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Life and death of the Westbury bears

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Remains of the middle Pleistocene cave bear, *Ursus deningeri* Reichenau, recovered from the cave deposits at Westbury-sub-Mendip near Bristol, England, are described. The age structure of the samples, based on evidence of dental eruption and wear stages, indicates that females both gave birth in the cave and sought shelter there with yearling cubs. The presence of two size classes in the permanent teeth also points to use of the cave by adults of both sexes. Wear stages on the deciduous teeth suggest that neonates were able to feed at times outside the cave during their first spring, while still using the cave as a den.

1. Introduction

The cave at Westbury-sub-Mendip is located in the Mendip Hills some 30 km south of Bristol (Fig. 1). The deposits were discovered in 1969 during limestone quarrying, and brought to the attention of local palaeontologists (Heal 1970, Bishop 1974, 1975). It is now clear that the mammalian assemblage is one of the most important known from the Middle Pleistocene of the British Isles (Stuart 1982), and a major report on the fauna based on collections made between 1969 and 1972 has been published by Bishop (1982).

We commence with a brief discussion of the deposits and the overall features of the assemblage, and go on to outline some of the behaviour patterns of extant bears that seem most relevant to interpretation in a palaeontological context. We then give details of the bear assemblage, with particular emphasis on the age structure of the dental samples from the units excavated by the BM(NH), and offer our interpretations based upon the behaviour of extant bears. Finally, we offer a brief assessment of the importance of the other large carnivores present at the site in the lives of the Westbury bears.

2. The Westbury deposits

Detailed descriptions of the character of the deposits and their taphonomic interpretations will be given elsewhere (Andrews 1990). Here we give only those details of the sediments and the character of the bone relevant to an understanding

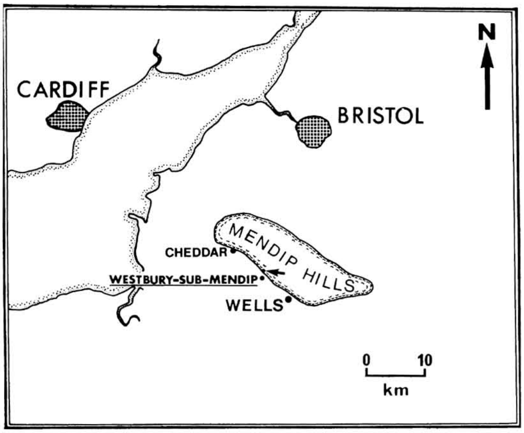

Fig. 1. Locality map showing the position of the Mendip Hills south of Bristol in western England. The cave site at Westbury-sub-Mendip is indicated by an arrow.

of processes that led to the formation of the bear assemblage. The cave consisted of two partially separated chambers (Fig. 2). The main chamber is infilled with basal siliceous deposits overlain by stratified cave breccias, and the side chamber has a continuation of the siliceous deposits wedging out across the floor and overlain by a different sequence of cave breccias.

In the side chamber the lowermost sediments with abundant bone were in units 2 and 5, which rest both on the surface of the siliceous member and on the limestone floor of the cave where the siliceous member pinches out in the western part of W3. Unit 5 is the lateral equivalent of unit 2, but since they are separated by an area of collapse there is no actual contact between them and therefore no way of directly correlating them. Both units consist of angular breccias derived almost exclusively from inside the cave system. Similarly, the upper part of the side chamber is infilled with angular breccia mainly derived from within the cave system. It proved possible to subdivide unit 2 into three lithological subunits, but there is no faunal change and for the present purpose the fauna from the unit, together with that from unit 5, is considered as a single entity.

In contrast to the deposition in the side chamber, much of the main chamber deposit was transported into the cave in the form of massive mud flows and so forms a mixture of material derived from both inside and outside the cave. Two units, 18 and 19 (equivalent in part to beds 3–5 described by Bishop 1982), can be distinguished in the mud flow, and they rest disconformably on the waterlain deposits of the siliceous member separated by a thick breakdown zone surrounding a massive series of roof fall blocks.

Table 1. Numbers and *percentages* of bone fragments from Westbury units arranged in size classes (cm).

