Harvesting Wild Boar –a study of prey choice by hunters during the Mesolithic in South Scandinavia by analysis of age and sex structures in faunal remains

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ABSTRACT: The hunting of wild boar during the Mesolithic was studied by analysis of age and sex distributions in faunal remains from four settlements situated in Scania, Southern Sweden. The results show that the harvest of wild boar varied between different settlements. Piglets dominate the age distribution in the faunal remains of the sites of Ringsjöholm and Tågerup, which indicate a hunting of wild boar reflecting the age composition of living populations. In the faunal remains from the sites of Ageröd I:HC and Bredasten the age distributions are different, with mainly individuals older than 36 months, which is interpreted as the result of a selective prey choice of adults by the hunters. The sex ratio based on the osteometry indicates that females made up about two thirds of the harvest of the adult wild boar. The hunting seems not to have been directed towards promoting a sustainable harvest, but rather to maximise the yield of the hunt.

KEYWORDS: WILD BOAR, MESOLITHIC, SOUTH SCANDINAVIA, HUNTING, AGE DISTRIBUTION, SEX DISTRIBUTION, PREY SELECTION

RESUMEN: La caza del jabalí durante el Mesolítico ha sido estudiada a través de análisis de edad y proporciones de sexo en restos faunísticos de cuatro yacimientos localizados en Escania, en Suecia meridional. Los resultados demuestran que la captura de jabalíes varió entre yacimientos. Los juveniles dominan la distribución de edades en los restos faunísticos estudiados en los yacimientos de Ringsjöholm y Tågerup, lo que indica una caza de jabalíes que refleja la estructura de edad de las poblaciones actuales. En los restos faunísticos de los yacimientos de Ageröd I:HC y Bredasten las estructuras de edad son diferentes dominadas por individuos de más de 36 meses. Esto se interpreta como el resultado de una selección de presas centradas en los adultos por parte de los cazadores. La proporción de sexos basada en la osteometría indica que las hembras constituyeron hasta 2/3 de las capturas de animales adultos. La caza no parece haber estado dirigida a la promoción de una cosecha sostenible sino más bien a maximizar la productividad de la cazería.

PALABRAS CLAVE: JABALÍ, MESOLÍTICO, ESCANDINAVIA MERIDIONAL, CAZA, DISTRIBUCIÓN DE EDADES, PROPORCIONES DE SEXO, SELECCIÓN DE PRESAS

INTRODUCTION

Bones and teeth from wild boar (*Sus scrofa*) are found on almost all Mesolithic sites in Southern Scandinavia where conditions for the preservation of osteological remains are appropriate. In three out of 16 Atlantic faunal assemblages from Scania, Sweden, wild boar is the most frequently occurring mammalian species and in ten out of 16 the second most common mammal after red deer (*Cervus elaphus*) or roe deer (*Capreolus capreolus*) (Larsson, 1978a; Lepiksaar, 1978, 1982, 1983; Hallström, 1984; Jonsson, 1986, 1988; Iregren & Lepiksaar, 1993; Jansson *et al*., 1998; Eriksson & Magnell, 2001a, 2001b). The large amount of bones and teeth of wild boar recovered from Mesolithic sites reflects the importance of the species during this period. The significance of hunting during the

period is, apart from the faunal remains, further indicated by the fact that tools associated with hunting and utilization of wild game, such as arrowheads, bone points, scrapers and blades with wear on the edges from butchering are a characteristic feature for Mesolithic settlements (Althin, 1954; Larsson, 1982: 39-45; Larsson, 1986: 31-35; Sørensen, 1996; Johansson, 1998; Andersen, 1999: 31-33; Knarrström, 2000: 45-52; Karsten, 2001: 105-108).

Although wild boar along with red deer and roe deer was the most frequently hunted wild game throughout the Mesolithic, the prey selection of wild boar by hunters in South Scandinavia has not been a subject for detailed studies. Most analyses of faunal remains from Mesolithic sites in South Scandinavia have focused on explaining palaeoecological conditions, the relative importance of the different species in the subsistence strategy and in identifying the season of occupation of settlements (Møhl, 1970; Aaris-Sørensen, 1976; Lepiksaar, 1978; Rosenlund, 1980; Lepiksaar, 1982, 1983; Hallström, 1984; Jonsson, 1988; Iregren & Lepiksaar, 1993; Rowley-Conwy, 1993, 1999; Noe-Nygaard, 1995).

In several studies age and sex distribution of faunal remains from red deer have been analysed in order to investigate the prey choice of Mesolithic hunters (Trolle-Lassen, 1990: 9-10; Noe-Nygaard, 1995: 109-110; Carter, 2001: 234-245). However, the hunting of wild boar has not been studied to the same extent as the hunting of red deer.

In order to study if the harvest of wild boar was selective for certain age groups or sex, the demographic composition in faunal remains from Mesolithic settlements was analysed. The study aims at identifying if the hunting of wild boar was practised in a way that resulted in a selective harvest that promoted a sustainable yield or to maximize the short-term harvesting.

Predation and hunting affect the density of prey populations and may, if pressure is high enough, drive these populations to extinction (Hedrick, 1984). Based on the density and large size of several Mesolithic settlements together with analogies of the demography of sedentary hunter-gatherers in contemporary and historical sources, it is assumed that the population density of humans was relatively high in certain areas of South Scandinavia during the Late Mesolithic (Larsson, 1980: 12-16; Rowley-Conwy, 1983:114-123; Price & Gebauer, 1993; Karsten & Knarrström, 2003: 212-218). One implication of sedentary settlements with relatively

large groups of humans is that the hunting pressure must have affected the wild game populations in the areas around the settlements. The abundance of wild game becomes depleted in the hunting zones near the settlements of contemporary hunter-gathers in Ecuador, Venezuela and Paraguay (Hames & Vickers, 1983; Hill et al., 1997).

