0	0	1	5	5	5	Atlantic	Ertebølle
Kassemose*	17	25	33	20	20	31	Atlantic	Ertebølle
Tybrind Vig (Trolle-Lassen in litt.)	5	2	4	3	0	2	Atlantic	Ertebølle
Havelse*	4	7	4	8	8	8	Atlantic	Ertebølle
Vester Ulstev	1	5	1	2	2	3	Atlantic	Ertebølle

Table 1. Mesolithic sites studied in approximate chronological order. Numbers 1-6 refer to measurements defined in the text. N = number of specimens.

*) In addition these sites may contain Early Subboreal material. However, in all border-line cases the bulk of the bone material derives from Mesolithic layers.

RESULTS

The Boreal sample is regarded as being representative of the continental Danish roe deer population, whereas data from the Atlantic chronozone subsequent to island formation have been divided into two geographically distinct samples, one from Jutland and the other from the Danish islands. In the following, the sample from Jutland will be referred to as the mainland Atlantic sample/population and the Danish island sample as the insular Atlantic sample/population. Dice-Leraas diagrams of the subfossil and recent material for parameters 1-6 are shown in Fig.

1. Accompanying descriptive statistics of the measurements are given in Table 2.

It can be seen that the mean values of the subfossil material in all parameters studied are greater than those for the recent material. This observation confirms that the roe deer during the Mesolithic period were larger than their present-day conspecifics.

In general, the pattern of change is very uniform in all six parameters. Applying the convention of the use of 95% confidence limits as a partial replacement of Student's t-test, it is noted that the Boreal sample in all cases differs significantly from the insular Atlantic sample. On

	N	range	x	s.d.	95%
1					
Boreal	31	14.5-17.0	15.84	0.64	0.23
Mainland Atlantic	30	14.5-17.0	15.77	0.75	0.28
Insular Atlantic	106	13.5-17.4	15.19	0.70	0.13
Recent	54	12.5-16.0	14.45	0.65	0.18
2					
Boreal	132	25.0-32.4	29.39	1.36	0.23
Mainland Atlantic	60	26.6-33.4	29.46	1.36	0.35
Insular Atlantic	193	24.5-30.6	27.77	1.27	0.18
Recent	54	23.1-30.3	27.08	1.19	0.32
3					
Boreal	135	25.9-32.0	29.13	1.23	0.21
Mainland Atlantic	49	26.7-32.0	28.68	1.20	0.34
Insular Atlantic	196	24.3-31.6	27.82	1.29	0.18
Recent	54	24.2-29.0	26.22	1.00	0.27
4					
Boreal	111	27.5-34.7	31.06	1.40	0.26
Mainland Atlantic	60	27.1-33.2	30.90	1.22	0.32
Insular Atlantic	167	26.8-32.4	29.44	1.25	0.19
Recent	54	25.8-30.4	27.84	1.01	0.28
5					
Boreal	109	17.1-22.3	19.65	0.90	0.17
Mainland Atlantic	60	18.0-21.6	19.76	0.87	0.22
Insular Atlantic	164	17.0-21.0	18.79	0.88	0.14
Recent	54	16.3-19.9	17.83	0.74	0.20
6					
Boreal	42	61.3-70.7	66.55	2.81	0.88
Mainland Atlantic	50	60.2-74.2	64.81	2.42	0.69
Insular Atlantic	143	55.7-68.5	61.29	2.68	0.44
Recent	54	54.8-65.8	58.66	2.28	0.62

Table 2. Parameters 1–6: Descriptive statistics. For details see text.

the other hand, only one parameter (greatest length of the fused calcaneus) shows no overlap between the Boreal and the mainland Atlantic samples. Thus the remaining parameters have been subjected to Student's t-test in order to determine the degree of significance between the sample parameters. The results of the t-tests are shown in Table 3. It appears that the comparison of the Boreal-mainland Atlantic samples may be considered different at the 0.05 level of probability in two parameters (greatest breadth of the distal humerus and greatest length of the

	T	d.f.	P	result
Parameter 1	0.4043	059	>0.05	not significant
Parameter 2	0.3150	190	>0.05	not significant
Parameter 3	2.1743	182	<0.05	significant
Parameter 4	0.7346	169	>0.05	not significant
Parameter 5	0.7547	167	>0.05	not significant

Table 3. Selected t-tests: comparison between Boreal and mainland Atlantic sample parameters.

fused calcaneus), whereas the Boreal-insular Atlantic samples differ significantly in all six parameters. Furthermore, the difference between the two geographically distinct samples of the Atlantic chronozone is significant in all six parameters.

