

5 The taphonomy of the small mammal faunas

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INTRODUCTION

Small mammals are found throughout the Mumbwa sequence. It is our purpose here to describe these remains and to try to identify the taphonomic agents responsible for their accumulation. Taxonomic identifications have been made by Margaret Avery (chapter 6) and will not be considered here other than at an ordinal level. Taphonomic processes under consideration here mainly relate to predation and the effects of breakage and digestion on the small mammal remains. Post-depositional damage is extremely extensive, which has led us to limit analysis to the most robust skeletal elements, which are the only ones to survive this damage, namely mandibles, incisors and molars, femora and humeri. Other cranial and postcranial elements are almost totally lacking in the Mumbwa assemblages: for example, only a single rodent maxilla was found compared with 129 rodent mandibles. The taphonomic processes and the modifications they produce follow the definitions and convention laid out in Andrews (1990).

The Mumbwa Caves stratigraphy is described in detail in chapter 2. Since we are concerned with taphonomic change throughout the sequence, we selected the single most complete record available from the 1994–1996 excavations, which is that in square D9. The sequence sampled is restricted to the Middle Stone Age and encompasses unit VII at the top (Stage 5) to unit XII at a depth of 684 cm below datum. Of the 78 levels excavated in D9, we sampled 55 with small mammals, providing a total of 5703 identified bones. In levels of microfaunal richness, we investigated 50 per cent samples. In addition, a sample of 5045 identifiable elements was analysed from the 1994 collection, mostly from the Later Stone Age and the Iron Age in the Mumbwa sequence. These came from the Area III squares D12-1-1, D12-1-2, D11-2-1 and D11-1-1 (unit I, Iron Age) and square D11-5-5, D11-6-1 to 8, D11-7-1, D11-8-1 (unit II, early Holocene Later Stone Age).

Avery (1996) has identified 27 small mammal species from the Mumbwa sequence, consisting of four insectivores, two bats and 21 rodents. Without considering possible taphonomic alteration of species composition, Avery concluded that the environment during the

Middle Stone Age was grassy dambos (low-lying flooded edaphic grasslands) with woodland on the higher ground with savanna away from the dambos. During the Later Stone Age there was riverine vegetation and savanna woodland, replaced by savanna grassland in the Iron Age. The environment today is similar to these reconstructions, with the limestone massif in which the caves were formed rising out of a grassland dambo with low scrubby woodland on the slopes away from the dambo. The woodland is greatly altered by human activity, however, and with the presence of isolated larger trees of *Ficus*, *Schlerocarya* and *Albizia*, all in the immediate vicinity of the cave, the indications are that the woodlands were much denser in the past before human clearances and human-induced fire.

TAPHONOMIC MODIFICATIONS

Preliminary observations in the field during the 1995 field season led us to believe there was some taphonomic variability in the Mumbwa sequence. Differences in degrees of digestion were observed in the D9-9 levels, with some having next to no digested bones and others having greater degrees of digestion, and this led to the hypothesis that different predators may have occupied the cave at different times. In this event, the faunal analysis would need to take these differences into account, for predators with different hunting habits produce different faunal composition in their prey assemblages even when hunting in the same area. The detailed analysis that follows is designed to test this hypothesis.

Breakage

The bones from all levels at Mumbwa are extremely broken, with great loss of elements. This is attributed to post-depositional damage because it is similar at all levels. Similarly, the majority of bones are either heavily stained or show considerable all-over surface corrosion, both of which are also attributed to post-depositional processes. As a result, bone breakage and the all-over corrosion of the bone surfaces are not primary indicators of mode of accumulation at Mumbwa, since any pattern resulting from initial accumulation has been destroyed by the later, post-depositional, breakage. As a result of this, most skeletal elements are either not

preserved at all, or, if present, are usually less than 1 per cent of the expected number calculated from the estimated number of individuals. Only the femur and humerus for the postcranial skeleton are preserved in any numbers, and the mandible and incisors (rodent only) for cranial remains.