During the Mesolithic, the hunters may selectively have avoided killing animals of a certain age and sex in order to reduce the depletion of the wild game populations. A hunting in order to ensure a sustainable harvest is expected to be selective of prey animals which have a low reproductive capacity. This means that juveniles and adult males would be the preferred choice and adult females spared. Young animals have a low reproductive value, because the mortality is high for these individuals and few will reach reproductive age (Alvard, 1995: 793).

If the hunting was directed towards optimising the short-term return of the hunt, a prey choice of animals of a large body size is to be expected, resulting in a gain of large amounts of meat and fat from each kill. Hunting following this model will be selective for adults instead of juvenile animals and males instead of females because of the large body size in adults and in males. Animals of large size have been observed to be the preferred prey among hunter-gatherers, such as the Hadza in Tanzania and Piro in Peru (Woodburn, 1968: 53; Alvard, 1995: 795-800). Prey selection may also be affected by the gain of social prestige to hunters when killing many or large sized animals. If social prestige was involved in hunting during the Mesolithic in South Scandinavia, it was probably prestigious for hunters to kill adult males of wild boar with impressive tusks and large body sizes.

MATERIALS

This study is based on age estimations of mandibles and loose mandibular molars, sexing based on morphology of canines and the osteo-metry of postcranial bones of wild boar from four Mesolitic settlements from Scania, Sweden (Figure 1). The selection of material focused on settlements with relatively large quantities of faunal remains, but also on settlements with different chronologies and location in order to cover for eventual differences in the hunting of wild boar. The dating of the settlements covers the period from the Late Maglemose Culture to the Early Ertebølle Culture (7800-

	Ageröd I:HC	Ringsjöholm	Tågerup	Bredasten
Dating of faunal remains (inter-quartile range of ^{14}C dating)	7715-7480 BP[+]	7670-7280 BP	7575-7270 BP	Ertebølle Culture (archaeological dating)
Minimal period of occupation	Autumn-Winter[#] (Sept-Dec)	Summer-Winter (July-Feb)	Summer-Autumn (June-Oct)	Spring-Summer[#] (April-July)
Frequency of wild boar of mammal remains (NISP)	25 %	28 %	31 %	60 %
Wild boar NISP / MNI	842 / 34	625 / 14	490 / 15	1334 / 25

TABLE 1

Description of sites and faunal remains used in the analysis. NISP= number of identified specimens, MNI= minimum number of individuals. The table is based on the following literature; Ageröd I:HC (Larsson, 1978b), Ringsjöholm (Sjöström, 1997; Jansson *et al.*, 1998), Tågerup, this study deals only with layers dated to the Kongemose Culture (Eriksson & Magnell, 2001a; Karsten & Knarrström, 2003), Bredasten (Larsson, 1986). [+]New radiocarbon dating of bones. [#]Revision of previous interpretations by the author, based on ageing of juveniles (unpublished data).

6000 BP), which corres-ponds to the Early Atlantic Chro-nozone (Table 1). The settlements were situated inland around lakes or by the former coast during the Mesolithic (Figure 1). The faunal remains from Ageröd I:HC, Ringsjöholm and Tågerup mainly originate from refuse layers on former shores of lakes or the sea. The bones from Bredasten originate from features such as pits, postholes and a ditch linked to a hut structure.

The age distributions of the faunal remains of wild boar were compared to the demographic structure of three modern populations. The demography of the wild boar from Kampinos National Park in Poland was studied in detail by capturing, tagging and re-capturing individuals during the period from 1965-1970 (Jezierski, 1977). This study was used as a reference of the age structure of a wild boar population. The demography of wild boar is dynamic and changes with season, from year to year and between different areas due to climate, acorn crops, predation from carnivores and hunting pressure. However, all populations of wild boar are characterised by the same basic age distribution of mainly piglets, yearlings and relatively few adults. Wild boar from Våxtorp, Sweden, were captured, tagged and the number of tagged individuals found dead counted during the period from 1989-1997 (Lemel, 1999). Since 94 % of the recovered tagged wild boar were killed in hunts, this study was used as a reference for modern harvesting of wild boar in Sweden. Finally, the age structure of the archaeo-logical materials was also compared to the harvest of wild boar in Bialowieza Primeval Forest, Poland, during 1970-80 and the population structure in the same area based on the counting of animals at feeding places during the spring of 1981 (Milkowski & Wojcik, 1984).

FIGURE 1

Map showing South Scandinavia and Scania in Southern Sweden with the localities of the four Mesolithic settlements used in the study: 1. Ageröd I:HC; 2. Ringsjöholm; 3. Tågerup; 4. Bredasten.

METHODS

Age estimation

The age estimation was based on the development, eruption and wear of the mandibular deciduous fourth premolar and the permanent molariform teeth. Three methods for age estimation were used in order to get as reliable data of the age structures as possible. Efforts were also made in order to analyse increments in dental cementum to assess the age and season of death, but due to diagenetic changes of the cementum in the sampled teeth, this method could not be used. Age estimation based on tooth eruption is dependent on mandibles with more or less complete tooth rows. In order to increase sample size, the age estimation of loose teeth based on tooth development and wear was likewise included in the analysis. Another reason to study loose teeth is to get a more representative sample of the populations. In comparison with the dense mandibles of adult wild boar, those of juveniles are fragile. This implies that mandibles of adults are more often preserved than mandibles of juveniles, which usually are rare in archaeological samples. Usually only loose teeth of the mandibles of juveniles are found in ravaged bone assemblages and most archaeological assemblages (Munson & Garniewicz, 2003: 410-415).

