

## The Mesolithic mammal fauna of Great Britain

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### INTRODUCTION

When Britain was covered almost completely in woodland, about 7000 years ago (Bennett, 1988), the mammal fauna must have been very different from what it is now; not only were several now-extinct large mammals present, and none of the now-abundant introduced species, but the community relations (large carnivores suppressing small ones, woodland species much more abundant than grassland ones) would have been very different. It is then an interesting speculation to try to work out just how different the fauna might have been. To attempt this requires some estimate of the vegetation cover then, and some figures for plausible densities of mammals in those habitats. The latter need to derive, where possible, from a balanced mammal community living in a habitat complex something like that which was present then in Great Britain. The fauna of the Białowieża National Park in Poland approximates to that community, and is sufficiently well described to allow this speculation (Jędrzejewska & Jędrzejewski, 1998). It develops a previous attempt to discuss just the large ungulate fauna (Yalden, 1996).

### AREAS OF HABITAT

For present purposes, an area of 220 111 km<sup>2</sup> has been used, representing Great Britain without Orkney, Shetland or the Outer Hebrides. It is therefore smaller than the 230 367 km<sup>2</sup> used by Harris *et al.* (1995), which included the offshore islands, beyond the reach of Mesolithic mammals. An estimate of the extent of habitats within this has been derived by taking the pollen scores from a representative set of 22 sites, scattered well across the country, adjusting the raw pollen scores for the differential production of pollen, and recalculating the percentages of the total to estimate, crudely, the overall extent then of woodland, grassland, fenland and heathland. For some species, the separate extents of birch, pine and mixed deciduous woodlands have been useful, and for Mountain Hare the extent of open montane vegetation and birch woodland, in Highland Scotland only, was estimated from the map in Bennett (1988). Lengths of river and lake shore were as assumed by Harris *et al.* (1995).

### ESTIMATING MAMMAL NUMBERS

For the ungulates, Lynx and Wolf, density figures are given by Jędrzejewski *et al.* (1992) and for smaller carnivores and their prey by Jędrzejewski & Jędrzejewska (1993). As previously, it is assumed that Aurochs in Britain had the same density that Bison now have in Białowieża, and that if this is an artificially low density, the other ungulates have increased accordingly to reach some ecological balance (cf. Yalden, 1996). Other small mammals were scaled to the known densities of Bank Vole and Yellow-necked Mouse from the proportions trapped in

Jędrzejewski *et al.* (1994). Riparian mammal densities came from Sidorovich *et al.* (1996). Otters in fresh water were estimated by applying their density of 0.22/km; coastal Otters were assumed to occupy half the coastline (implicitly western Britain) at the density of 0.6/km found around Shetland by Kruuk (1995). A few species remain uncertain. Wildcat are absent from Białowieża, and Mountain Hares are very scarce; densities in favourable habitat in Scotland were used. Similarly, no data from Białowieża for Dormouse, Red Squirrel, Mole and Hedgehog were available, and equivalents from Britain were used. Brown Bears are now extinct in Białowieża, and nowhere in Europe is a balanced community of all three large carnivores present. It was assumed, on the basis of limited data from Canada, that bears would be twice as numerous as Wolves. Wolf densities are suppressed at Białowieża by persecution, and can reach 0.9/km<sup>2</sup> (Jędrzejewska *et al.*, 1996); it was also assumed that the bears would substitute for the missing biomass of Wolves, though they are in fact largely herbivorous. Water Voles are strangely scarce in Białowieża, but the Mesolithic record from Britain suggests that they were then as common as Field Voles, so this equivalence was used. It is not certain that Root Voles still existed in Great Britain at the target date, but evidence suggests that in Europe they tend to occur allopatrically from Field Voles (De Jonge & Dienske, 1979) and they are the common *Microtus* in Białowieża. It was assumed that Field Voles occurred then in grasslands, at about the density they now achieve in British grasslands, and Root Voles only in fenland, but at half the density of Field Voles (they are rather larger). Generally, Wood Mice and Yellow-necked Mice do not occur together in Białowieża, but the archaeological record from Britain is too scant to suggest the appropriate division of habitats or densities in Britain. The calculation is based on densities of Yellow-necked Mice in Poland, with no distinction attempted for Mesolithic Britain. The chiropteran fauna of Białowieża has not been documented systematically, and the bats are omitted from this paper. Four species dominate in woodland there (Noctule, Leisler's, Pipistrelle and Brown Long-eared Bats; Jędrzejewska & Jędrzejewski, 1998), but other species were also numerous in Mesolithic Britain (Yalden, 1992).