The femur is the most abundant element in all levels, with 686 specimens for the whole Middle Stone Age sequence in square D9 (table 5.1). Of these, 94.8 per cent consist of just the proximal end, usually with a small portion of the shaft. Mid-shaft diaphyses are the next most abundant, and distal ends are rare, only 14 specimens or 2.1 per cent. Complete specimens, where parts of proximal and distal ends are preserved with the diaphysis, make up 3.1 per cent of the sample (diaphyses were not counted separately). Similar figures were found for Iron Age and Later Stone Age levels, although the number of distal ends was slightly higher than in the Middle Stone Age. The only other common limb element in the Middle Stone Age levels was the humerus. There were 512 specimens of which 95.7 per cent had just the distal end with part of the shaft, 3.7 per cent complete and 0.9 per cent proximal ends. In the case of the humerus, proximal ends were considerably more common relative to distal ends in the Later Stone Age and especially in the Iron Age compared with the Middle Stone Age (table 5.1), suggesting a slightly lower degree of breakage at these levels. The only other limb element at all common in the Middle Stone Age was the tibia, but these were not separately recorded. They were relatively more abundant in the Iron Age and Later Stone Age, with 253 and 96 specimens respectively, and at all levels the distal end makes up around 50 per cent of the sample with almost no complete elements.

The minimum number of individuals indicated by these specimens is 343 in the Middle Stone Age based

on the femur, taking into account lefts and rights but not size differences or species identifications. In the Later Stone Age, the MNI is 62 and for the Iron Age it is 174, based on the humerus in both cases. Both the humerus and femur occur in greater numbers than the mandible in most levels. In the Middle Stone Age, only 176 mandibles were found, 129 rodents and 47 insectivores, more than from other levels, and they were more broken than in either the Iron Age or the Later Stone Age deposits (table 5.1). This is similar to the pattern seen for the femur and humerus. The mandibles are extremely fragmentary in all the deposits, with few retaining any part of the ascending ramus and most with broken inferior borders and missing incisors. In this particular instance, the Middle Stone Age breakage is slightly less than in other levels. The lower numbers of mandibles is interesting, and if this is a true reflection of the original faunal composition, it suggests that there may have been a bias against cranial elements in the Mumbwa Caves faunas (but see below).

Rodent incisors are by far the most abundant skeletal element, with 4093 specimens recorded from the Middle Stone Age in the D9 section. The Iron Age count is lower, 1220 specimens, and the Later Stone Age is the lowest with only 230 specimens. These numbers are misleading as indicators of abundance, however, for all incisors were broken. From a small subset of 100 rodent incisors, it is estimated that on average the rodent incisors in the Middle Stone Age were broken into 3.4 fragments per individual. The MNI based on rodent incisors therefore is 1043 for the Middle Stone Age based on left/right and upper/lower, and this is reduced to 307 taking breakage into account. This number is marginally fewer than the MNI based on the femur, but it is greater than that indicated by the humerus ($N=512$, $MNI=256$). The estimated MNIs for incisors in the Iron Age deposits is 90 and for the Later Stone Age is only 17, both being considerably below the numbers of postcranial elements (table 5.1). This supports the suggestion above that there was a bias against cranial elements in the two upper levels, but in the Middle Stone Age the number of incisors is similar to those for humeri and femora and the evidence is equivocal. Molars are much less common, 53 only from the whole Middle Stone Age sequence and 85 from the Iron Age. The marked disparity in numbers could reflect a sampling error caused during excavation, but a 0.5 mm fabric mesh was used for screening all sediments in Areas II and III.

It is hard to account for the shortfall in mandible numbers compared with numbers of isolated incisors. This is all the more so since about 22 per cent of the rodent mandibles still had their incisors present in the jaw. Even more dramatic is the near absence of maxillae, with only 19 rodent maxillae being found in the Mumbwa

sequence. These are more prone to destruction than mandibles, and the conclusion must be that post-depositional destruction was so great that approximately 80 per cent of mandibles and 97 per cent of maxillae were so totally destroyed that no evidence of their existence remained in the Mumbwa deposits except the broken remains of their incisor teeth.