Age estimation based on tooth development has been used for ageing humans as well as cattle and various species of deer (Brown *et al.*, 1960; Liliequist & Lundberg, 1971; Demirjian *et al.*, 1973; Brown & Chapman, 1991a, 1991b; Carter 1997). A method for ageing wild boar based on the mandibular tooth development has been developed by Carter and Magnell (unpublished). The ages at which eight developmental stages of teeth occur, from the formation of a crypt to the final root formation and the closing of the apex, were studied from radiographs of modern specimens of known age or known kill date (Table 2). This method has certain advantages over ageing based on eruption and wear. Tooth development has shown to be less affected by environmental factors than either tooth eruption or wear (McCance *et al.*, 1961: 220; Brown & Chapman, 1991a: 95). The method can be used for ageing complete mandibular tooth rows as well as loose teeth with relatively high accuracy (Carter, 1997, 1998, 2001). However, the root of loose teeth in archaeological samples is often damaged. This means that the roots must be examined in order to identify any breakage to avoid that the loose teeth are assessed to the wrong tooth development stages. If the roots are damaged it is only possible to estimate the age of a tooth as older than the age that can be observed from the tooth development.

The ageing based on tooth eruption according to Matschke (1967) is used with adjustment of the eruption of the third molar (Table 3). The ages at eruption of the third molar were corrected in order to cover the variation observed in the eruption of this tooth in different populations of wild boar (Genov *et al.*, 1991: 400; Magnell, in print a). The study by Matschke (1967: 113) considers only the eruption of the mesial cusps of the third molar and not the whole tooth crown. In order to cover the complete eruption of the tooth, data of the ages when the distal cusps of the third molar erupt according to Boitani and Mattei (1991) were also used.

Tooth developmental stage	dp_4	M_1	M_2	P_3	P_4	M_3
1. crypt formation	(*in utero*)	0-1	1-2	5-7	5-6	5-7
2. mineralization within the crypt	(*in utero*)	(1-3)	2-5	6-8	5-7	7-12
3. mineralization of all cusps	(*in utero*)	1-3	5-6	8-12	7-10	12-14
4. crown formation complete	(*in utero*)	2-5	7-12	8-12	8-12	14-18
5. early root formation	0-1	2-5	10-14	12-14	12-14	18-24
6. mid-root formation	0-2	(2-5)	12-18	(14-18)	12-14	24-30
7. full root length (open apex)	2-3	5-7	12-18	14-18	14-18	30-48
8. full root length (root apex closed)	>2	>6	>18	>18	>18	>36

TABLE 2

The ages (months) at tooth development of molariform teeth of wild boar according to Carter and Magnell (unpublished). Ages in brackets are tooth developmental stages missing in the sample, but the ages have been estimated based on the age range of the previous and following stages.

dp_4	M_1	M_2	P_2-P_4	M_3*	M_3+
0-1	5-6	12-14	14-18	19-24	25-36

TABLE 3

Ages at eruption (months) of deciduous and permanent teeth in wild boar used for age estimation according to Matschke (1967), with adjustment of the eruption of the third molar. *Eruption of the mesial cusps. + Eruption of the distal cusps of the third molar according to Boitani and Mattei (1991).

TWS	dp_4	M_1	M_2	M_3
C	-	0-1	5-11	7-13
V	-	0-5	7-12	9-24
E	0-1	5-6	12-13	19-24
$\underline{}$	0-1	(5-6)	12-13	19-24
Ū	(2-6)	5-8	12-18	(24-36)
a	(2-6)	7-13	14-24	24-36
b	(2-6)	7-13	14-24	25-48
c	2-6	7-13	14-36	>36
d	5-11	9-24	>14	>36
e	7-14	9-36	>36	>36
f	7-14	>14	>36	>36
g	7-14	>14	>36	(>36)
h	7-14	>14	>36	(>36)
j	7-14	>19	>36	>36
k	7-14	>36	>36	(>36)
l	7-14	(>36)	(>36)	-
m	7-14	>36	>36	-
n	-	>36	(>36)	-

TABLE 4

The age in months within tooth wear stages (TWS) found in four modern North European populations of wild boar. Ages in brackets are tooth wear stages that have not been observed, but the ages have been estimated based on the known ages of the previous and following stages.

The age estimation of tooth wear in the archaeological samples was based on the relationship between age and tooth wear in modern samples from four North European populations of wild boar; Scania in Southern Sweden, Schleswig-Holstein in Germany and Kampinos National Park and Bialowieza Primeval Forest in Poland (Magnell, in print a). The tooth wear stages were scored according to Grant (1982). The age ranges within tooth wear stages (TWS) are expected to be found with a confidence interval of 95 % in the four modern populations that were used for the age estimation based on tooth wear (Table 4).

The age of each specimen was estimated to as limited age ranges as possible by combining the methods based on tooth development, eruption and wear (Table 2, 3 & 4). The aged specimens were ordered into four age groups based on the life history of wild boar and age division commonly used by hunters today in northern Europe: piglets (0-12 months), yearlings (13-24 months), subadults (25-36 months) and adults (>36 months).

Piglets are characterised as being dependent on their mother for survival during their first months and not behaving independently until at 8-9 months of age. The mortality is high and piglets have a rapid growth of body size. No marked sexual dimorphism is found in piglets and by the end of their first year, at 7-10 months of age, the wild boar is sexually mature.

During the second year, as *yearlings,* the mortality is still high and the females usually have their first litter, while males leave the maternal kernel group. The wild boar reaches about 75 % of its full body mass and the sexual dimorphism becomes pronounced by the end of their second year.

Subadults are adults that have not reached their full body size. The mortality of subadults is lower than for younger wild boar and the reproduction is fully developed, but individuals in this cohort are usually of subordinate social status in the kernel groups.

A*dults* have reached their full body size and form the socially dominating age group. Normally it is first as adults that the males become sexually reproductive. The level of reproduction is high and the mortality is low, but increases with age (Herre, 1986; Briedermann, 1990: 321-324).

Sex assessment

The sex ratios of wild boar in the faunal remains were estimated by quantification of male and female canines as well as by osteometric analysis. The distinct morphological differences between the canines of male and female wild boar were used for sex estimations (Mayer & Brisbin, 1988). The minimum numbers of mandibular and maxillar canines were estimated. The lower canines of male wild boar were often worked into tools and ornaments during the Mesolithic in South Scandinavia (Larsson, 1978a: 50; Andersen, 1999: 39). This means that the frequency of canines of males may not be representative of the hunted sex ratio of wild boar depending on whether the areas of production and deposition of artefacts made of canines are excavated or not on a site.

