CARNIVORE ACTIVITY AT KLASIES RIVER MOUTH: A RESPONSE TO BINFORD

by

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ABSTRACT

Environmental and behavioural factors contributed to variability in the relative abundance of *Raphicerus* (grysbok/steenbok) represented in Late Pleistocene and Holocene deposits at the complex of caves at Klasies River Mouth and at Nelson Bay Cave in the southern Cape Province, South Africa. Binford has used the relative abundance of *Raphicerus* in an index assumed to measure the degree of hunting by Middle Stone Age hominids. However, the occurrence of relatively high numbers of *Raphicerus* with leopards and baboons in some layers is likely to have been associated, at least in part, with leopard activity, particularly at times when relatively large ungulates were not common in the palaeoenvironment and when the cave sites were not frequently occupied by hominids with control over fire. Binford's indices are re-assessed in the light of other indices which are designed to identify assemblages that have a relatively high probability of having been accumulated by leopards and/or other carnivores.

INTRODUCTION

Many factors can contribute to patterning observed in assemblages of faunal remains excavated from cave deposits (Brain 1981). Binford is one among many palaeo-anthropologists who have attempted to recognize a distinction between such contributing factors. In fact, his objective in examining faunal remains from the complex of caves at Klasies River Mouth (KRM) in South Africa (Klein 1976; Singer & Wymer 1982) was to learn something "relevant to the unambiguous recognition of scavenging versus hunting from archaeological bone assemblages" (Binford 1984: 17). Under the assumption that the agents of accumulation were hominids, he has attempted to quantify aspects of hominid behaviour on the basis of a "relationship between the frequency of Cape grysbok, considered as a hunted animal, and the eland, believed to be an unambiguous index to the role of scavenging" (Binford 1984: 236). Assuming that the bluebuck was another scavenged animal, he has also made use of an index based on the proportion of this antelope relative to grysbok in an attempt to quantify the degree of hunting *versus* scavenging. Changes in these indices (Binford 1984: figs 5.9 & 5.10) were interpreted as "a general shift in subsistence strategies, with increased hunting of small animals" (Binford 1986: 60).

Although *Raphicerus* (the genus to which grysbok as well as steenbok belong) may well have been hunted by Middle Stone Age (MSA) and Later Stone Age (LSA) hominids, a problem not closely examined by Binford is whether bones of these small antelope were also introduced to the cave by carnivores, including leopards and brown hyaenas which are known to prey on *Raphicerus* as well as other fauna. This problem is addressed here in relation to indices which have been designed to identify particular assemblages that have a high probability of having been accumulated, at least in part, by carnivores.

MATERIALS AND METHOD

This study is concerned primarily with faunal indices based on minimum numbers of individuals (MNI) of certain taxa cited in previously published reports of fauna from Klasies River Mouth as well as from Nelson Bay Cave, situated 100 km further west (Klein 1972, 1976). Carnivore/ungulate ratios, a "leopard index" (LI) and a generalised "leopard/brown hyaena index" (LBH) have been designed to facilitate the identification of certain assemblages that have relatively high probabilities of having been accumulated, at least in part, by carnivores. The proportion of *Raphicerus* in these assemblages is compared against corresponding values obtained from other assemblages, in an attempt to address the question as to whether grysbok/steenbok were accumulated, at least in part, by leopards or hyaenas. For purposes of standardisation, each of the faunal indices has been expressed relative to the total number of ungulates represented in each sample (ungulates being the most common taxa in all of the 26 assemblages under consideration).

CARNIVORE/UNGULATE RATIOS

The proportion of carnivores relative to ungulates represented in faunal assemblages from cave deposits has been used as a means of distinguishing carnivore lairs from human occupation sites (Brain 1981; Klein 1975; Thackeray 1979). Assemblages with high proportions of ungulates relative to carnivores appear to be associated primarily with hominid occupation;

Table 1. Minimum numbers of individuals of various taxa from Klasies River Mouth (KRM) and Nelson Bay Cave (NBC) (Klein 1972, 1976), used here as a basis for calculating various faunal indices (Table 2). UNG refers to the total number of ungulates and C refers to the total number of carnivores (except seals) in each sample. The minimum number of individuals of *Raphicerus campestris/Raphicerus melanotis* (steenbok/grysbok) in each assemblage is listed under R. Also listed are leopards (L), baboons (BAB), brown hyaenas (BH), small carnivores (SC) which are known to be items in the diet of brown hyaenas, and hyrax (H).

