

New Approaches in Interpreting Archaeological Faunal Assemblages with Examples from Southern Africa

J. F. Thackeray

Anthropology Department, Yale University, Box 2114, Yale Station, New Haven, Connecticut 06520, U.S.A.

Faunal relationships in contemporary ecosystems have been analysed with a view to interpreting the significance of faunal assemblages at archaeological sites. Preservational bias against small fauna, selective predation, and environmental changes are considered, with examples being given for several sites in Southern Africa. It is shown that the extinction of certain ungulates may have happened before the Terminal Pleistocene, possibly at the hands of Middle Stone Age peoples and other predators. Palaeoenvironmental data are required to determine the extent to which environmental changes may have contributed to the extinctions recorded for the Terminal Pleistocene.

Faunaverwantskape in hedendaagse ekosisteme is ontleed met die oog op 'n vertolking van die betekenis van faunaversamelings op argeologiese terreine. Die neiging dat minder klein fauna behoue bly, selektiewe jag deur roofdiere, en omgewingsveranderings word oorweeg, en voorbeelde word gegee wat van verskeie terreine in Suider-Afrika afkomstig is. Daar word aangetoon dat die uitsterwing van sekere hoefdiere voor die Eind-Pleistoseen kon voorgekom het, moontlik deur die toedoen van mense van die Middel-Steentyd en roofdiere. Gegewens oor die paleoömgewing is nodig om te bepaal in watter mate omgewingsveranderings bygedra het tot die uitsterwing wat vir die Eind-Pleistoseen gevind is.

The analysis of faunal assemblages from archaeological sites is of interest not only in assessing how human populations have adapted to changing environments, but also in deducing how faunal communities have become modified through time. Interpreting archaeological faunal assemblages is difficult because many factors may contribute to the accumulation of material in the deposits. The nature and importance of these factors may be hard to identify. One possible approach in reconstructing the dynamic nature of palaeo-communities is to use analyses of modern counterparts to establish relationships that throw light on those in the past. Studies of contemporary communities (which are undertaken in the context of whole ecosystems) and of archaeological faunal assemblages (which are based on relatively long-term successions) can contribute mutually to evolutionary ecology and palaeo-anthropology.

This paper aims to describe some of the environmental factors that are important in determining the composition of faunal communities, using census data for modern ungulates in South West Africa/Namibia.¹ It also makes use of results from recent analyses of faunas from archaeological sites in Southern Africa, and indicates the potential that modern environmental and faunal studies have for the interpretation of ancient assemblages. As there are sampling uncertainties in the modern and archaeological data, emphasis is given here to the identification of general trends for several variables, rather than to obtaining

exact relationships. Particular attention is given to Terminal Pleistocene extinctions, first documented in Southern Africa by Klein.² The interpretation of these extinctions is difficult on account of the multiplicity of factors which may have been responsible. While both environmental and cultural influences may have been important, we can attempt to resolve this issue by quantifying the environmental variables (for example temperature and rainfall) involved; these are more amenable to quantification than behavioural factors, such as predation. This approach may eventually enable us to obtain an indirect assessment of the extent to which predation by human and/or carnivores contributed to these extinctions.

Modern faunal communities in South West Africa/Namibia

A census of large mammals in 16 districts in South West Africa/Namibia was undertaken by Joubert and Mostert.¹ These were distributed in northern, central, and southern S.W.A., and varied in area from approximately 20 000 to 60 000 km². Despite the uncertainties and limitations of this census, the data provide useful information on distribution patterns, relative abundances and species diversity.