Digestion

Small proportions of rodent teeth and postcrania show signs of digestion throughout the Mumbwa sequence (see figs 5.1, 5.2 and 5.3). This is seen particularly in the rodent incisors. Only one molar was observed showing digestion (from level D9-7-9 in unit VIII). Six proximal femora also showed signs of digestion, always when digestion is also present on the rodent incisors from the same level. Of the 4093 rodent incisors, 158 showed signs of digestion, which comes to just under 4 per cent. Most of these had a very slight degree of digestion, defined as category 1 digestion in Andrews (1990). Ten of the 55 fossiliferous levels that we examined had rodents with no evidence of digestion, but many of these had rather small samples (table 5.2) and it is possible that larger samples would have shown evidence of some degree of digestion. Twenty-five levels having rodent incisors with digestion had levels of digestion less than 5 per cent and only three levels had the percentage occurrence of digestion greater than 20 per cent. For example, levels D9-1-4 and D9-1-5 both have high proportions of digestion, and they both have at least some teeth digested to a greater degree, but the sample sizes are small, 16 and 23 rodent incisors respectively, and the significance of this is uncertain. Level D9-9-3 is the only other level with a high proportion of digestion, but in this case it is all category 1.

The majority of levels in the D9 sequence have samples of incisors sufficient in size to give a reliable estimate of the presence or absence of digestion. It would appear, therefore, that most levels show rodent remains with only low proportions and low degrees of digestion, and the most likely predator to produce these is the barn owl (*Tyto alba*). The evidence of higher digestion in three levels could indicate a different predator in this stage of the sediment accumulation, but the evidence is not convincing, either because sample sizes are too small or because the degree of digestion is no greater than at other levels. What might be indicated at these levels is that the same predator was present, but that at these stages it was nesting. It has been demonstrated (Andrews 1990) that nesting barn owls produce small mammal samples with a higher degree of digestion than roosting adult individuals, because the pellets produced by nestlings contain more digested bones than do pellets from adults.

The data for the Later Stone Age and Iron Age levels

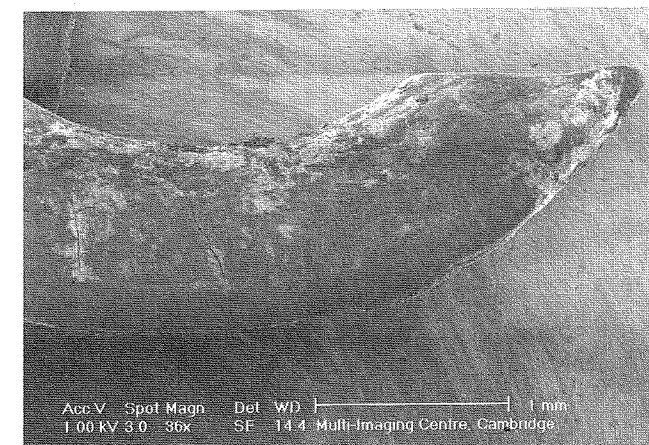


Figure 5.1 SEM micrograph of rodent incisor with light digestion on the tip. This gradual corrosion of the enamel tip is a very distinctive form of digestion.

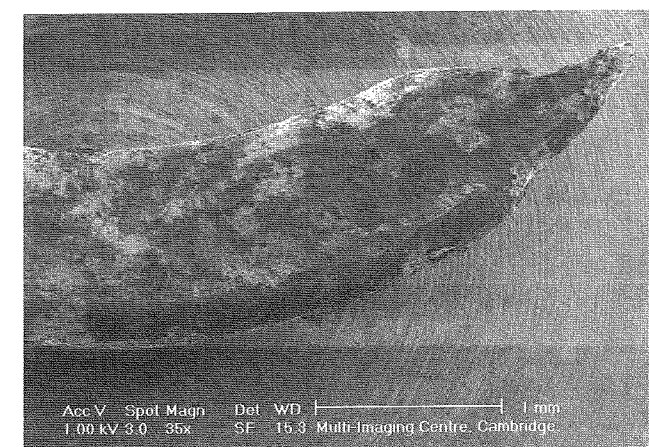


Figure 5.2 SEM micrograph of rodent incisor with moderate digestion on the enamel tip, and also further along in the middle of the incisor.