SITE	INDUSTRY	LEVELS	UNG	C	R	L	BAB	BH	SC	H
KRM 1	WILTON (LSA)	1-12	46	4	8	1	2	0	1	2
KRM 1	MSA IV	13	19	0	0	0	1	0	0	3
KRM 1	MSA II	14	95	13	21	4	3	1	6	15
KRM 1	MSA II	15	45	5	14	1	1	1	2	5
KRM 1	MSA II	16	73	8	5	1	1	1	3	15
KRM 1	MSA II	17a	49	5	6	1	0	0	3	3
KRM 1	MSA II	17b	39	4	3	2	0	0	1	6
KRM 1	MSA I	37	62	2	4	1	1	0	0	2
KRM 1	MSA I	38/39	45	1	0	0	0	0	1	2
KRM 1A	MSA III	1-9	32	3	4	1	2	0	1	13
KRM 1A	HOWIESONS POORT	10-11	26	1	1	0	0	0	1	4
KRM 1A	HOWIESONS POORT	13-16	21	1	6	0	2	0	0	4
KRM 1a	HOWIESONS POORT	17-21	33	3	2	0	1	0	3	4
KRM 1A	MSA II	22-27	25	1	1	0	0	0	0	4
KRM 1A	MSA II	28-34	28	0	5	0	0	0	0	4
KRM 1B	MSA 1	1-10	28	2	7	1	0	1	2	11
NBC	WILTON (LSA)	IC	41	6	21	1	0	0	4	20
NBC	WILTON (LSA)	BSC	36	11	14	2	0	0	8	27
NBC	WILTON (LSA)	RC	80	8	47	3	11	0	5	27
NBC	ALBANY (LSA)	J	24	3	7	1	0	0	2	6
NBC	ALBANY (LSA)	BSBJ	36	3	7	1	2	0	2	8
NBC	ALBANY (LSA)	CS	26	1	5	0	2	0	1	6
NBC	ALBANY (LSA)	GSL	30	1	3	0	1	0	1	7
NBC	ROBBERG (LSA)	BSL	23	0	1	0	2	0	0	5
NBC	ROBBERG (LSA)	YSL	42	4	4	0	2	1	3	25
NBC	ROBBERG (LSA)	YGL	31	0	5	0	1	0	0	14

Table 2. Faunal indices based on data presented in Table 1. (See text.)

SITE	INDUSTRY	LEVELS	RAP	C/U	LBH	MUB	LI	HYR	DVC
KRM 1	WILTON (LSA)	1-12	17,39	8,70	8,70	215	6,52	4,35	19,75
KRM 1	MSA IV	13	0,00	0,00	5,26	540	5,26	15,79	0,00
KRM 1	MSA II	14	22,10	13,68	14,74	574	7,37	15,79	56,84
KRM 1	MSA II	15	31,11	11,11	11,11	294	4,44	11,11	71,11
KRM 1	MSA II	16	6,85	10,96	8,22	628	2,74	20,55	41,10
KRM 1	MSA II	17a	12,24	10,20	8,16	336	2,04	6,12	42,86
KRM 1	MSA II	17b	7,69	10,26	7,69	656	5,13	15,38	30,77
KRM 1	MSA I	37	6,45	3,23	3,23	667	3,22	3,22	24,19
KRM 1	MSA I	38/39	0,00	2,22	0,00	606	0,00	4,44	28,89
KRM 1A	MSA III	1-9	12,50	9,38	12,50	430	9,37	40,62	37,50
KRM 1A	HOWIESONS POORT	10-11	3,85	3,85	3,85	685	0,00	15,38	15,38
KRM 1A	HOWIESONS POORT	13-16	28,57	4,76	9,52	227	9,52	19,05	33,33
KRM 1A	HOWIESONS POORT	17-21	6,06	9,09	12,12	484	3,03	12,12	33,33
KRM 1A	MSAII	22-27	4,0	4,00	0,00	656	0,00	16,00	32,00
KRM 1A	MSA II	28-34	17,86	0,00	0,00	443	0,00	14,28	67,86
KRM 1B	MSA 1	1-10	25,00	7,14	10,71	383	3,57	39,28	60,71
NBC	WILTON (LSA)	IC	51,22	14,63	14,63	121	4,88	48,78	51,22
NBC	WILTON (LSA)	BSC	38,89	30,56	30,56	181	8,33	75,00	38,89
NBC	WILTON (LSA)	RC	58,75	10,00	23,75	84	17,50	33,75	58,75
NBC	ALBANY (LSA)	J	29,17	12,50	12,50	140	4,17	25,00	29,17
NBC	ALBANY (LSA)	BSBJ	19,44	8,33	13,89	199	8,33	22,22	19,44
NBC	ALBANY (LSA)	CS	19,23	3,85	11,54	135	7,69	23,08	19,23
NBC	ALBANY (LSA)	GSL	10,00	3,33	6,67	243	3,33	23,33	10,00
NBC	ROBBERG (LSA)	BSL	4,35	0,00	8,70	253	8,69	21,74	4,35
NBC	ROBBERG (LSA)	YSL	9,52	9,52	14,29	265	4,76	59,52	9,52
NBC	ROBBERG (LSA)	YGL	16,13	0,00	3,23	298	3,22	45,16	16,13

conversely, sites with relatively low proportions of ungulates have been interpreted as carnivore lairs. An assemblage at Swartklip in the southern Cape is one example where a relatively high carnivore/ungulate ratio has been associated with hyaena rather than with hominid activity (Klein 1976). However, at Klasies River Mouth and other sites, the situation is complicated by the fact that hominids as well as carnivores may have occupied the same caves, although not necessarily at the same time.