Unit:	2		5		18		19	
0 - 1	673	*55*	11275	*84*	1770	*53*	3670	*70*
1 - 2	297	*24*	1817	*14*	1152	*34*	1065	*20*
2 - 3	144	*12*	263	*2*	318	*10*	338	*6*
3 - 5	75	*6*	20	*0*	92	*3*	132	*3*
5 - 10	30	*3*	9	*0*	27	*1*	37	*1*
Totals	1219		13384		3359		5242	

Table 2. Bone element counts for bear remains at Westbury.

Unit:	2	5	18	19
Mandible	6	8	1	1
Maxilla	1	0	1	3
Incisors	44	18	2	26
Canines	33	18	16	37
Molars and premolars	103	38	86	107
Deciduous canines	3	0	212	149
Distal humerus	2	1	0	0
Proximal radius	3	1	0	1
Proximal ulna	3	1	0	0
Femur head	5	3	0	1
Proximal femur	2	3	0	1
Distal femur	2	0	0	0
Distal tibia	2	1	0	0
Pelvis	1	0	0	0
Calcaneus	5	1	0	1
Astragalus	1	5	1	0
Phalanges	42	21	10	13
Metapodia				
complete	16	0	4	6
proximal	17	10	6	7
distal	13	9	4	5
shaft	8	0	4	0
Vertebrae	14	2	3	4
Ribs	55	0	2	3
Indet. fragments	1219	13384	3359	5242

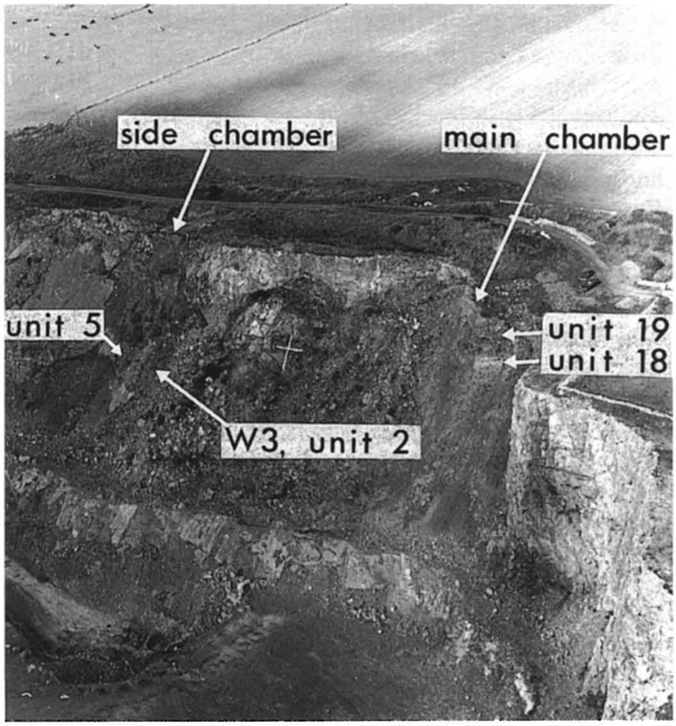

Fig. 2. Aerial view of the cave exposures at Westbury. The main chamber with units 18 and 19 are shown on the right, and the side chamber with units 2 and 5 on the left. The vertical arm of the cross in the centre of the deposits is 12 m and the horizontal arm is 8 m.

3. Description of the Cave Bear bones

The abundant bone in units 2 and 5 of the side chamber is entirely of bear and is highly fragmented with few specimens larger than 5–10 cm (Table 1). In the main chamber, the bone from units 18 and 19 was also broken, but generally speaking tended to be less intensively fragmented than that from the side chamber. When all four units are compared this point can be seen more clearly: Table 1 shows the number of fragments in each unit that fell within the various size classes.

The only common complete items from units 2 and 5 are foot bones and teeth (Table 2). All physical features of the bone and the damage inflicted upon it, together with the fact that most parts of the skeleton appear to have been present, the absence of evidence for post depositional sorting by water and the fact that roof falls do not appear to have been a significant cause of damage, suggest breakage in situ by trampling of substantially complete skeletons. Koby (1943) proposed the term "charriage a sec" to describe such a phenomenon, whereby the defleshed and largely dried-out bones of previous mortalities were apparently trampled and broken by later inhabitants of the cave. Puncture marks in some of the bones of unit 5, evidently produced by the teeth of a large carnivore, suggest that scavenging may also have played a part in the process of destruction. Bone loss is greater in units 18 and 19 (Table 2), despite the fact that bone fragmentation in the latter units is less than in units 2 and 5 of the side chamber (Table 1). In the main chamber bear is no longer the sole species present, but it dominates the faunal list. The pattern of the skeletal part representation of bear in units 18 and 19 is similar to the overall pattern for the total assemblage in those units, and the greater degree of bone loss can probably be attributed to the effect of transport of sediment and bone.