## RESULTS

The areas of vegetation used in these calculations are summarized in Table 1, and the areas assumed relevant to each mammal species are given in Table 2. The total number of wild mammals then in Britain is estimated to be 535 million, nearly twice the present-day estimate of 282 million, but the biomass then was 2.4 times greater, due to the abundance of large

**Table 1.** Estimates of the vegetation cover of Mesolithic Britain. The figures on the left represent the average of the pollen rain at 7000 b.p., from 22 sites distributed across Great Britain, modified to allow for the differential production of pollen. (*Quercus* and *Salix* unchanged; *Pinus*, *Betula*, *Alnus*, *Corylus* all  $\times 4$ ; *Tilia*  $\times 4$ ; Gramineae  $\times 3.33$ ; Cyperaceae  $\times 2$ ; Ericaceae  $\times 5$ , after Faegri & Iversen, 1975). The separate extents of birch woodland and moorland in the Highlands come from the map by Bennet, 1988; lengths of river and lake shore are as assumed by Harris *et al.*, 1995

Birch <i>Betula</i> woodland (B)	9.28%	20 426 km <sup>2</sup>	Rivers 66 766 km	
Pine <i>Pinus</i> woodland (P)	6.00%	13 207 km <sup>2</sup>	Lakes 6824 km	
Mixed deciduous woodland (D)	43.23%	95 154 km <sup>2</sup>	Coast 18 836 km	
Grassland Gramineae (G)	19.25%	42 371 km <sup>2</sup>		
Fenland Cyperaceae (F)	8.11%	24 234 km <sup>2</sup>	Highlands moor (ex-H = M)	3564 km <sup>2</sup>
Heathland Ericaceae (H)	8.49%	18 687 km <sup>2</sup>	Highlands birch (ex-B = M)	6969 km <sup>2</sup>
Other (herbs, ferns, sphagnum)	5.65%	6032 km <sup>2</sup>	Hazel (ex-D = Z)	51 682 km <sup>2</sup>
Total (T)		220 111 km <sup>2</sup>		

**Table 2.** An estimate of the Mesolithic terrestrial mammal fauna of Great Britain. Species presence derived from the archaeological record, numbers estimated by comparison with the fauna of Białowieża National Park, Poland and other sources where that ecosystem is not helpful. The habitats to which the density estimates were applied are abbreviated as in Table 1