There is considerable variability in the carnivore/ungulate (C/U) ratio calculated for assemblages from Klasies River Mouth as well as Nelson Bay Cave (Tables 1, 2). The index has been obtained by dividing the total number of carnivores (except seals) by the corresponding number of ungulates in each assemblage, and multiplying this quotient by 100 to express it on an arbitrary scale between 0 and 100:

$$C/U = \frac{\text{Number of carnivores}}{\text{Number of ungulates}} \times 100 \quad \text{.........................Equation 1}$$

Within the sequence of deposits at Cave 1 at Klasies, there is a general increase in C/U values from the oldest layers (38/39, thought to date to at least 120 000 B.P.), through to layer 14. A similar increase is observed in a sequence of assemblages in Cave 1A. At Nelson Bay Cave, there is also a general increase in the C/U ratio in a sequence of deposits spanning the end-Pleistocene and part of the Holocene. The highest value for this index has been obtained for layer BSC. Of all the samples listed in Table 1, this is the only assemblage having a C/U value comparable to that obtained for the inferred carnivore-lair assemblage at Swartklip (C/U = 28,93). The highest ratio at the Klasies cave complex is comparable to the value of 16,95 obtained from a cave assemblage at Herolds Bay in the southern Cape (Brink & Deacon 1981), thought to have been accumulated primarily by brown hyaenas as well as porcupines.

Since the probability of finding rare taxa in any assemblage is to some extent a function of sample size, and since carnivores are among the rare taxa in many of the assemblages at KRM as well as at NBC, one cannot rely on the C/U index as a means of quantifying the extent to which the relatively small-sized samples from KRM and NBC were accumulated by carnivores. Another limitation of the C/U index is that it does not serve to make a clear distinction between potential carnivore agents of accumulation. However, in the case of assemblages from KRM and NBC, the problem of recognizing carnivore activity deserves attention since assemblages with relatively high C/U ratios, potentially associated with some degree of carnivore activity, also have high percentages of *Raphicerus* (Table 2). The question arises as to which, if any, carnivore species may have contributed to the accumulation of *Raphicerus*. This problem is addressed by first considering predation patterns of leopards.

LEOPARDS

Brain (1981) has drawn attention to the fact that antelopes such as reedbuck and impala (within Brain's size class II) have been frequently reported in observed leopard kills in savanna environments. However, Pienaar (1969) has stated that "in the absence of large mammalian fauna, leopards revert to a diet of smaller fauna." They will prey upon baboons (*Papio ursinus)* and hyrax (*Procavia capensis*) when these animals are relatively abundant and when other (larger, preferred) fauna are not available. A recent study of scats recovered from areas in the southern and western Cape (Norton *et al.*, 1986) has indicated that hyraxes are the most important prey items of leopards in the corresponding regions, and small antelope (including *Raphicerus* and rhebok, *Pelea capreolus)* are also preyed upon where these ungulates occur.

Raphicerus melanotis (grysbok) is relatively common in "fynbos" regions of the southern Cape Province, where larger ungulates more usually associated with savanna do not occur. Leopards in these more southern regions are generally much smaller than leopards from other (savanna) areas to the north. For example, the mean mass of male individuals in Zimbabwe is 59,7 kg, contrasting with a corresponding value of only 30,9 kg in the Cape Province (Smithers 1984: 370). This difference may be related to the availability of prey, apart from other factors.

In the light of what is known about leopard behaviour patterns, one would expect that assemblages accumulated solely by leopards would be characterized by having relatively high proportions of ungulates of size class II, unless these samples accumulated under conditions when animals of this size were not available. Under such conditions, one would expect to find higher proportions of smaller fauna, including antelopes of size class I. Assemblages with leopards, baboons and relatively high proportions of small ungulates could therefore relate to periods when larger ungulates were not common in the original environment in the vicinity of a site, and when leopards turned to animals on the smaller side of the range of animals preyed upon by these carnivores.

Changes in the relative abundance of ungulates of different sizes can be quantified by means of an index which has been termed "mean ungulate bodymass" (MUB), referring to the mean mass of ungulates represented in an assemblage or community (Thackeray 1977, 1980). The same index has been used by Vrba (1976) in her assessment of cave assemblages at sites in the Sterkfontein valley, including Swartkrans where leopards and other agents are known to have contributed to the accumulation of faunal remains. In that study, assemblages associated primarily if not entirely with leopard activity were characterized by relatively low MUB values, indicative of assemblages with a higher proportion of small ungulates (notably antelope of Brain's size class II). The evidence from Swartkrans suggests that at least some hominids (*Australopithecus robustus*)

were likely to have been the victims of leopard predation (Brain 1970, 1981). In the case of Klasies and Nelson Bay Cave, it is entirely possible that the assemblages were accumulated in part if not entirely by *Homo sapiens*, but the main issue addressed here is whether there is any basis for suggesting that leopards contributed to the accumulation of assemblages which include *Raphicerus*.

LEOPARD ACTIVITY AT KLASIES RIVER MOUTH?

Leopards are represented in several of the faunal assemblages from Klasies River. Articulated remains of an almost complete skeleton of a leopard were found in Cave 1 (Singer & Wymer 1982: 15), suggesting that at least some leopards died in the cave. Hendey & Volman (1986) suggested that the individual represented by an articulated skeleton may have died as a result of a landslide.