Measurement	Male			Female			Mean diff. (%)
	min-max	mean	n	min-max	mean	n	
Scapula - GLP	46.1 - 49.8	48.0	2	40.1 - 48.1	43.4	6	10.6
Scapula - BG	31.5 - 34.8	33.2	2	27.0 – 33.6	30.6	6	8.5
Humerus - Bd	49.8 - 55.2	53.0	3	44.6 – 50.5	47.4	7	11.8
Humerus - HTC	23.8 - 24.0	23.9	3	21.4 – 23.3	22.2	7	7.7
Tibia - Bd	36.6 - 40.5	37.9	3	35.0 – 37.5	36.3	2	4.4
Tibia - Dd	32.7 - 37.7	35.0	3	31.7 – 34.2	32.8	5	6.7
Astragalus - GLl	51.4 - 55.3	53.1	3	49.1 – 52.7	50.4	5	5.4
Astragalus - BTp	24.3 - 27.5	25.9	3	23.3 – 25.7	24.0	5	7.9

TABLE 5

Sexual dimorphism in bone measurements (mm) of recent wild boar from Bialowieza Primeval Forest, Poland. Measurements of bones taken from individuals aged 36 months or older.

The sex distributions based on the osteometry were also estimated in order to test whether the result of the quantification of male and female canines could be considered representative.

Many mammalian species exhibit a pronounced sexual dimorphism in body size, which is reflected in the skeleton and has been used in the assessment of sex in faunal remains (Boessneck, 1956; Bosold, 1968; Klein & Cruz-Uribe, 1984; Noble & Crerar, 1993; Weinstock, 2000). This sexual dimorphism in body size for wild boar is pronounced. The body weight and withers height in adult wild boar from Bialowieza Primeval Forest, Belorussia, are respectively 52 % and 14 % larger in males than in females (Briedermann, 1990: 64-65). Differences between males and females are thus also found in the size of postcranial bones of wild boar (Table 5), (Teichert, 1969; Payne & Bull, 1988; Magnell, in print b).

Two dimensions of the scapula, humerus, tibia and astragalus from the faunal assemblages were measured in order to enhance the osteometric separation between the sexes in bivariate plots and make sex estimations more reliable (Figure 2). Bivariate plots are preferred over histograms, since they enhance sex differences in comparison with values in isolated parameters (Weinstock, 2000: 1193).

Bone elements exhibiting a large sexual dimorphism and resistant to fragmentation, thus permitting for a larger series of measurements to be taken, were selected for the osteometric analysis. Six osteometric parameters were measured according to von den Driesch (1976): scapula: greatest length (GLP) and breadth (BG) of the glenoid process; humerus: breadth of the distal end (Bd); tibia: breadth (Bd) and depth (Dd) of the distal end; astragalus: greatest length of the lateral half (GLl). The diameter of the trochlea of the humerus (HTC) was measured according to Payne & Bull (1988) and an additional measurement of the astragalus was defined. This is the medio-lateral breadth of the proximal trochlea (BTp) measured at the right angle to the rotation of the joint at the central parts of the trochlea at its narrowest point (Figure 2).

Only bones with fused epiphyses were used in the study. Bones from a cluster of small sized astragalus, indicating that they originated from juveniles, were excluded from the analysis.

Bivariate plots were made from each bone element and the number of bones clustering as males or females was counted directly from the plots. Due to the small sample size, the number of specimens counted either as males or females for the four bone elements was added up and used as an approximation of the sex ratio.

The separation between the sexes is not total in the bivariate plots and measurements between males and females overlap (Table 5 & Figure 2). This overlap has been noticed for reindeer and red deer and is assumed to be the result of subadult males not having reached full size and falling in the gap between adult males and females. Measurements of adult males and females from Bialowieza Primeval Forest show that the overlap is also the result of the expected normal distribution of measurements, with a few large sized females and some males of relatively small size (Table 5 & Figure 2). Since the sex estimation of bones that fall into the gap between the clusters of males and females is uncertain, these bones were not included in the estimation of the sex ratio.