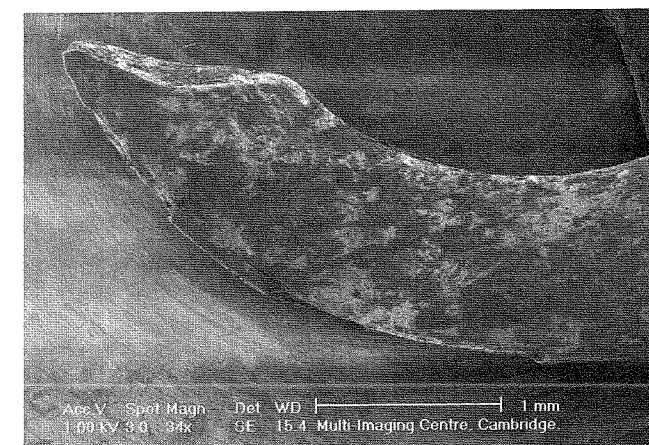


Figure 5.3 SEM micrograph showing rodent incisor with moderate digestion. This image illustrates clearly the intermittent corrosion that can occur along the incisor leaving islands of enamel.

Table 5.1 Breakage of skeletal elements in the Mumbwa Caves sequence

Skeletal element	Iron Age	Late Stone Age	Middle Stone Age
femur N	233	117	686
proximal	164	86	651
distal	33	16	14
complete	36	15	21
humerus N	348	123	512
proximal	106	17	4
distal	205	77	490
complete	37	29	18
mandible N	270	54	176
complete	9	4	4
no ramus	62	9	92
inferior bdr broken	180	34	80

Table 5.2 Distribution of digested bones in the D9 sequence at Mumbwa Caves. The context is based on square, locus, level designations from appendix 1; N is the number of rodents incisors; Cat. 1 etc refers to the category of digestion (Andrews 1990); total I is the total number of rodent incisors in the Mumbwa sequence divided by 3.4 (see text)

Context no	N	Cat. 1	Cat. 2	Cat. 3	Cat. 4	Total I	Cat1/N	Cats. 1-4/N	Cats. 1-4/1203
D9-1-1	23	2	1			1203	8.7	13.0	0.25
D9-1-2	26					1203	0.0	0.0	0.00
D9-1-3	4					1203	0.0	0.0	0.00
D9-1-4	16	3		1	1	1203	18.8	31.3	0.42
D9-1-5	23	3	1	1		1203	13.0	21.7	0.42
D9-2-1	2					1203	0.0	0.0	0.00
D9-2-2	2					1203	0.0	0.0	0.00
D9-2-3	28		1	1		1203	0.0	4.2	0.17
D9-4-4	96	4		1		1203	4.2	5.2	0.42
D9-4-7	215	1				1203	0.5	0.5	0.08
D9-4-8	106					1203	0.0	0.0	0.00
D9-6-1	44					1203	0.0	0.0	0.00
D9-7-1	24					1203	0.0	0.0	0.00
D9-7-2	43					1203	0.0	0.0	0.00
D9-7-3	196	3				1203	1.5	1.5	0.25
D9-7-4	21					1203	0.0	0.0	0.00
D9-7-5	45					1203	0.0	0.0	0.00
D9-7-7	232	2				1203	0.9	0.9	0.17
D9-7-8	160	3				1203	1.9	1.9	0.25
D9-7-9	84	3				1203	3.6	3.6	0.25
D9-7-10	54	4				1203	7.4	7.4	0.33
D9-7-11	44	1				1203	2.3	2.3	0.08
D9-7-12	141	2				1203	1.4	1.4	0.17
D9-7-13	116	3				1203	2.6	2.6	0.25
D9-7-14	57	1				1203	1.8	1.8	0.08
D9-7-15	42	2				1203	4.8	4.8	0.17
D9-7-16	34	3				1203	8.8	8.8	0.25
D9-7-17	43	2				1203	4.7	4.7	0.17
D9-7-18	56	1				1203	1.8	1.8	0.08
D9-7-19	73	2				1203	2.7	2.7	0.17
D9-7-20	56	2				1203	3.6	3.6	0.17
D9-9-1	113	4				1203	3.5	3.5	0.33
D9-9-3	45	9				1203	20.0	20.0	0.75
D9-9-4	144	6		2		1203	4.2	5.6	0.67
D9-9-5	121	6		3		1203	5.0	7.4	0.75
D9-9-6	98	2				1203	2.0	2.0	0.17
D9-9-7	80	5				1203	6.3	6.3	0.42
D9-9-8	76	2				1203	2.6	2.6	0.17
D9-9-9	52	1				1203	1.9	1.9	0.08
D9-10-1	78	4				1203	5.1	5.1	0.33
D9-10-2	66	2				1203	3.0	3.0	0.17
D9-10-3	59	1	1			1203	1.7	3.4	0.17
D9-10-5	136	5				1203	3.7	3.7	0.42
D9-10-6	92	4	2	2		1203	4.3	8.7	0.67
D9-10-7	120	4				1203	3.3	3.3	0.33
D9-10-8	101	5		4		1203	5.0	8.9	0.75
D9-10-9	98	3				1203	3.1	3.1	0.25
D9-11-2	120	3				1203	2.5	2.5	0.25
D9-11-4	64	4				1203	6.3	6.3	0.33
D9-12-3	51	3		2		1203	5.9	9.8	0.42
D9-12-5	120	6		1		1203	5.0	5.8	0.58
D9-13-2	133	7				1203	5.3	5.3	0.58
Totals	4093	133	6	18	1	1203	3.25	3.86	13.13