Layer 14 in Cave 1 does not have any evidence of extensive hearth features, although "occasional small lumps of charcoal and numerous flecks were recovered" (Singer & Wymer 1982: 14). The same layer yielded the highest number of leopard individuals at Klasies. Leopards are also represented in adjacent layers which contain limited evidence of prehistoric fire. By contrast, no leopards were represented in the Howiesons Poort layers which are characterised by numerous hearth features. On the basis of these observations, one may suggest that the probability of leopards occupying a site at Klasies was inversely proportional to the extent to which it was occupied by hominids having control over fire.

The occurrence of abundant stone artefacts in most of the Klasies deposits attests to occupation of the cave complex by hominids. Recent excavations at Caves 1 and 1A have shown that relatively high concentrations of stone artefacts occur in layers associated with the Howiesons Poort Industry. The apparent absence of leopards in these layers, having high concentrations of artefacts, is another potential indication of an inverse relationship between the extent to which hominids and leopards made use of the cave.

In some instances leopards are represented together with bones of baboons in the Klasies cave deposits (Table 1). As noted above, leopards are known to prey upon these primates. Although other agents may also have been responsible for the accumulation of baboon remains, the occurrence of leopards and baboons in the same layers at Klasies is strongly suggestive of leopard occupation, as in the case of certain assemblages at Nelson Bay Cave (Klein 1976).

At Klasies, the abundance of leopards and baboons varies in relation to the number of ungulates from layer to layer. For example, some layers have neither leopards nor baboons, while others (notably layer 14) have relatively high numbers of baboons together with leopards (Table 1). Such changes have been quantified by means of a "leopard index" (LI), calculated by summing together the minimum numbers of individuals of leopards and baboons represented in an assemblage, standardising this figure in relation to the total number of ungulates in the same sample:

$$LI = \frac{[MNI \text{ (leopards)} + MNI \text{ (baboons)}] \times 100}{MNI \text{ (ungulates)}} \quad \text{.........Eq.2}$$

Since the sample sizes of leopards and baboons are so small in each of the archaeological samples, it is not intended that the LI index should be regarded as an accurate measure of the degree to which leopards may have contributed to the accumulation of faunal remains in the cave deposits. However, the LI index is used here simply to identify certain assemblages which have a relatively high probability of having been accumulated, at least in part, by leopards.

The faunal assemblage from Layer 14 at Klasies River has a relatively high LI value, and the same assemblage includes relatively high proportions of *Raphicerus*. Bones from Layer 14, examined for damage that might have been inflicted by leopards or other carnivores, included a distal humerus of a baboon. This specimen has a pair of puncture marks, both 5 mm in diameter. If they were made simultaneously, they could have been caused by carnivore canines (upper or lower) with tips separated by a distance of about 29 mm, corresponding closely to bone damage to a hominid parietal from Swartkrans (SK54), which has a pair of holes (each 6 mm in minimum diameter) separated by about 33 mm, and which are thought to have been caused by a leopard (Brain 1970).

An arbitrary LI value of 4,5 divides the 26 assemblages listed in Table 2 into two equal groups: those having values less than this figure, and others having LI values greater than or equal to 4,5. Those faunal assemblages with "high" indices (LI > 4,5) have been compared against ones with "low" values (<4,5). Particular attention is directed at the relative abundances of *Raphicerus* and at variability in the size distribution of ungulates represented in these two groups of assemblages. However, before attempting to make behavioural inferences on the basis of such comparisons, it is necessary to examine whether the two groups of assemblages reflect a different range of ungulate fauna (potentially associated with different palaeo-environmental conditions), and whether the two groups consist of assemblages of similar sample sizes.

Ungulates are consistently the most common taxa in both groups of assemblages. Although samples vary in size, the range of variability in this parameter is similar within the two groups. The mean size of ungulate samples from assemblages associated with high LI values (LI > 4,5) is 41,23, with a corresponding standard deviation (σ) of 22,42 (n = 13 assemblages). This result is almost identical to the mean sample size of 38,38 (σ = 15,45) obtained for the 13 assemblages associated with low probabilities of having been accumulated by

PROBABILITY OF
CARNIVORE ACTIVITY
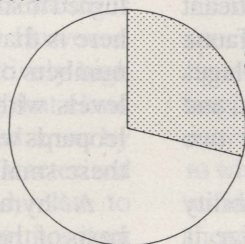
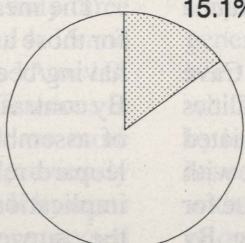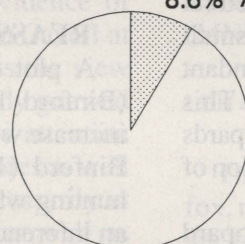28.9% *Raphicerus*

HIGH

LI ≥ 4.5 AND LBH ≥ 9.0

15.1% *Raphicerus*

INTERMEDIATE

LI ≥ 4.5 OR LBH ≥ 9.0

8.6% *Raphicerus*

LOW

LI < 4.5 AND LBH < 9.0

Figure 1.   Pie-charts illustrating increase in the proportion of *Raphicerus* in faunal assemblages from Klasies River mouth corresponding to an increase in probability of carnivore related activity.

leopards (LI < 4,5).