Summing up, it can be said that a gradual decrease in mean body size of Danish roe deer during the Mesolithic period has been ascertained in the Boreal – insular Atlantic samples. However, the Boreal – mainland Atlantic samples do not show the same reduction in mean body size. Since both Atlantic samples differ significantly from the present-day sample in all six parameters, the reduction in body size of roe deer continued into post-Mesolithic times.

DISCUSSION

In looking for factors underlying changes in mean body size of Mesolithic roe deer, an attempt has been made to correlate evidence of environmental changes with the observed size development of the species in question during the Boreal and Atlantic chronozones.

The isolation of the Danish islands from Jutland and Scania, which took place at the beginning of the Atlantic chronozone as a result of the Littorina transgressions, had an important bearing on the distribution and evolution of the terrestrial mammalian fauna (Aaris-Sørensen 1980). The changes in the land-sea configurations resulted in faunal impoverishment on the Danish islands, with the extinction of brown bear (*Ursus arctos*), polecat (*Mustela putorius*), badger (*Meles meles*), lynx (*Lynx lynx*), elk (*Alces alces*) and aurochs (*Bos primigenius*) during the Atlantic-Early Subboreal chronozones (Aaris-Sørensen 1980, 1985). In contrast to the situation on the islands, a continental Boreal-type of mammalian fauna was retained in Jutland and Scania during the Atlantic chronozone (Aaris-Sørensen 1980).