Table 5.3 Distribution of digested bones in the three stages represented in the Mumbwa Caves sequence. Abbreviations as in table 5.1

Context	N	Cat. 1	Cat. 2	Cat. 3	Cat. 4	Cat. 5	% digestion
Iron Age	1220	40	0	11	16	3	5.7
LSA	189	9	0	1	3	0	6.9
MSA (table 1)	4093	133	6	18	1	0	3.9

are similar to those for the Middle Stone Age just described. What we show in table 5.3, therefore, is a summation of digestion proportions by these three stages. The Later Stone Age and Iron Age have slightly higher degrees of digestion, but the difference is small and throughout the Mumbwa sequence it appears that the barn owl is the predator accumulating small mammal remains.

DISCUSSION

Two main taphonomic processes have been identified in the Mumbwa sequence. These are post-depositional breakage and corrosion, and digestion by the predator accumulating the assemblage. Some of the breakage could have been caused by the predator, but so great has been the later breakage that this could not be identified. The barn owl is considered to be the only likely predator accumulating the small mammal remains in the cave, and variations in digestion in some levels is attributed more to changes in behaviour of the owl, nesting as opposed to roosting, than to a different predator being involved. There may still be a change in the food items owls bring to their nestlings, although there is little evidence that this occurs, but the principal bias in the accumulation of the small mammal fauna at Mumbwa is that introduced by the barn owl. This makes the ecological interpretation relatively straightforward, and it justifies the conclusions of Avery (1996b), although there are still issues to be addressed in the behaviour patterns of the barn owl.

The barn owl is a small to medium-sized owl that feeds mainly on mammals, taking the most abundant prey in its habitat. Many insectivores are included in its diet as well as rodents, but few birds are eaten, although it must be said that some individual barn owls may specialise on particular prey (Andrews 1990:29). This is the exception, however, and in general barn owls take a representative sample of prey in relation to their hunting territory, but they select their prey within a relatively narrow size range. Both larger and smaller rodents are

under-represented in the owl's prey assemblage, and very small animals such as insects or other invertebrates are much less common than their actual abundance in the habitat. In addition, barn owls hunt generally by slow flight over relatively open ground, and their prey assemblages reflect this, sampling open country species to a greater extent than closed country ones. Indeed, species that may be common in thick woodland within the hunting area of a barn owl may be greatly under-represented because they are only rarely taken as the owl flies along the edges of the woodland. All these are limiting factors to barn owl behaviour that introduce elements of selectivity to its prey assemblages. On the other hand, barn owl activity patterns are broader than those of many other predators, for they are not as strictly nocturnal as most other owls and so are not limited only to prey with nocturnal habits.

Given the biases to the Mumbwa faunas introduced by the common predator, the barn owl, some doubt remains about the ecological conclusions of Avery (1996b). The general conclusions about open habitats such as grassland and savanna may be correct when one considers the preferred hunting habits of the owl, since these are the habitats barn owls like to hunt in, but it leaves open the question as to what other kind of habitats may have been present that the owl did not hunt in because they are not suited to its method of hunting. Avery's (1996b) conclusion about Iron Age habitats at Mumbwa was that the most likely environment was savanna grassland, and at earlier levels her conclusions were similar, but given the nature of barn owl hunting methods these conclusions may not be the whole story. It is likely that the barn owls living at Mumbwa today would provide similar indications, but the present-day area is woodland with dambos, much altered by human activity, and it is certain that sampling current barn owl prey assemblages would not be representative of the range of habitats present. Neither would they have been in the past. These issues are addressed in chapter 6.