In order to test whether the two sets of assemblages represent fauna from different kinds of palaeo-environments, comparisons have been made between faunal indices reflecting the proportion of taxa associated with a high degree of vegetation cover (one of the most important parameters influencing the distribution and abundance of ungulates in modern African environments (Greenacre & Vrba 1984)). Such an index, potentially associated with the degree of vegetation cover, has been called DVC. It has been calculated by summing the MNI values of kudu, eland, bushbuck and *Raphicerus* together, then expressing this sum as a percentage of the total number of ungulates in each sample. High DVC values have been obtained for several assemblages from Nelson Bay Cave and the Klasies River cave complex. Within the Nelson Bay sequence, the increase in DVC from the Last Glacial Maximum to the Holocene is likely to have been associated with an environmental change from

grassland to fynbos habitats (Klein 1972), though behavioural factors can also have contributed to changes in the relative abundance of fauna represented in the cave deposits. At Klasies River Mouth, there is an increase in DVC within the Late Pleistocene sequence in Cave 1. Such changes may be associated with Late Pleistocene environmental factors comparable to those affecting fauna during the end-Pleistocene and Holocene at Nelson Bay Cave (Klein 1972), though in both cases behavioural factors (including leopard predation) can have contributed to variability in the relative abundance of *Raphicerus* and other fauna represented in these cave sequences.

The mean DVC index obtained for 13 assemblages associated with a high probability of having been accumulated by leopards (LI > 4,5) is 29,18 (σ = 19,26). A slightly higher mean DVC value of 36,36 (σ = 19,76) has been calculated for the 13 assemblages associated with low LI values. In relation to the almost identical but

relatively large standard deviations (reflecting a similar range of variation in the proportions of bush-loving fauna represented in both sets of assemblages), the difference in mean DVC values obtained for these two groups of assemblages is negligible. There is no significant difference in the proportions of bush-loving fauna represented in the two groups. Both contain assemblages with high (as well as low) values of the DVC index, and the variation in DVC is almost identical in the two groups.

An implication of these results is that variability associated with different habitats and sample size is sufficiently controlled for purposes of making comparisons between the two groups of assemblages, with the objective of identifying behavioural processes that might have contributed to differences in the composition of fauna represented in the two groups.

Taking results from Klasies and Nelson Bay Cave together, one finds that assemblages with high probabilities of leopard-related predation are generally associated with relatively low MUB values in comparison with other samples in this analysis. The mean MUB value for samples with high values of the LI index is 298 kg. By contrast, assemblages grouped together on the basis of low values of the same index have a mean MUB value of 451 kg. In other words, for those assemblages associated with a high probability of having been accumulated (at least in part) by leopards, one finds that relatively small ungulates (including *Raphicerus*) are more abundant than they are in the other group of assemblages. This observation is compatible with the suggestion that leopards were responsible, at least in part, for the accumulation of assemblages associated with high LI values.

There is no strong correlation between the "leopard index" and the percentage of *Raphicerus* (RAP, calculated in relation to the total number of ungulates in each assemblage), but a correlation need not be expected, considering that grysbok and steenbok may have been preyed upon by hominids, leopards as well as other agents of accumulation which occupied the same sites at different times. However, for assemblages with high LI values, the mean value of the percentage occurrence of *Raphicerus* is relatively high (22,28%), contrasting with a corresponding value of 12,98% calculated for assemblages with low LI values.

Together these observations support the suggestion that leopards contributed to the accumulation of remains of *Raphicerus* in Klasies River cave deposits, notably in those samples characterised by high LI values. However, this suggestion does not discount the possibility that other agents of accumulation may also have been responsible for their accumulation.

TEST IMPLICATIONS

As noted above, leopards have preferences for ungulates of size class II (e.g. springbok and impalas) when animals of this size class are available. If leopards really were responsible for the accumulation of *Raphicerus* in

the Klasies cave deposits (notably those characterized by high LI values), one would expect that they were doing so under conditions when larger fauna were not abundant in the palaeo-environment, and when they turned to small game (cf. Pienaar 1969). A test implication here is that one might expect to find an increase in the numbers of hyrax and/or other small fauna in the very levels with relatively high numbers of *Raphicerus*, *if* leopards were in fact contributing to the accumulation of these small prey items.

A "hyrax" (HYR) index has been calculated on the basis of the number of individuals of *Procavia capensis* expressed as a percentage of the total number of ungulates represented in each assemblage. Values of this HYR index are listed for each assemblage in Table 2.

The mean HYR value of 30,39% has been obtained for those assemblages which have a high probability of having been accumulated, at least in part, by leopards. By contrast, the corresponding value for the other group of assemblages (associated with a low probability of leopard-related predation) is only 18,15%. The test implication is thus upheld, providing further support for the suggestion that leopards contributed to the accumulation of *Raphicerus* in assemblages with high LI values under conditions when relatively larger animals were not abundant in local palaeoenvironments.