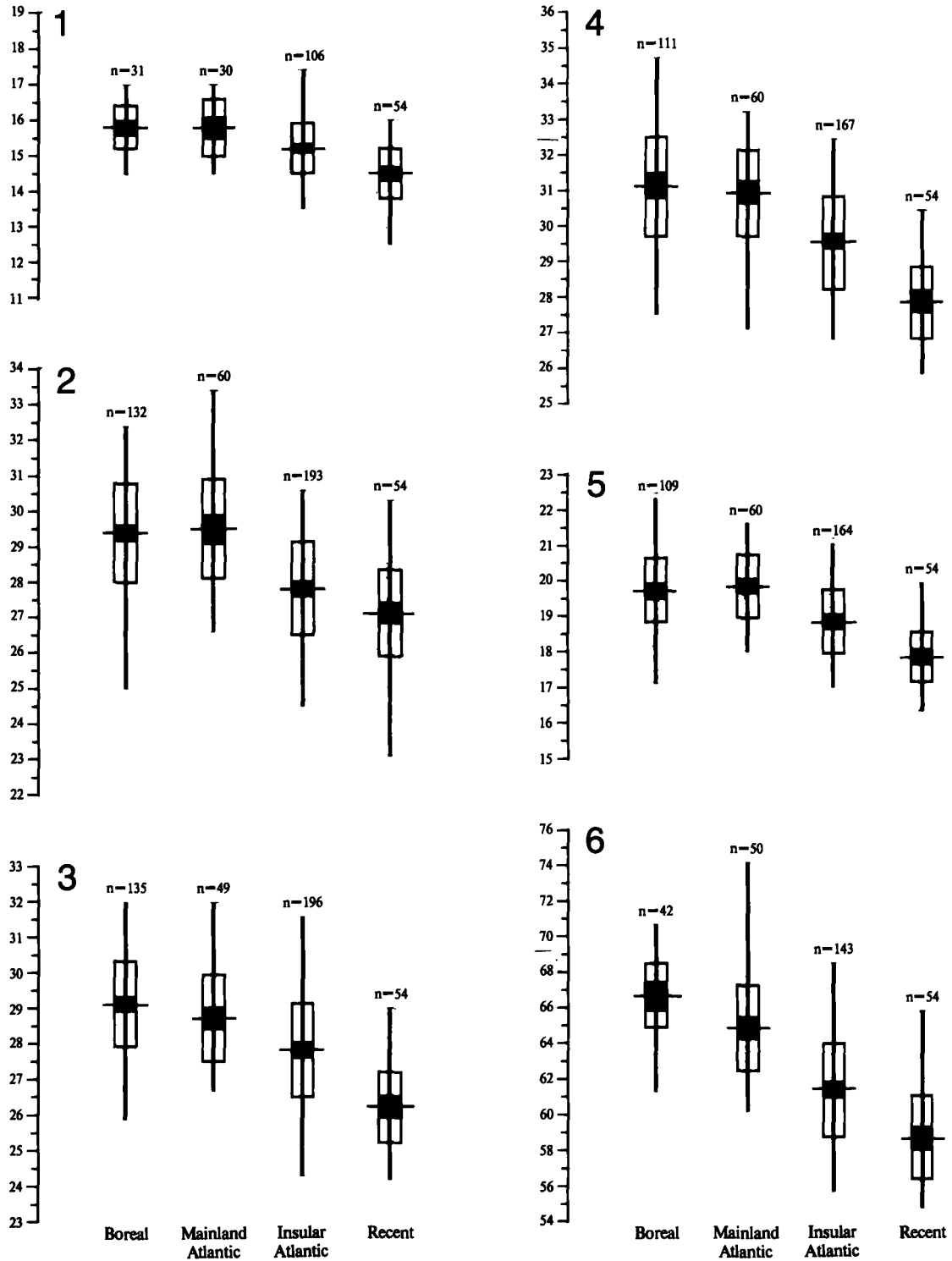


Fig. 1. Parameters 1-6: Dice-Leraas diagram showing temporal variation. For details see text.

Regional differences in mean body size of Mesolithic roe deer have been observed concurrent with the faunal impoverishment of the insular mammalian fauna. Although showing some fluctuations in two parameters, the body size of the mainland Atlantic population remained relatively stable compared to that of Boreal roe deer, whereas the insular Atlantic population experienced a marked decline in body size.

Foster (1964), in a study on body size trends of recent mammals on islands as compared to mainland conspecifics, noted that insular ungulates tend to become dwarfed. Foster suggested that all morphological changes of insular mammals are adaptive and that island adaptations are probably attained more rapidly due to the smallness of the gene pool and the restriction of gene flow from other populations. Foster envisaged limited food supply as a factor causing size decrease of mammals on islands. Kurtén (1965, 1968), working on size development of Late Quaternary mammals, suggested that insular dwarfing represents an adaptation which enables the maintenance of viable populations in spite of severe limitations in habitat and/or food resources. Similarly, Marshall & Corrucini (1978) stress that by decreasing body size, chances of survival through periods of environmental perturbations are significantly increased.

On the basis of the interpretation of Danish pollen diagrams Iversen (1973) proposed a general reduction in the alimentary base of the ungulates at the Boreal-Atlantic transition. The open hazel-pine woodlands of the Boreal provided abundant quantities of forage for ungulates, as opposed to the closed Atlantic climax forest, dominated by shade-tolerant deciduous tree species, which only offered favourable food conditions for wild boar (*Sus scrofa*). According to this scenario, roe deer and red deer (*Cervus elaphus*) decreased in numbers, and elk and aurochs disappeared from the faunal record on the islands due to reduced availability of fodder. However, the decrease in population of the larger game animals during the Atlantic chronozone has been questioned by Aaris-Sørensen (1988). Moreover, numerous finds of roe deer and red deer remains associated with Kongemose and Ertebølle sites in Jutland and on the islands cast doubt on the validity of Iversen's (1973) assumption. It therefore seems that the postulated population decline of the two species is based on inconclusive evidence. Hence it follows that it is not possible to establish whether limited food supply was the main factor that triggered off the observed decrease in body size of the Boreal – insular Atlantic roe deer.