It is important to stress clear that any sex estimation based on the osteometry does not allow for the sexing of isolated bones, but instead indicates the relative distribution of males and females in the samples.
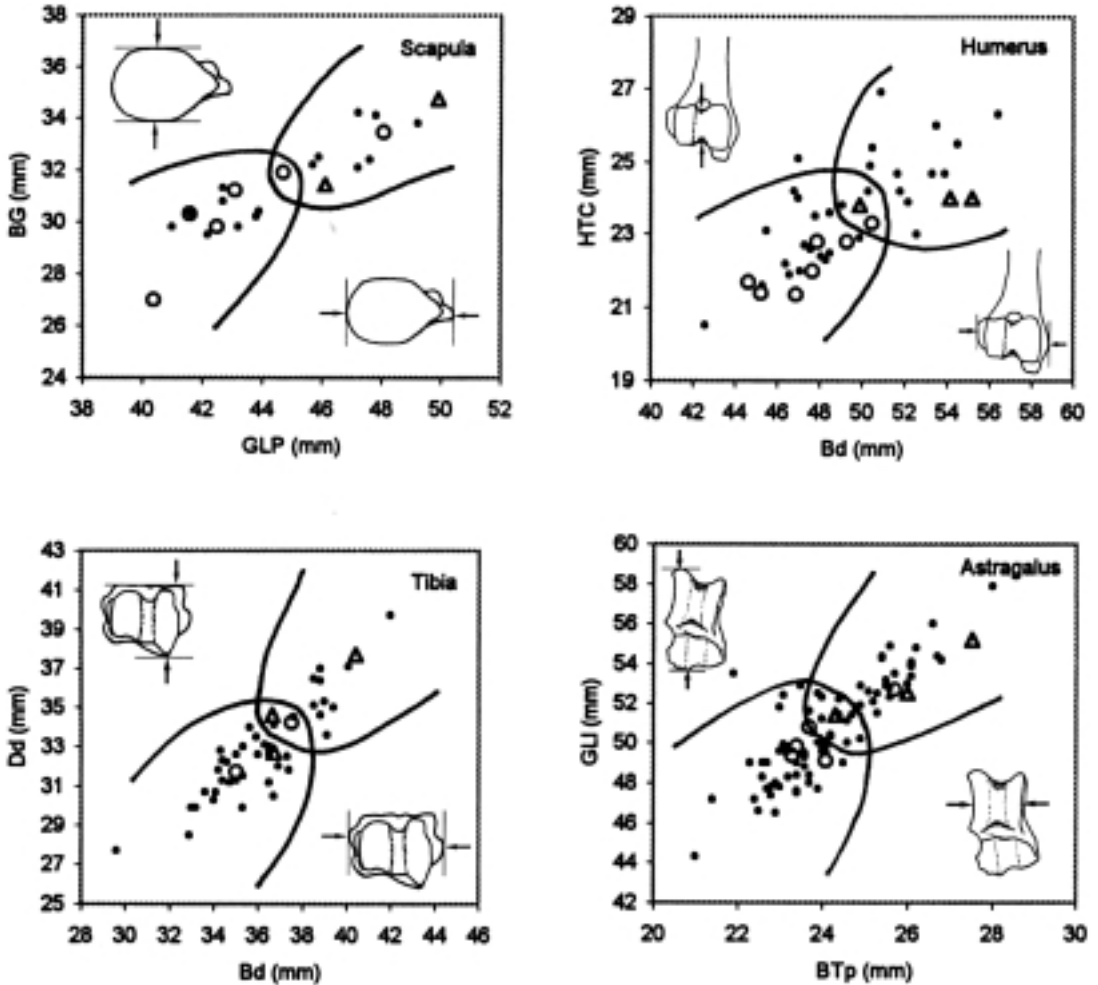
FIGURE 2

Scatterplots of measurements of scapula, humerus, tibia and astragalus indicating specimens counted as males, unknown sex (intermediate) and females from four Mesolithic sites (black dots), adult (>36 months) males (triangles) and females (circles) from recent time Bialowieza Primeval Forest, Poland.

RESULTS

Age distributions

The age distributions of wild boar show that the harvest differs considerably between the four sites (Figure 3). In the sample from Ringsjöholm, piglets are the most frequently occurring age group, followed by adult individuals older than 36 months, while yearlings and subadults are relatively scarce. The large proportion of piglets (56 %) reflects the age distribution of modern populations of wild boar, of which piglets usually make up 40-66 % of the population (Andrzejewski & Jezierski, 1978: 314).

The survivorship curve of the harvest of wild boar from Ringsjöholm shows similarities with Tågerup and the modern populations from Kampinos National Park and Våxtorp, but differs in having a mortality profile with few yearlings and a relatively large proportion of adult individuals (Figures 3 & 4). In a Kolmogorov-Smirnov test, the age distribution of the sample from Ringsjöholm was proven to be significantly different from all samples except those of Tågerup and Kampinos National Park (Table 6).
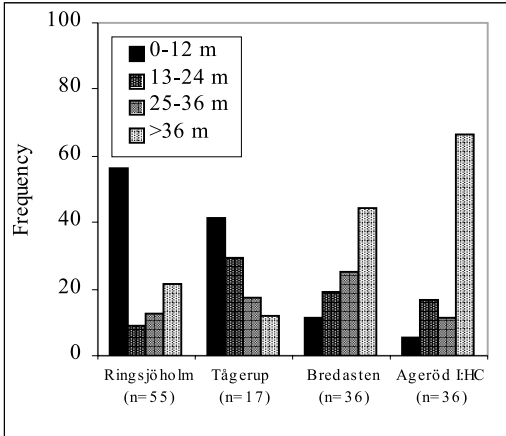
FIGURE 3

The age distribution of number (NISP) of mandibles and loose mandibular molariform teeth of wild boar from four Mesolithic settlements in South Scandinavia.

	RH	TÅG	BRE	AgI:HC	K.N.P.
Ringsjöholm					
Tågerup	0.152				
Bredasten	0.453***	0.401*			
Ageröd I:HC	0.508***	0.548**	0.221		
Kampinos N.P.	0.148	0.117	0.498***	0.580***	
Våxtorp	0.226 *	0.079	0.480***	0.562***	0.191***

TABLE 6

Kolmogorv-Smirnov test of the age distribution of wild boar from four Mesolithic sites and two modern populations. Significance level: ***= *P*<0.001; **= *P*<0.01; *= *P*<0.05.

The wild boar remains from Tågerup have an age distribution with a high proportion of piglets and yearlings (70%) and few adult individuals in comparison with the other Mesolithic bone assemblages. The age profile from Tågerup demonstrates some general similarities with the remains of wild boar from Ringsjöholm, but differs by having somewhat fewer piglets, relatively more yearlings and few adults (Figures 3 & 4). There is a striking resemblance in the age distribution between the sample from Tågerup and modern hunting in Våxtorp, Sweden (Figure 4).