REASSESMENT OF BINFORD'S INDICES

A plot of changes in the grysbok/bluebuck index (Binford 1984: fig. 5.9) shows an apparent general increase within part of the Cave 1 sequence of deposits. Binford (1984: 234) regards this as "a measure of hunting when biome is held constant". However, such an inference is questionable, not only because grysbok may have been introduced to the site by leopards and/or other carnivores, but also because these small antelope are generally associated with relatively closed habitats while the historically extinct bluebuck was evidently associated with grassland habitats more open than situations preferred by other (extant) Hippotraginae (roan and sable) (Klein 1974). Although both grysbok and bluebuck occurred in "fynbos", as noted by Binford, this certainly does not imply that the ratio based on the relative abundance of these two taxa necessarily holds "biome constant".

Various factors, including carnivore predation, may have contributed to variability in the proportion of grysbok relative to eland. According to Binford (1984: figure 5.10), the grysbok/eland index (standardised on a percentage scale) increases from less than 30% in the basal MSA I layers of Cave 1 to more than 50% above layer 17a; the highest value is shown in excess of 80% for layer 15. Although there are errors in his graph of changes in this index (in actual fact, the index is only 58,3% for layer 15 and it is *less* than 50% for *all* the underlying layers in Cave 1), Binford is correct in showing that layers 14 and 15 have the highest numbers of grysbok relative to eland in the Cave 1 sequence of

Late Pleistocene assemblages. According to Binford, the high number of grysbok relative to eland in layer 15 would be interpreted in terms of hominid behaviour, specifically in terms of a period when hunting reached its climax within the Cave 1 sequence of assemblages associated with Middle Stone Age layers. However, since layer 15 as well as layer 14 have relatively high values of the "leopard index", and knowing that eland fall outside the size range of antelope preyed upon by leopard, one may suggest that these layers (characterized by relatively low numbers of eland) could relate to periods when leopards played a relatively more important role in the accumulation of faunal assemblages in Cave 1.

BROWN HYAENAS

Klein (1976) recorded brown hyaenas in only three layers in Cave 1 at Klasies, notably in layers 14, 15 and 16. No specimens were reported from Caves 1A or 1B. Their apparent absence may be related to differences in the nature of the sites. Caves 1A and 1B are more exposed to the elements, and have in fact been previously referred to as "shelters" rather than as caves. If hyaenas used the sites to rear their cubs, one might have expected that there was a higher probability of their choosing Cave 1, rather than 1B or 1A on account of the greater degree of cover and seclusion.

As noted by Binford (1984) there is evidence of carnivore damage on bones of ungulates from Cave 1 at Klasies River. There is no reason to dismiss the view that hominids transported some bones already gnawed by carnivores to the cave deposit, but close attention should be given to the possibility that carnivores as well as hominids utilized the same sites (not necessarily at the same time), and that both carnivores as well as hominids contributed to the accumulation of material in the deposits.

Primarily scavengers, brown hyaenas can account for the accumulation of bones of many different kinds of animals, ranging in size from small mammals to very large ungulates. Adults are known to rear their cubs on baboons as well as small carnivores such as bat-eared fox, honey badger and mongooses. Indeed, Brain (1981: 80) said "I suspect that cub-rearing brown hyaenas purposely select small carnivores and, in some areas, primates as food for young cubs, since their skeletons are more crunchable than those of bovids of the same size". The fact that baboons are also a component of the diet of brown hyaenas raises the question as to whether the LI index is necessarily a good reflection of leopard predation rather than that of other carnivores, including brown hyaenas. However, it is apparent that baboons tend to occur with leopards more frequently than they do with hyaenas in the archaeological assemblages listed in Table 1, suggesting that these primates may have been more frequently associated with leopard predation in at least some contexts.

One of the differences between predation patterns of leopards and those of brown hyaenas is that small carnivores (including bat-eared boxes) are an important component in the diet of brown hyaenas (Mills 1974; Mills & Mills 1977) whereas they do not appear to be as common in reports of leopard predation (Brain 1981). There may be some degree of overlap in the range of species included in the diets of leopards and brown hyaenas, particularly under conditions when large ungulates are not common in an environment, and it may be difficult if not impossible to resolve the extent to which leopards and brown hyaenas contributed to the accumulation of faunal remains in cave deposits such as those in certain layers at Klasies and Nelson Bay Cave. (The fact that both carnivores are represented in some levels, notably layers 14, 15 and 16 in Cave 1 at Klasies, raises the question of competition between hyaenas and leopards in relation to the use of the site). However, a generalised "leopard/brown hyaena index" (LBH) has been generated in an attempt to identify assemblages which have a high probability of having been accumulated by leopards and/or brown hyaenas. The index has been based on the occurrence of these carnivores together with animals that are known to be important in the diet of one or other or both of these large carnivores. It has been calculated from the minimum numbers of individuals of leopards (MNI:L), brown hyaenas (MNI: BH), small carnivores (MNI:SC), and baboons (MNI: BAB), standardized in relation to the total number of ungulates (MNI: UNG) in each assemblage:

$$LBH = \frac{(MNI:L + MNI:BH + MNI:SC + MNI:BAB \times 100}{MNI:UNG} \quad \ldots\ldots\text{Equation 3}$$

The "small carnivore" category includes bat-eared fox, mongooses, honey badger and caracal, all of which are known to be items in the diet of brown hyaenas.