4. Modern guide-lines to bear behaviour

The Middle Pleistocene cave bear *Ursus deningeri* is regarded as the most plausible ancestor of the later Pleistocene cave bear *Ursus spelaeus* Rosenmuller & Heinroth, although it is not certain that the two taxa indeed represent distinct species rather than earlier and later forms of the same taxon. Kurtén (1968: 120) left room for some doubt on the issue, although Schütt (1968) took the view that species-level distinction was appropriate. Bishop (1982) strongly endorsed Schütt's opinion. Whatever the correct interpretation, both fossil taxa appear to have been most closely related to the brown bear, *Ursus arctos* Linnaeus, among extant species. For this reason, the brown bear is perhaps the best model upon which to base reconstructions of life style in the two extinct taxa, as proposed by Kurtén (1955, 1958), although features of the ethology of the American black bear, *Ursus americanus* Pallas may also shed light on the subject.

Both the brown bear and the American black bear hibernate during winter. The females give birth during this period, with a typical litter size of two (Bunnell & Tait 1981). Delayed implantation occurs sometime in November, following mating in June–July, leading to parturition most typically in January–February. The young bears are heavily dependent upon their mothers in the first few months of their lives, and will die with her in the den if she cannot survive until the spring. The cubs continue to suckle for some time, and appear still dependent upon the mother during the following winter, since without her they may be unable to enter dormancy (Pulliainen 1972:205). The minimum birth interval for females is therefore two years (Bunnell & Tait 1981:table 3, Herrero 1978:table 1, McCullough 1981:183).

Since adult brown bears have few natural enemies except wolves (Herrero 1978), and the young receive considerable protection from their mothers, many deaths are likely to occur in the winter during hibernation. However, adult male brown bears kill cubs despite the protection afforded by the mother (McCullough 1981), and it would be unwise to assume that all juvenile deaths necessarily occur in the den. The relative frequency of adult male and female deaths in dens is not known, although the extra hazards and burdens of pregnancy and lactation might be expected to have some effect upon the incidence of deaths among females.

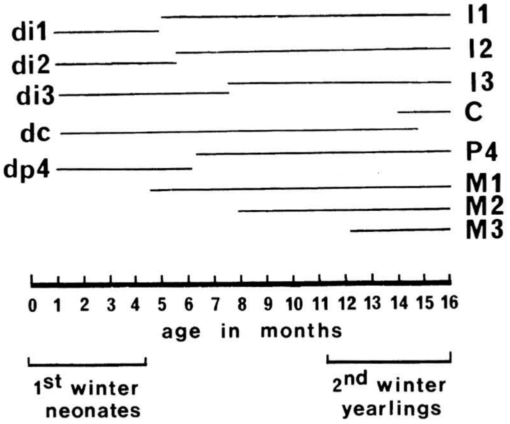

Fig. 3. Dental eruption sequence in brown bears (after Dittrich 1960). Expected teeth from neonates in the cave include all erupting and erupted (but unworn) deciduous teeth together with unerupted or erupting permanent molars and incisors; death of yearling cubs should yield worn deciduous canines, slightly worn permanent first and second molars and incisors, and unworn/erupting canines and third lower molar.

The sequence of eruption and replacement of the teeth is shown in Fig. 3, based on details given by Erdbrink (1953) and Dittrich (1960). The milk dentition is replaced during the period 6–14 months. None of the deciduous teeth is shed during the first winter, but the deciduous premolars begin to be lost soon after the time of emergence from the den, assuming birth occurred in January. The permanent dentition erupts during the first year of life and into the early part of the second. Dentally immature animals will therefore overwinter with their mothers twice. On the first occasion, as neonates, they retain their full, unworn deciduous dentition, with the upper and lower first permanent molars beginning to erupt. In their second winter, as yearlings, they have upper and lower M1s, P4 and M2 all in wear, heavily worn deciduous canines, and the unworn crowns of the other permanent teeth in various stages of eruption.