The harvest of wild boar seems to have been rather similar on the sites Ageröd I:HC and Bredasten with few piglets and a large proportion of adults (Figure 3, Table 6). The age distributions with 44% and 67% adult individuals respectively differ from the modern populations of wild boar where adults usually make up only about 10% of the population (Jezierski, 1977: 340). The survivorship curve of the sample from Bredasten is similar to the harvest of wild boar in Bialowieza Primeval Forest, Poland during 1970-80, but is quite different from the population structure in that same area based on the counting of animals near feeding lots (Milkowski & Wojcik, 1984: 342).
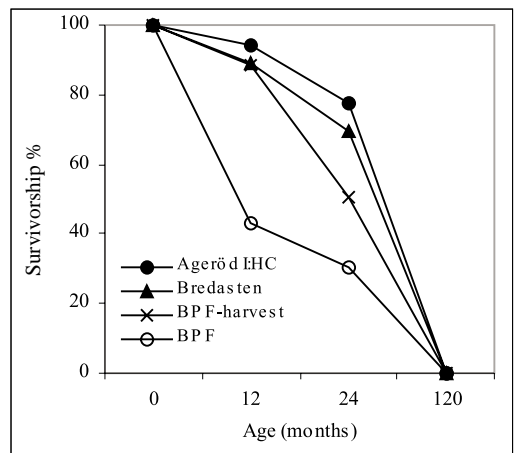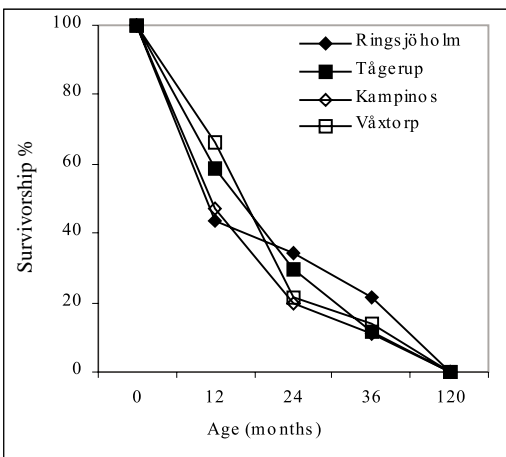

FIGURE 4

Survivorship curves of wild boar from four Mesolithic sites in comparison with three modern populations from Kampinos National Park, Poland and Våxtorp, Sweden and population structure (BPF) and harvest (BPF-harvest) of wild boar from Bialowieza Primeval Forest, Poland. Note that the age units differ between the two survivorship curves due to limitations in the age data available from the modern populations.

Sex distribution

The sex distribution based on the morphology of the canines shows that the tusks of males are most frequent in all bone assemblages. Males make up about 60 % of the canines from Ringsjöholm and Tågerup and 70 % of the canines from Bredasten and Ageröd I:HC (Table 7 & Figure 5).

Sample sizes are relatively small thus distributions may be due to random variation. In three of the faunal assemblages, it is evident that the number of males is relatively larger if the lower canine is taken into consideration instead of the upper canine (Table 7). This indicates that the sex ratios probably are not representative and that the use of mandibular tusks for making tools and ornaments has biased the sex distribution of the canines.

	Ringsjholm		Tgerup		Bredasten		Agerd I:HC	
	M	F	M	F	M	F	M	F
Maxillar canines	2	4	2	6	3	0	10	7
Mandibular canines	5	1	9	1	4	3	20	7

TABLE 7

The sex distribution of wild boar from four Mesolithic sites based on minimal numbers (MNE) of canines from males (M) and females (F).

The result of the osteometrical analysis indicates somewhat different proportions between the males and females (Table 8). In the sample from Ringsjöholm, the sex ratio between males and females is of 1:0.7 for the canines and of 1:1.1 according to the osteometry. The two methods provide contradictory results, but it is important to emphasise that the sex distributions in both cases are not statistically different from a 1:1 sex ratio in a Chi-squared test.

At Tågerup the sex ratio based on both the morphology of the canines and the osteometry is of

	Ringsjholm		Tgerup		Bredasten		Agerd I:HC	
	M	F	M	F	M	F	M	F
Scapula (GLP x BG)	5	4	1	0	2	3	2	7
Humerus (Bd x HTC)	1	2	1	2	1	3	4	11
Tibia (Bd x Dd)	3	5	2	0	1	3	4	12
Astragalus (GLl x BTp)	6	8	6	5	7	9	13	20
Calcaneus (GL x Bp)	1	0	2	0	3	4	8	14

TABLE 8

The sex distribution of wild boar from four Mesolithic sites based on selected osteometric parameters.

1:0.6 and may indicate a selection of males. Still, these sex distributions were not found to be significantly different from a 1:1 distribution of males and females.

The sex distributions are similar in the samples from Bredasten and Ageröd I:HC, with more canines from males than females, but with more females than males according to the osteometry (Figure 5 & Figure 6). As noted above, the sex ratio based on the morphology of the canines is most likely biased and the sex distributions based
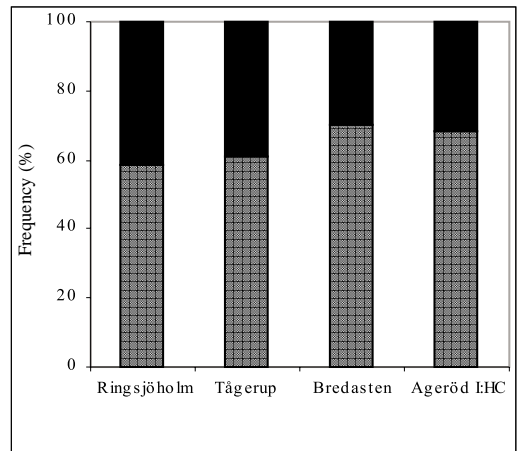

FIGURE 5

The frequency of male (grey) and female (black) wild boar from four Mesolithic sites based on the morphology of the upper and lower canines.
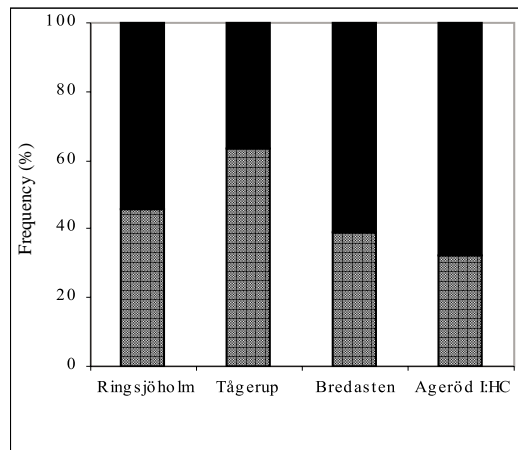

FIGURE 6

The frequency of male (grey) and female (black) wild boar from four Mesolithic sites based on the distribution of measurements of four bone elements.

on the osteometry are probably a better reflection of the real situation. The sex distribution based on the osteometry from Ageröd I:HC is the only case that is significantly different from an equal distribution between males and females in a Chi-squared test ($?^2$= 4.88, p= 0.05). The sex ratio of 1:1.9 indicates that in the wild boar from Ageröd I:HC, females consistently made up a larger proportion than males.