An arbitrary LBH value of 9 divides the assemblages listed in Table 2 into two equal groups: firstly, those having a relatively high probability of having been accumulated by leopards and/or brown hyaenas (i.e. assemblages having LBH values greater than or equal to 9,0), and secondly, those with a lower probability of having been accumulated by these agents (such assemblages are distinguished by having LBH values less than 9,0). As in the case of LI indices, the sample sizes of ungulates in the two groups of assemblages are almost identical. However, comparing the relative abundance of *Raphicerus* (RAP) in these two groups, one finds that assemblages with high LBH values generally have relatively high proportions of *Raphicerus*. This is reflected by the mean RAP value of 27,04% for 13 assemblages with a high probability of having been accumulated by leopards and/or brown hyaenas; by contrast, *Raphicerus* is generally much less common in the 13 assemblages with a lower probability of having been accumulated by these agents (the mean RAP value for this group is only 8,22%). An inference drawn from this contrasting situation is that *Raphicerus* could have been introduced to certain of the Klasies assemblages as a result of carnivore activity.

PROBABILITIES OF CARNIVORE ACTIVITY BASED ON LI AND LBH VALUES

Values of the "leopard index" (LI) and the generalized "leopard/brown hyaena index" (LBH) calculated in this study can be used together to show that the percentage occurrence of *Raphicerus* in certain assemblages increases in relation to the probability of an assemblage having been accumulated, at least in part, by leopards and/or hyaenas. Figure 1 indicates that the mean percentage occurrence of *Raphicerus* is relatively very low (RAP = 8,6%) for the group of nine assemblages which have low LI as well as low LBH values. By contrast, the mean percentage occurrence of *Raphicerus* is relatively high (RAP = 28,9%) for the group of nine assemblages associated with high LI and high LBH values. An intermediate mean percentage occurrence of *Raphicerus* (RAP = 15,1%) has been calculated for the eight assemblages with high LI or high LBH values. The progressive increase in mean percentage occurrence of *Raphicerus* in this set of assemblages corresponds to an increase in the probability of assemblages having been accumulated by leopards and/or brown hyaenas (Fig. 1).

How do these changes relate to the DVC index, calculated from proportions of fauna which generally prefer closed environmental conditions (Table 1)? The mean DVC value of 31,2% calculated for assemblages associated with low LI and low LBH values (cf. a "low" probability of carnivore activity) is only slightly different from the corresponding value of 33,0% obtained for assemblages associated with an "intermediate" probability of carnivore-related activity (Fig. 1). Assemblages with high LI and high LBH values have a mean DVC value of 38,3%. The scale of variation in mean DVC is thus very small relative to the scale of variation in the mean proportions of *Raphicerus* in assemblages associated with "low", "intermediate" and "high" probabilities of carnivore activity, based on LI and LBH values. The threefold increase in proportions of *Raphicerus*, from 8,6% for assemblages with a low probability of carnivore activity, to 28,9% in assemblages with a high probability of such activity, contrasts with a relatively small increase in mean DVC (from 31,2% to 38,2%), reflecting changes in the proportions of bush-loving fauna represented in the corresponding assemblages. It is therefore unlikely that the major increase in *Raphicerus* in particular assemblages (notably those here associated with a high probability of carnivore activity) is simply a function of environmental changes of the kind associated with a shift from open grassland to closed habitats.

CONCLUSION

Binford's interpretation of faunal remains from Klasies has been based in part on an assumption that *Raphicerus* was hunted by hominids, and on an assumption that proportions of *Raphicerus* relative to other ungulates could be used as an unambiguous index of human behaviour. However, this study has drawn attention to the fact that his indices based on *Raphicerus* and other ungulate fauna represented at Klasies do not unambiguously reflect hominid behaviour.

If grysbok were introduced by leopards and/or other agents at Klasies River Mouth, as suggested from this study, it follows that neither Binford's grysbok/eland index nor his grysbok/bluebuck ratio can be used unambiguously as a reflection of the degree of hunting by hominids in prehistory.

The suggestion that carnivores contributed to the accumulation of remains of *Raphicerus* and other fauna represented in cave deposits in the southern Cape is strengthened by various observations. Carnivore-ungulate ratios which have previously been used to distinguish between hominid and carnivore agents of accumulation are relatively high in assemblages for which the mean percentage occurrence of *Raphicerus* is also relatively high. The pair of puncture marks on a baboon humerus, from an assemblage with a high carnivore-ungulate ratio and a high LI index (and a relatively high proportion of *Raphicerus*), strongly suggests leopard activity.

Recent studies have indicated that leopards prefer ungulates of the size of springbok, but will turn to hyrax and other small fauna under conditions when springbok-sized fauna are not available. This study of fauna from Klasies River has drawn attention to the fact that hyraxes are generally more abundant in the very assemblages with relatively high proportions of *Raphicerus*, leopards and baboons. An inference drawn here is that these assemblages were accumulated, at least in part, by leopards during periods when larger fauna were not abundant in the local palaeoenvironment.