The later wear stages of the permanent cheek dentition appear remarkably even, based on our own study of brown bears in the collections at the BMNH and at the Finnish Museum of Natural History in Helsinki. For example, with the first molars showing slight wear on the enamel of the highest cusps, the second molars exhibit only very slight wear while the lower third molars remain unworn. Moderate wear on the first molars, revealing patches of dentine, is matched by slight to moderate wear on the second molars and slight wear on the third molar. Heavy wear on the first molars, involving substantial planation of the teeth, is matched by heavy wear on the second molars and by moderate wear on the third molar. Some of these points are illustrated in Fig. 4.

Pregnant females tend to seek dens away from other bears, especially from males. The same is apparently true of females with yearling cubs. However, the extent of overlap in home ranges and territories is unclear (Herrero 1978, Bunnell & Tait 1981), so that it is not possible to say that a given den would fall within the range of a given number of bears at any one time. Female black bears at least may seek a different den each year (Rogers 1980), so that a given locality could potentially be occupied by females one year and males the next.

Adult brown bears are extremely sexually dimorphic in body size (Bunnell & Tait 1981:table 1), and this is most clearly apparent in the relative sizes of the permanent canines (Kurtén 1958, details reproduced here in Fig. 5). Figure 5 also shows the ranges for canine widths of populations of prehistoric brown bears collected from Tornewton Cave in Devon (Sutcliffe & Zeuner 1958) compared with ranges for two populations of cave bear, *Ursus spelaeus* (Kurtén 1976) and the Westbury sample.

Many of the features of bear lifestyle summarised above are likely to be recorded in the fossil record. Young who die in the den will be represented by deciduous or immature permanent dentitions and immature skeletons, although the skeletons in the case of neonates in particular are likely to stand up less well to any subsequent processes such as trampling by later occupants of the den. Such juveniles will have been accompanied by their mothers, and contemporaneous adult deaths in the same levels should therefore be of females. Hibernation deaths may give rise to separation of bear remains into growth stages, as for instance has been observed at Dragon Cave near Mixnitz, Austria. In this cave the numerous cave bear remains grouped into neonates, yearlings, two-year olds, and so on, together with fully adult females. Life tables for cave bear populations from a number of caves indicate that as much as half the population of juveniles may have died during the first two winters of life (Kurtén 1976), death during the first winter yielding full sets of deciduous teeth and some unerupted permanent teeth (see Table 3), and death during the second winter yielding deciduous canines and erupting or slightly worn permanent teeth. Where adult males occur in caves, they should not be accompanied by juveniles.

A major problem in applying these observations to the fossil record is that deposition over time in a single den may tend to obscure the basic features of behaviour in the skeletal record, particularly if a different den tended to be sought by each animal each winter. It is also clear that the middle Pleistocene carnivore fauna in Europe included a vastly greater number of species able to kill bears than is presently the case, and the proportion of deaths that occurred outside the dens may have been greater than in modern bears.

5. The Westbury Bears

Bishop (1982) noted the abundance of deciduous bear teeth in the total assemblage then available. His sample came exclusively from his beds 3–5, which are laterally equivalent to our units 18 and 19. Bishop also distinguished males and females on the basis of size distributions in width measurements of permanent lower canines (1982:45), with 75 % of the adult sample consisting of females. He interpreted this as indicating motherly care of the young. In the BM(NH) collections from units 18 and 19, the bear samples are similar to those described by Bishop, but the side chamber samples from units 2 and 5 are very different. We shall discuss the two areas separately.