THE RELIABILITY OF USING AGE AND SEX DISTRIBUTION IN FAUNAL REMAINS AS ESTIMATIONS OF PREY SELECTION: THEORETICAL AND PRACTICAL CONSIDERATIONS

Are the results of the age and sex distributions reliable estimates of the prey selection made by the hunters of these settlements? Studies of mortality profiles by random sampling of age data from faunal assemblages have shown that a sample size of 30 or more is adequate for reconstructing reliable age distributions, when ten age classes are specified and average life expectancy of newborns of the taxon is about three years (Lyman, 1987: 136-138). Based on that study, the sample sizes of three of the faunal assemblages should be large enough to give reliable results (Figure 3). The sample from Tågerup includes only 17 aged mandibles and teeth. However, statistically significant correlations between age profiles and random drawn samples have been found in sample sizes as low as 15 to 20 specimens (Lyman, 1987: 137-138).

A problem when including loose teeth in the reconstruction of the age profiles is that a higher degree of fragmentation of mandibles of certain age groups, for example piglets and yearlings, may result in a higher frequency of loose teeth in these age groups in relation to older cohorts and produce a biased age profile. In order to investigate whether the pooling of loose teeth and mandibles resulted in biased age profiles, age distributions based on MNE (minimal number of elements) were also tested. The overall age profiles are similar when the age distribution based on MNE and the total number of loose teeth and mandibles are compared and no statistically significant difference could be identified in a Kolmogorv-Smirnov test.

During the long chain of events taking place from the killing of the wild boar to the recovery of

their bones, the relationship between the age distribution of the harvested animals and the faunal remains will be affected by several taphonomic factors. Ravaging of faunal remains by scavengers is a taphonomic process which is known to change the mortality profile through the age-correlated differential survival of mandibles from juveniles and adult animals. Observations of mandibles ravaged by dogs show that only 17 % of mandibles of lambs aged 3-4 months and 63% of deer aged 5-6 months did survive, while the survivorship of mandibles of deer aged 17-18 months and older than 29 months was of 94 % and 100 % respectively (Munson & Garniewicz, 2003: 410).

The occurrence of carnivore tooth marks on 4-11 % of the wild boar bones with bone surfaces permitting for the identification of modifications the bone assemblages indicates that either dogs or other scavengers have most likely affected the composition of the faunal remains (Table 9).

	Correlation between % MAU and bone density	Frequency of tooth marks
Agerö I: HC	0.739**	11 %
Ringsj|oholm	0.776***	11 %
Tågerup	0.768***	11 %
Bredasten	0.479*	4 %

TABLE 9

The frequency of tooth marks and Spearman´s r correlation values between skeletal part frequencies (%MAU) and bone density of wild boar remains from four Mesolithic sites. Significance level: ***= $P<0.001$; **= $P<0.01$; *= $P<0.05$.

A significant correlation between skeletal part frequencies (%MAU) and the structural density of bones was found for the four faunal assemblages (Table 9). This relationship means that the less dense immature mandibles most likely have survived in lower frequencies than the more dense mature mandibles and that the youngest cohorts are probably lower in the faunal assemblages in relation to the original frequencies of harvested piglets and yearlings. The relatively large proportion of piglets in two of the bone assemblages indicates that by considering loose teeth in the age distribution analyses, teeth of fragmented immature mandibles have probably been included in the age profiles. By including loose teeth in the analyses it has been possible to more faithfully reconstruct age profiles of the actual harvest of wild boar in spite of the density-mediated attrition acting on the

assemblages. Experiments have shown that the survival rates of individual teeth are much higher than those of mandibles in ravaged bone assemblages and that age profiles based on individual teeth are to be preferred over ageable mandibles (Munson & Garniewicz, 2003: 412).

The frequencies of carnivore tooth marks and the correlations between skeletal part frequencies and the structural bone densities are similar in the faunal assemblages from Ageröd I:HC, Ringsjöholm and Tågerup (Table 9). This indicates that the density-mediated attrition in the faunal assemblages is comparable and cannot be used in order to explain differences in the age structures. On the other hand, the frequencies of carnivore tooth marks and the correlation between skeletal part frequencies and the structural bone density in the sample from Bredasten are lower than in the other assemblages (Table 9). However, since teeth and mandibles from piglets are relatively few at Bredasten, the indications of a less intensive ravaging by scavengers and of a density-mediated attrition do not seem to have resulted in a higher survivorship of mandibles and teeth of juveniles on this site when compared to the other three assemblages.

The frequency of piglets is remarkably low at Ageröd I:HC, which is probably partly due to recovery biases of loose teeth during the excavation of this site. Ageröd I:HC was mainly excavated during the 1940s and the soil was not sieved to the extent done in the 1980-90s excavations of the other three sites. To what extent the limitations of sieving have affected the age profile from Ageröd I:HC is difficult to evaluate. The proportion of piglets would certainly have been larger but the age distribution with a very large proportion of adult wild boar is difficult to dismiss.

As noted above, sex ratios based on the morphology of canines are most likely biased since the lower tusks of males were used for the production of tools and ornaments. Sex distributions based on osteometric data of postcranial bones is probably more reliable, but the method requires relatively large series of measurements to be taken in order to establish reliable sex ratios. Sample sizes are small for three of the assemblages. Only the Ageröd I:HC assemblage (n= 78) had a sex distribution that was significantly different from that of an equal sex ratio.