The fact that high proportions of leopards and baboons occur in the very assemblages with low artefact concentrations and limited evidence for fires suggests that leopards and baboons made use of the caves (not necessarily intensive use) during periods when people did not frequently occupy the sites. It is apparent that the same periods included intervals when local palaeo-environments supported populations of small fauna (including *Raphicerus*). Notably, in assemblages BSC and RC at Nelson Bay Cave, and in assemblages from layers 14 and 15 at Klasies River Mouth, relatively high proportions of leopards and baboons coincide with high proportions of *Raphicerus*.

Leopards need not have been the only agent contributing to the accumulation of faunal remains of *Raphicerus* and other animals in cave deposits at Klasies River Mouth. However, the evidence presented here, taken together, strongly supports the suggestion they were among a number of agents that contributed to the accumulation of faunal assemblages, notably those from layer 14 and 15 at Klasies River Mouth, and levels BSC and RC at Nelson Bay Cave.

As suggested by Binford (1984), Middle Stone Age hominids could have scavenged bones of ungulates killed by carnivores. Did the hominids at Klasies scavenge leopard kills, and is it possible to resolve the extent to which hominid behaviour as opposed to other behavioural

as well as non-behavioural factors contributed to observed patterning in faunal assemblages from the cave deposits? Certainly these are challenging questions, but indications from this study are that the situation at Klasies is likely to have been more complex than Binford realised. Carnivore activity is likely to have been a significant component which cannot be ignored, and which deserves to be studied further.

REFERENCES

BINFORD, L.R. 1984. *Faunal remains from Klasies River Mouth*. New York: Academic Press

BINFORD, L.R. 1986. Reply to comments by R. Singer and J. Wymer. *Current Anthropology* 27:57-62.

BRAIN, C. K. 1970. New finds at the Swatkrans australopithecine site. *Nature* 225:1112-19.

BRAIN, C.K. 1981. *The hunters or the hunted? An introduction to African Cave Taphonomy*. Chicago: University of Chicago Press.

BRINK, J.S. & DEACON, H.J. 1981. A study of a Last Interglacial shell midden and bone accumulation at Herolds Bay, Cape Province, South Africa. *Palaeoecology of Africa* 15:31-39.

GREENACRE, M.J. & VRBA, E.S. 1984. Graphical display and interpretation of antelope census data in African wildlife areas, using correspondence analysis. *Ecology* 65: 984-997.

HENDEY, Q.B. and VOLMAN, T.P. 1986, Last Interglacial sea levels and coastal caves in the Cape Province, South Africa. *Quaternary Research* 25: 189-198.

KLEIN, R.G. 1972. The late Quaternary mamalian fauna of Nelson Bay Cave (Cape Province, South Africa); its implications for megafaunal extinctions and environmental and cultural change. *Quaternary Research*. 2:135-142.

KLEIN, R.G. 1974. On the taxonomic status, distribution and ecology of the blue antelope, *Hippotragus leucophaeus* (Pallas 1766). *Annals of the South African Museum* 65: 99-143.

KLEIN, R.G. 1975. Palaeaonthropological implications of the nonarchaeological bone assemblage from Swartklip 1, south-western Cape Province, South Africa. *Quaternary Research* 5:275-88.

KLEIN, R.G 1976. The mammalian fauna of the Klasies River Mouth sites, southern Cape Province, South Africa. *South African Archaeological Bulletin* 31: 75-98.

MILLS, M.G.L. 1974. Brown hyaena in the Kalahari Gemsbok National Park: Ecology. *World Wildlife Yearbook 1973-4*: 140-48.

MILLS, M.G.L. and MILLS M.E.J. 1977. An analysis of bones collected at hyaena breeding dens in the Gemsbok National Parks (Mammalia: Carnivora). *Annals of the Transvaal Museum* 30: 145-55.

NORTON, P., LAWSON, A.B., HENLEY, S.R. and AVERY, G. 1986. Prey of leopards in four mountainous areas of the south-western Cape Province. *South African Wildlife Research*. 16: 47-52.

PIENAAR, U. DE V. 1969. Predatory-prey relationships amongst the larger mammals of the Kruger National Park. *Koedoe* 12: 108-187

SINGER, R. and WYMER, J. 1982. *The Middle Stone Age at Klasies River Mouth in South Africa*. Chicago: University of Chicago Press.

SMITHERS, R.H.N. 1984. *The Mammals of the Southern African Subregion*. University of Pretoria, South Africa.

THACKERAY, J.F. 1977. *Towards a clarification of the extent to which environmental change contributed to Terminal Pleistocene extinctions*. Unpublished MSc. thesis, University of Cape Town, Cape Town.

THACKERAY, J.F. 1979. An analysis of faunal remains from archaeological sites in southern South West Africa (Namibia). *South African Archaeological Bulletin* 34: 18-33.

THACKERAY, J.F. 1980. New approaches in interpreting archaeological faunal assemblages with examples from southern Africa. *South African Journal of Science* 76: 216-23.

VRBA, E. 1976. The fossil Bovidae of Sterkfontein, Swartkrans and Kromdraai. Mem. Transvaal Museum, No. 21.