A re-assessment of the potential environmental carrying capacity of the Atlantic climax forest is needed to clarify these matters.

It is well-known that changes in temperature through time may influence body size of mammals in agreement with Bergmann's rule. Several authors (*e.g.*, Kurtén 1965, 1968; Davis 1977, 1981; Klein & Cruz-Urbe 1984) have correlated the observed size decrease of a number of mammalian species to the Late Pleistocene – Holocene temperature elevation. Taking into consideration the marked size differential between the mainland and insular roe deer populations of the Atlantic chronozone, it seems most unlikely, however, that temperatures acted as a body size-determining factor in this particular case. The mean July temperatures during the period under review averaged 2 degrees Celsius above those of today, rising slightly towards the end of the Atlantic chronozone (Iversen 1944, 1973). The summer temperatures have been inferred from finds of mistletoe (*Viscum alba*) and ivy (*Hedera helix*) pollen (Iversen 1944) and from subfossil occurrences of European pond terrapin (*Emys orbicularis*) and other thermophilous vertebrate species beyond their present-day northern limits (*e.g.*, Degerbøl & Krogh 1951; Iversen 1973; Aaris-Sørensen 1988). Although the July temperatures were stable during the Mesolithic period, the climate itself underwent changes. The Boreal was associated with a dry, continental climate, but as a consequence of the formation of the North Sea and the sea-level rise in the western Baltic Sea, humidity rose, resulting in an oceanic-type of climate at the beginning of the Atlantic chronozone (Iversen 1973). Whether the climatic changes during the Mesolithic period had any influence on the body size of roe deer is, however, doubtful.

Klein & Strandgaard (1972) studied differences in body size of recent Danish roe deer and showed that size is most directly related to population density. The largest deer today are those from areas with lower population densities, lower ratios of agricultural land to forest, and poorer soil fertility. The mechanisms by which population density influences body size are social pressure and intraspecific competition during spring and early summer. At this time, high quality forage is limited, but the dietary requirements of roe deer are greatest. Klein & Strandgaard also noted that the smaller European subspecies occur in association with intensive agriculture, abundance of food, and high population densities, unlike the Siberian subspecies, which are found in areas with more extensive forests and frequent food shortages, coinciding

with low population densities. Extrapolating their findings backwards in time, Klein & Strandgaard suggest that size reduction in Danish roe deer took place after the introduction of agriculture. The latter brought about great increases in the abundance of forage and in turn led to greater population densities than those of pre-Neolithic times. Although the above model may hold true with regard to the reduction in body size during the Neolithic and later periods, it is considered unlikely that population densities were the decisive factor responsible for the observed body size trends of Mesolithic roe deer.

As a corollary, it is proposed that factors other than population density were involved in the regulation of the body size of roe deer during the period under consideration. Bearing in mind the geographical size differential in the Atlantic chronozone, the above discussion indicates that the body size of roe deer was not controlled by any one factor. At least, the environmental evidence does not support such a view. Thus, changes in body size of roe deer during the Mesolithic period should be viewed rather as a result of several environmentally-induced factors working together on the phenotype. Prevented from gene exchange with adjacent populations from Jutland and Scania, direct environmental stress due to the effects of insularity probably accounted for the size decrease of the insular Atlantic roe deer population.

Further studies on body size changes of other game animals recovered from Danish Mesolithic sites such as red deer and wild boar may reveal whether the observed geographical size differential of roe deer is an isolated phenomenon pertaining only to this particular species or whether it is a general trend.

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Appendix

Sexual dimorphism in recent roe deer (*Capreolus capreolus*):

	Male (N=23)	Female (N=31)	Difference
M₃	14.54	14.38	1.1%
Scapula	27.31	26.90	1.5%
Humerus	26.56	25.96	2.3%
Astragalus 1	28.04	27.68	1.3%
Astragalus 2	18.16	17.58	3.2%
Calcaneus	58.81	58.22	1.0%

Difference between male and female means expressed as a percentage of male mean.

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