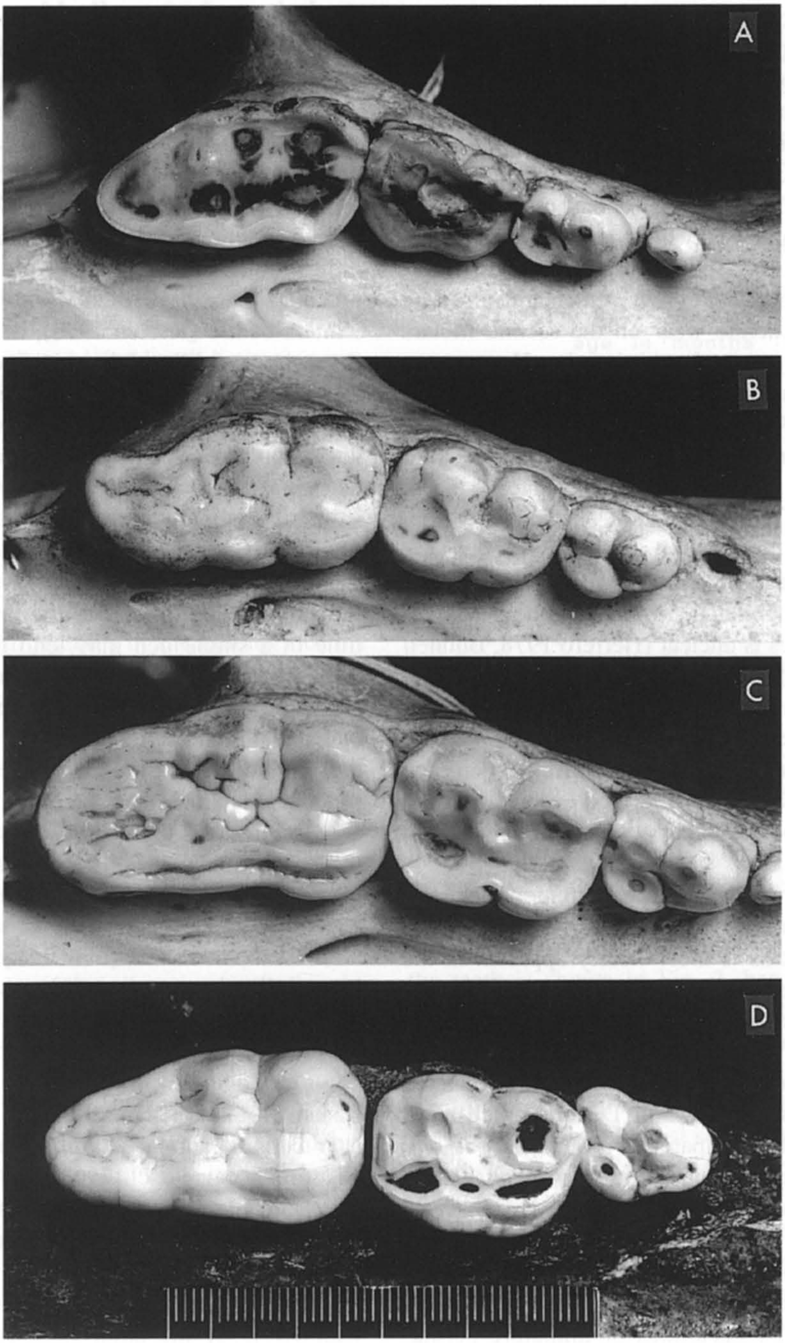

Fig. 4. Tooth rows of three brown bears (*Ursus arctos*) compared with a specimen from W3 at Westbury, showing the correspondence of wear stages on P4–M2 on the right upper tooth rows. — A. Specimen 31.2.2.1, heavily worn, with flattened dentine exposed over whole of crown of all teeth. — B. Specimen 43.268, moderately worn, with dentine beginning to appear on lingual surfaces of all teeth. — C. Specimen 31.7.14.2, moderately worn as for B but with some dentine exposure extending to the buccal cusps of all teeth. — D. M33530 at equivalent wear stage to C. Scale in mm.