Species	Density (per km <sup>2</sup> )	Area of Habitat (km <sup>2</sup> )	Numbers	Source for density (Habitat)
Hedgehog	80	42 371	3389 680	Kristiansson, 1990 (G)
Common Shrew	885.4	171 158	151 543 000	Jędrzejewski <i>et al.</i> , 1994 (T-F,H)
Pygmy Shrew	102.2	171 158	17 492 348	Jędrzejewski <i>et al.</i> , 1994 (T-F,H)
Water Shrew	9.3	161 759	1504 369	Jędrzejewski <i>et al.</i> , 1994 (D + G + F)
Mole	200 (woodland)	95 154	(19 030 800)	Gorman & Stone, 1990 (D)
	230 (grassland)	42 371	(9745 330)	Gorman & Stone, 1990 (G)
			28 776 130	
Mountain Hare	40	10 533	421 320	Krebs, 1986 (M)
Beaver	1.1/km	73 590 km	80 949	Sidorovich <i>et al.</i> , 1996
Red Squirrel	76 (deciduous)	95 154	(7231 704)	Kenward <i>et al.</i> , 1998 (D)
	344 (conifer)	13 207	(4543 208)	Kenward <i>et al.</i> , 1998 (P)
			11 774 912	
Dormouse	500	51 682	25 841 031	Harris <i>et al.</i> , 1995 (Z)
Bank Vole	1070	128 787	137 802 000	Jędrzejewski & Jędrzejewska, 1993 (D)
Field Vole	1000 (grassland)	42 371	(42 371 000)	Tapper, 1979 (G)
	18 (woodland)	95 154	(1 712 772)	Jędrzejewski <i>et al.</i> , 1994 (D)
			44 083 772	
Root Vole	500	24 234	12 117 000	0.5 × Field Vole (F)
Water Vole	1000	42 371	42 371 000	= Field Vole (G)
Wood Mouse	566.6	95 154	53 914 256	Jędrzejewski <i>et al.</i> , 1994 (D)
Red Fox	0.33	220 111	72 637	Jędrzejewski & Jędrzejewska, 1993 (T)
Wolf	0.03	220 111	6603	Jędrzejewski <i>et al.</i> , 1994 (T)
Weasel	2.2	220 111	484 244	Jędrzejewski & Jędrzejewska, 1993 (T)
Stoat	0.3	220 111	66 033	Jędrzejewski & Jędrzejewska, 1993 (T)
Polecat	0.5	220 111	110 055	Jędrzejewski & Jędrzejewska, 1993 (T)
Pine Marten	0.67	220 111	147 474	Jędrzejewski & Jędrzejewska, 1993 (T)
Otter	0.22 (fw)	73 590 km	(16 630)	Sidorovich <i>et al.</i> , 1996
	0.6 (marine)	9418 km	(5651)	Kruuk, 1995
			22 281	
Badger	0.1	137 525	13 752	Jędrzejewski & Jędrzejewska, 1993 (D+G)
Brown Bear	0.06	220 111	13 207	2 × Wolf (T)
Wild Cat	0.3	220 111	66 033	Corbet & Harris, 1991 (T)
Lynx	0.03	220 111	6603	Jędrzejewski <i>et al.</i> , 1993 (T)
Wild Boar	5.9	161 759	954 378	Jędrzejewski <i>et al.</i> , 1993 (D + F + G)
Roe Deer	4.7	177 190	832 793	Jędrzejewski <i>et al.</i> , 1993 (T-F,H)
Elk	0.3	215 389	64 617	Jędrzejewski <i>et al.</i> , 1993 (T-M)
Red Deer	6.4	195 877	1 253 613	Jędrzejewski <i>et al.</i> , 1993 (T-F)
Aurochs	0.5	167 791	83 896	Jędrzejewski <i>et al.</i> , 1993 (T-B,P,H)
Man	0.01	220 111	2500	McEvedy & Jones, 1978 (T)
Total		220 111	535 312 486	

ungulates (Table 3). However, if the considerable biomass of Humans and domestic ungulates is included in the present fauna, the British countryside currently sustains about 22 times the biomass of mammals (about 12 times if Humans are excluded). This is a measure of the enhanced productivity of the agricultural grasslands that have replaced the woodlands. Only 2% of the biomass is wild mammals, however, and only 1% is of native species.

**Table 3.** Comparison of estimates for the numbers and biomass of terrestrial mammals in Great Britain in the mesolithic period and now. Recent numbers from Harris *et al.* (1995), Yalden (1999); but with a total that includes feral and introduced species, not otherwise listed. Masses used to compute biomasses come from Corbet & Harris (1991) and sources in Table 2. Domestic and human numbers refer to breeding 'adult' populations (over 18 years for humans) to maintain comparability with the estimates for wild mammals