One further problem with sexing based on osteometry of samples spanning over relatively long time periods, is that size may change over the lapse of deposition. Thus, a decrease in size over time could result if the bones of small sized males of younger dating were to be interpreted as females by comparison with the bones of older periods. This should not be a problem in this study since no change in size has been recorded on wild boar from Scania, Southern Sweden, during the Atlantic (Magnell, in print b).

The exclusion of bone values falling into the gap between the clusters that are interpreted as females and males from the analysis is problematic since most of these bones are normally expected to be from subadult males (Legge & Conwy-Rowley, 1988; Weinstock, 2000: 1189). This implies that the sex ratios based on the osteometry could be biased towards females. Measurements of bones with late fusing epiphyses have shown to be more useful than early fusing epiphyses in order to avoid the overlap of subadults between the sexes (Legge & Rowley 1988; Weinstock 2000). Since few bones with late fusing epiphyses were measurable in the faunal remains used in this study, such measurements could not be taken into consideration.

DISCUSSION

The age profile from Ringsjöholm indicates a harvesting of wild boar that to a great extent reflects the age composition of modern populations of wild boar where piglets constitute the largest age group. The dominance of piglets and the relatively large proportion of adults are probably the result of hunting directed towards groups of females with their offspring. A female and its offspring form the basic structure of the matriarchal social groups of wild boar, which may also include some yearlings and other subadults or adult females with their own piglets (Briedermann, 1990: 334-336). The relatively large proportion of adult individuals, the biologically most productive cohort, indicates a hunting strategy not focused on maintaining a sustainable harvest, but instead at optimising the return of the hunt by directing it towards groups of females and their farrows.

The harvesting of wild boar at Tågerup is liewise similar to the age structure of modern populations of wild boar. The age distribution is almost identical to the harvesting of wild boar by recent day hunters at Våxtorp, Sweden. The low frequency of adults at Tågerup differs from those of the other Mesolithic samples, but is similar to that of modern populations of wild boar. The low

frequency of adults (12%) could be a reflection of the age structure of a population under high hunting pressure allowing few individuals to reach to an adult age. Modern wild boar populations have similar age distributions with few adults (11-14%) with hunting being the main mortality agent (Jezierski, 1977: 340; Okarma *et al.*, 1995: 204; Lemel, 1999: 29).

The settlement of Tågerup was large, covering over 10000 m^2, and was situated at the coast on an isthmus by the outlet of two streams in an area with several other contemporary sites (Karsten & Knarrström, 2003). It is likely that a relatively large group of people inhabited the area around Tågerup during the Mesolithic and that these people exerted a high hunting pressure allowing few wild boar to reach to an adult age.

The harvest of wild boar around Ageröd I:HC and Bredasten, on the other hand, seems to have been more or less the same with few piglets and adults being the most common age group. The age distributions from both settlements are radically different from the age profile of modern wild boar populations and are most likely the result of a selective prey choice by the hunters. Adult individuals were probably preferred to piglets and yearlings because of their larger body size and the strategy would thus aim at an optimisation of the return amount of meat and fat per kill.

Sex ratios show that more subadult and adult females than adult males were hunted. This is probably not the result of a deliberate selection by the hunters, but rather a combined reflection of the sex distribution of the wild boar populations coupled with an opportunistic hunting. Modern populations of wild boar have equal sex ratios in adults and are the result of a higher mortality of males during their first four years of life (Jezierski, 1977: 341-342; Garzon-Heydt, 1992: 490-491).

Age profiles at Ageröd I:HC and Bredasten exhibit large similarities with the harvest of wild boar in Bialowieza Primeval Forest, Poland, during 1970-1980. The hunting at Bialowieza Primeval Forest is assumed to have had an effect on the population structure of wild boar causing a lowering of the average population age thus the productivity of the population. The average carcass weight of wild boar decreased during this period due probably to an inadequate hunting (Milkowsli & Wojcik, 1984: 344-345). Whether hunting pressure on wild boar around Ageröd I:HC and Bredasten was intensive enough to generate the same negative effects as in Bialowieza Primeval Forest during the 1970s is not possible to tell with the data available. However, it is possible to dismiss that a hunting strategy ensuring a sustainable harvest was practised at these two settlements while hypothesizing that the hunting probably was directed towards optimising the return of meat and fat for each kill.

The harvest of wild boar from Ringsjöholm and Tågerup fits well with the age distributions of living populations. This indicates a non-selective killing of wild boar that could be either the result of trapping with spring-bows and snares or of non-selective hunting techniques, such as game drives. The selective prey choice of adults from Ageröd I:HC and Bredasten implies that a more selective hunting technique, such as ambushing or stalking, was practised in order to make it possible for the hunters to choose their prey.

CONCLUSIONS

This study evidences that prey choice of wild boar varied from site to site during the Mesolithic in Southern Scandinavia.

The harvest of wild boar around Ringsjöholm was directed towards piglets, probably as an indirect indication for the hunting of groups of females with farrows. Piglets and yearlings were the most common prey at Tågerup. The age distribution with few adults is interpreted here to be the result of a high hunting pressure allowing few individuals to reach to an adult age in the areas around that settlement. The hunting of wild boar at Ageröd I:HC and Bredasten, on the other hand, was aiming at adult individuals, most likely in order to optimise the yield of meat and fat of each kill. The age and sex distributions show that the hunting of wild boar was not practised in a way that promoted a sustainable harvest. Instead it seems as though hunting was directed towards maximizing return rates.

No relationship could be detected between the dating and the geographic location of the settlement as indicators that cultural changes in the hunting strategy or different hunting at inland or coastal sites was in operation. The harvest seen in these faunal assemblages is thus probably the result of a combination of local hunting traditions and different structures in the wild boar populations brought about by the different hunting strategies together with local environmental conditions.

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