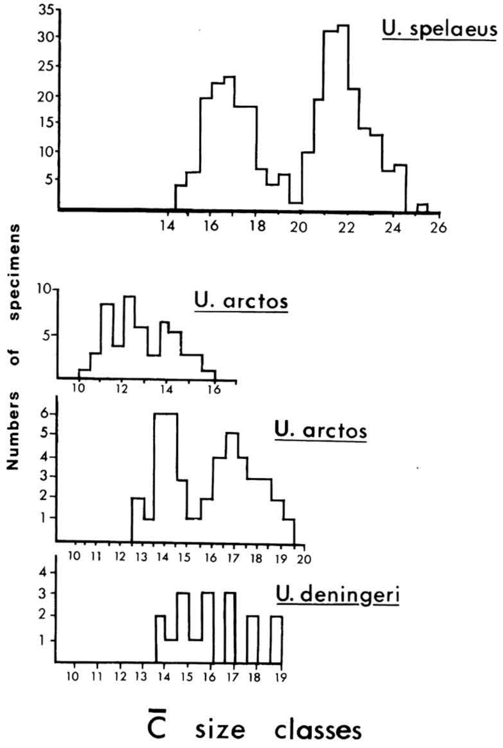

Fig. 5. Distribution of lower canine size classes, from bottom to top: the Westbury cave bear, *Ursus deningeri* (our data); fossilized brown bear *Ursus arctos* (our data); recent brown bear *Ursus arctos* (Kurtén 1958); and the later Pleistocene cave bear, *Ursus spelaeus* (Kurtén 1976). Measurements in mm.

Units 2 and 5

In the side chamber of the BMNH excavation, the only deciduous teeth found were three canines in unit 2. The permanent teeth of both units 2 and 5 showed a series of development and wear stages, the overall pattern of which is shown in Table 3.

Two points arise from these distributions. Based on the times of eruption of the permanent teeth, the unerupted/unworn M2s and M$_3$, as well as the slightly worn M1s and P4s, point to the presence of yearling bears (MNI = 7) denning during their second winter; that is, accompanied by their mothers. The presence of three deciduous canines points to the same conclusion. Many if not most of the worn, adult teeth might therefore be from females that also died during the hibernation period (MNI = 6). However, the distribution of tooth sizes among the adults in the side chamber suggests that the sequence of occupation was perhaps more complicated. Fig. 5 shows histograms of adult lower permanent canine widths for the units 2 and 5 sample combined with that from units 18 and 19. The sample size is too low to offer an accurate reflection of the precise size distributions, but it would appear that both sexes are present in the Westbury side chamber adult assemblage, and that males are more abundant than females. There is not the preponderance of females seen in the lumped samples considered by Bishop (1982:fig. 22). The even smaller sample of upper second molars from the side chamber sequence appears to consist entirely of males (Fig. 6) in contrast with the mixed sex assemblage from the main chamber.

Secondly, the unerupted permanent first molars and upper fourth premolars clearly point to the presence of young bears during their first winters as neonates (Table 3).This indicates that pregnant females also occupied that part of the cave. But such young bears should also have had deciduous teeth, teeth that should have been incorporated in the deposits if the bears died in the cave as they appear to have done. The minimum number of five neonate cubs would each have had their full complement of deciduous teeth, and the discovery of only three deciduous teeth

Table 3. Wear stages of bear permanent cheek teeth from Westbury units 2 and 5 combined (BMNH collections). Teeth present at different growth stages are shown in separate boxes, from left to right: neonates, yearlings, second years, adults.

	Unerupted	Unworn	Slight	Heavy	Totals
P^4	9	5	0	2	16
P_4	1	4	1	1	7
M^1	2	4	0	0	6
M_1	2	14	1	10	27
M^2	14	7	6	5	32
M_2	11	8	3	12	34
M_3	10	4	1	4	19
Totals	49	46	12	34	141

The wear stages are based on the following characters. Unerupted: teeth with little root formation; unworn: teeth with roots wholly or partly (more than half) developed but with no wear on the crown; slightly worn: with small facets on the surfaces of the crowns but no exposure of dentine; heavily worn: with large exposures of dentine on areas of wear.

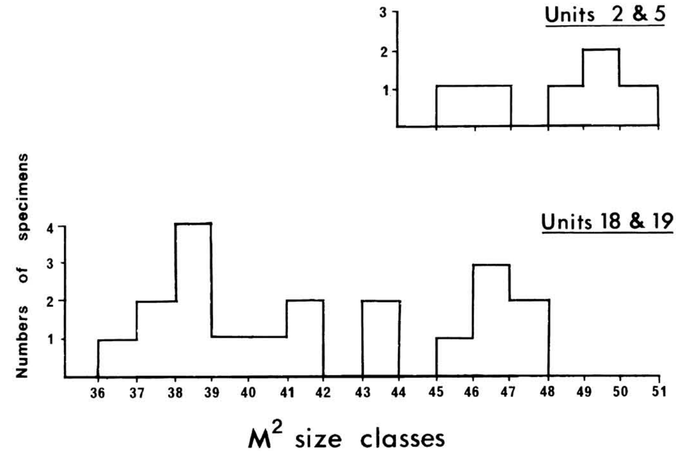

Fig. 6. Distribution of upper second molar size classes of *Ursus deningeri* from Westbury, units 2 and 5 above, and units 18 and 19 below. The latter appears to be a mixed sex sample, while the small sample from from units 2 and 5 includes only large (male?) teeth. Measurements in mm.