Species	Mesolithic		Recent		
	Numbers	Biomass (kg)	Numbers	Biomass (kg)	Mass (kg)
Hedgehog	3 389 680	4 067 616	1866 000	777 500	1.2
Common Shrew	151 543 000	1 515 430	41 700 000	417 000	0.01
Pygmy Shrew	17 492 348	69 969	8600 000	34 400	0.004
Water Shrew	1 504 369	22 566	1900 000	28 500	0.015
Mole	28 776 130	2 877 613	31 000 000	3 100 000	0.1
Mountain Hare	421 320	1 221 567	350 000	1 015 000	2.9
Beaver	80 949	1 618 980	0	0	20
Red Squirrel	11 774 912	3 532 474	160 000	48 000	0.3
Dormouse	25 841 031	510 821	500 000	10 000	0.02
Bank Vole	137 802 000	2 756 040	23 000 000	460 000	0.02
Field Vole	44 083 772	1 322 513	75 000 000	2 250 000	0.03
Root Vole	12 117 000	727 020	0	0	0.06
Water Vole	42 371 000	12 711 300	1169 000	350 700	0.3
Wood Mouse	53 914 256	1 078 285	38 000 000	760 000	0.02
Red Fox	72 637	435 822	240 000	1 440 000	6
Wolf	6603	211 296	0	0	32
Weasel	484 244	36 318	450 000	33 750	0.075
Stoat	66 033	16 508	462 000	115 500	0.25
Polecat	110 055	99 050	15 000	13 500	0.9
Pine Marten	147 474	221 211	3650	5475	1.5
Otter	22 281	178 248	7350	58 800	8
Badger	13 752	144 396	250 000	2625 000	10.5
Brown Bear	13 207	3 367 785	0	0	255
Wild Cat	66 033	297 149	3500	15 750	4.5
Lynx	6603	165 075	0	0	25
Wild Boar	954 378	76 350 240	0	0	80
Roe Deer	832 793	16 655 860	500 000	10 000 000	20
Elk	64 617	12 923 400	0	0	200
Red Deer	1 253 613	125 361 300	360 000	36 000 000	100
Aurochs	83 896	33 558 400	0	0	400
Man	2500	175 000	43 490 000	3 044 300 000	70
Horse			750 000	375 000 000	500
Pig			853 000	127 950 000	150
Cattle			3 908 900	2 149 895 000	550
Sheep			20 364 600	916 407 000	45
Total (native)	535 312 486	304 229 252	225 536 500	60 647 375	
(introduced)			56 803 200	68 458 425	
Total (wild + domestic)			348 698 200	6 742 657 800	

Among the notable differences within the fauna, the balance of small mammals was rather different, Bank Voles especially but also Water Voles, Wood Mice and Common Shrews being then much more abundant. Field Voles, Badgers and Red Foxes are among the major beneficiaries of the different habitats now available.

## DISCUSSION

These estimates are only as convincing as the analogy assumed between the Mesolithic British fauna and that of modern Białowieża, and also depend on the assumption that areas of vegetation then have been reasonably well estimated from the pollen record. The fauna of Białowieża now includes introduced American Mink (about 0.7/km of river) and Raccoon Dogs (about 0.05/km<sup>2</sup>), and their biomass ought to be shared among other carnivores (Polecat and Red Fox, respectively?), but this manipulation has not been attempted. Similarly, a large biomass of Water Voles has been added to the fauna, and may have no equivalent at Białowieża, but might well have sustained additional carnivores, probably Stoats and Polecats, in Mesolithic Britain. There are additional rodents and shrews in the modern Polish fauna, but their abundance is low, and they are unlikely to affect these estimates. Productivity in the more continental climate of Białowieża now may be higher than in Britain then, or milder winters here may have allowed greater densities of earthworm-feeding species such as shrews and Badgers.

At the least, these estimates suggest which parts of the mammal fauna have been most affected by the changes over the last 7000 years, and indicate some of the gaps in modern ecosystems. The impact of the large ungulates, in particular, needs to be assessed. Their trampling, grazing and browsing must have had profound effects on the suppression of woodland regeneration, the creation of glades, and the dispersal of propagules like acorns and crab apple pips. The estimates also put the modern fauna in an interesting perspective, highlighting the extent to which domestic ungulates and Humans now dominate the fauna, and suggesting that 'mesopredator release' (Crooks & Soulé, 1999) has had an important effect on Foxes and Badgers.

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