(all canines) in unit 2, and the absence of any in unit 5, is therefore at odds with the age distributions of the permanent teeth. The only logical explanation would appear to be that this is the effect of bone breakage in the cave, fragmenting most of the deciduous teeth beyond the point of recognition.

This interpretation is strengthened when we consider the relative intensity of fragmentation in the four units as shown in Table 1. The extent of fragmentation in unit 5, the largest sample and the one in which 98% of the specimens were less than 2 cm in length, suggests that in situ destruction may have removed the evidence of deciduous teeth in the side chamber. Less intensive fragmentation in unit 2 may explain the preservation of 3 deciduous teeth there, despite the smaller size of the sample, while in units 18 and 19 large sample sizes appear to have combined with less intensive fragmentation to lead to the preservation of even more deciduous teeth.

The picture that emerges for the side chamber deposits is one of periodic occupation by all-male groups and females with cubs. Despite the bias introduced by the probable loss of deciduous teeth, it is likely that the chamber was occupied more frequently by the males and only occasionally by the females with young.

Units 18 and 19

Numerous deciduous bear canines were found in both units 18 and 19, 212 of them in unit 18 compared with 104 permanent teeth, and 149 of them in unit 19 compared with 170 permanent teeth.

The pattern of bear permanent cheek-tooth eruption and wear in the two main chamber units is shown in Table 4. This distribution shows a higher proportion of teeth with slight wear than is seen in the side chamber assemblage (23% versus 9%), but the emphasis is still on unerupted and unworn teeth. Minimum numbers of individuals in the neonate, yearling and two-year old age classes are four, eight and four respectively, and the overall impression is therefore of a den where females with neonates and year-old cubs

Table 4. Wear stages of bear permanent cheek teeth from Westbury units 18 and 19 combined (BM(NH) collections).Teeth present at different growth stages are shown in separate boxes, from left to right: neonates, yearlings, second years, adults.

	Unerupted	Unworn	Slight	Heavy	Totals
P^4	3	3	1	4	11
P_4	4	4	7	0	15
M^1	7	8	7	9	31
M_1	6	3	8	11	28
M^2	5	7	4	13	29
M_2	16	5	9	10	40
M_3	6	6	3	3	18
Totals	47	36	39	50	172

These distributions are based on the eruption and wear stages given in Table 3.

tended to congregate. This finding tends to support the interpretation of maternal activity put forward by Bishop (1982). The distribution of sizes in the adult tooth sample, however, suggests that denning by females and young was not the sole cause of the accumulation. Figure 6 shows histograms for adult upper second molar widths for units 18 and 19, and although the sample size is again small, there is every indication that males are also represented in the units.

Since the young bears of the main chamber from which the immature permanent teeth came are also represented by milk teeth, we can examine the distributions of wear in that sample as a more detailed guide to the structure of the neonate and yearling portion of the assemblage. The deciduous canines have been divided up into the classes suggested by Kurtén (1958:9) for *Ursus spelaeus* deciduous canines, and the results are shown in Table 5. Not all of the Westbury deciduous teeth could be placed in discrete categories, so the table is based on 42 specimens from unit 18 and 149 from unit 19.

The most interesting features of the wear-stage distribution for the deciduous canines are the high frequencies of worn teeth (46%) and unworn/unerupted teeth (34 %). This distribution points to the presence in some numbers of both neonate and yearling cubs, and supplements the evidence of the permanent dentition in this respect. However, a further significant group may also be discerned, since 39 (20 %) of the teeth in Table 5 exhibit slight wear. Until emergence from the den, there is nothing in the diet of the young bears to cause the teeth to wear, and yet the animals evidently died in the den. The presence of these teeth may imply that the young animals were venturing outside the den to feed in the early spring of their first year, a time when grass is likely to have been the main plant food available.

Table 5. Wear stages in Westbury bear deciduous canines.

Unit:	18	19	Totals	
Unerupted	6	16	22	Neonates
Erupting	2	8	10	
Unworn	9	23	32	
Slight wear	9	30	39	
Heavy wear	14	66	80	Yearlings
Heavy wear with root resorbtion	2	6	8	
Totals	42	149	191	

The classes are as follows: unerupted, when the crown is formed but the root is not; erupting, when some root development has taken place; unworn, when the root is fully formed but the crown has no wear; slight to moderate wear; heavy wear; heavy wear with root resorbtion.

It can be concluded that the cave bear remains in units 18 and 19 of the main chamber sequence at Westbury are derived mainly from females with neonate and yearling young. This contrasts with the cave bear remains from the side chamber, although, as in that part of the cave, the main chamber was also occupied periodically by males. There is an added complication in the main chamber, however, in that the sediments were transported. Many of the bones were therefore probably brought from other parts of the cave as well, and it is likely that more than one occupation area may have been sampled in the unit 18–19 deposit.

6. Discussion

We have not attempted a more detailed study of the structure of the Westbury bear assemblage at this stage for a number of reasons. The first is the potential effect of excessive wear on the inclusion of teeth from older animals in the samples. A number of teeth were simply too worn to be measured: others were broken in the deposits. Breakage could be argued to be non sexually specific, but differential longevity between the sexes might have an effect upon the representation of the two sexes in an assemblage if the teeth of the longer-living sex became too worn to be measured. The second reason is the evident under-representation of deciduous teeth in the side chamber, and its unknown effects upon the apparent age structure of the sample from that part of the cave. In the main chamber, the derived nature of the deposits produce their own problems. The third reason is the unknown effect of the activities of other carnivores on the bear population.

In contrast with their modern relatives, and even with bears of the upper Pleistocene studied by Kurtén (1955, 1958, 1976), Westbury bears faced the potential dangers of a considerable range of other large carnivores. The wolf present was the relatively small *Canis mosbachensis* Soergel, but it was accompanied by the large, dhole-like *Xenocyon lycaonoides* Kretzoi. Also known from the site are the lion, *Panthera leo* L., the jaguar, *Panthera gombaszoegensis* Kretzoi, the sabre-toothed cat, *Homotherium crenatidens* Fabrini, the short-faced hyaena, *Pachycrocuta brevirostris* (Aymard), and the spotted hyaena, *Crocuta crocuta* Erxleben.

Any of these animals, and especially members of those species able to act co-operatively, such as the dogs, hyaenas and lions, may have posed a serious threat to immature, infirm or elderly bears. In view of the large number of potential predators, it is very difficult to assess the relative importance of within-den versus extra-den mortalities upon the structure of the bear population. No contemporaneous occurences of hyaena-accumulated bone samples containing ursid remains are even available to afford us some complementary view of the effects of hyaena predation/scavenging upon bears. It is also true that any such hyaena activity would be unlikely to present a true picture of the age structure of bears that fell victim, since the bones of juveniles would inevitably tend to be destroyed. This point is borne out by the general scarcity of juvenile bear remains in British Upper Pleistocene cave assemblages, the vast majority of which appear to have been accumulated by the spotted hyaena (Turner 1981, 1982). In his detailed study of the morphology of British Pleistocene bears, many of which were obtained from just such assemblages, Reynolds (1906) was unable to assemble a representative set of deciduous teeth for description.

Our view of the life and death of the Westbury bears is therefore necessarily incomplete. But a fossil assemblage represents animals that died, and in the case of a den those deaths evidently reflect denning behaviour. The best approach to an interpretation of the behaviour of the animals in such an assemblage is to consider suitable modern analogues, a method exemplified by Kurtén (1955, 1958), taking account as far as possible of taphonomic factors affecting age and sex ratios. By concentrating on the more robust relationships between the behaviour of living animals and the structure of similar death assemblages it has proved possible to provide tentative interpretations of the cave bear remains in the two chambers of Westbury Cave. Two different patterns of cave usage are indicated, all-male occupation predominating in the side chamber and female-cub occupation in the main chamber, and in both chambers there was periodic occupation by other age/sex groups. During the deposition of units 18 and 19, the conditions in spring may have been mild enough to permit the neonate bears to venture outside for long enough to nibble at the grass. We feel sure that such an interpretation would have delighted Björn Kurtén.

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