The faunal and floral communities are greatly influenced by rainfall and temperature, the former being particularly important in the dry southern region. Rainfall is less than 50 mm/yr in the Namib, increasing towards the north-east, which receives more than 500 mm/yr. Giess³ distinguishes several vegetation types within three main vegetation zones: desert in the west and south, savannas in the central areas, and woodland savannas in the north-east. Estimates of primary production (dry plant biomass expressed in terms of kilograms per hectare) have been

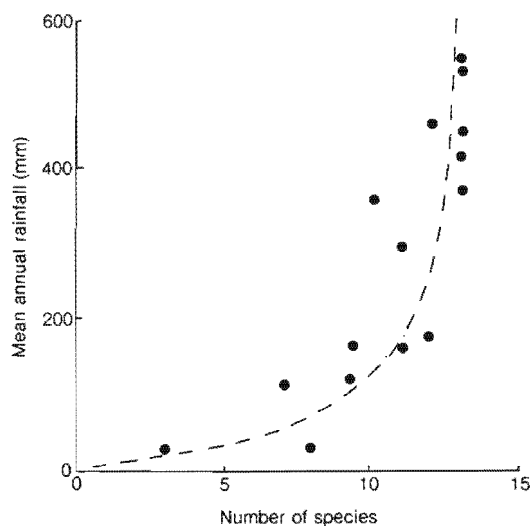


Fig. 1. Relationship between mean annual rainfall and species diversity for modern faunal communities in South West Africa/Namibia.

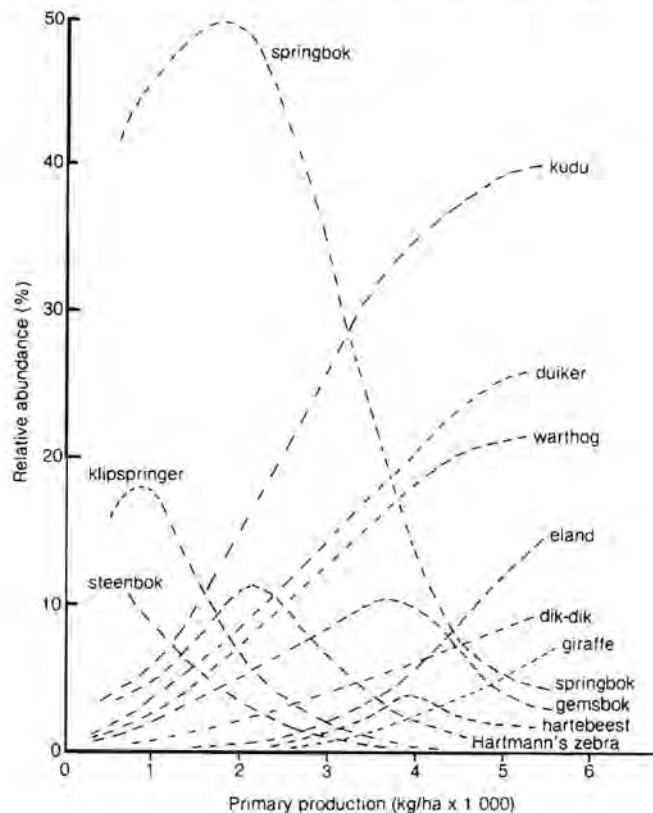


Fig. 2. Changes in relative abundances of 13 ungulate species along a gradient in primary production in S.W.A. These relationships have been interpolated from data for 16 districts. The strongest relationships are obtained for kudu ($r = 0.9$) and springbok ($r = -0.9$).

given by Rutherford.⁴ These indicate that primary production increases from the south-west to the north-east of S.W.A., and is strongly correlated with mean annual rainfall ($r > 0.9$).

The term 'modern faunal community' here refers to the large ungulates investigated in ref. 1. Census data indicate that the number of species in each community is highest in the north of the territory and depends on rainfall (Fig. 1). (A close correlation between species number and mean annual rainfall has been reported for mammal communities in South Africa⁵ and North America.⁶) The number of species in ungulate communities increases from the desert regions of S.W.A. as far as the mixed savanna areas, which receive 300 mm/yr; for regions which receive more than 300 mm/yr, there appears to be a levelling off in the number of species. Simpson⁶ suggested that the diversity of species in a community is not determined by rainfall alone; temperature and topography may also be important. However, the influence of temperature in limiting the distribution of species is particularly important in southern S.W.A. where cloud cover is minimal, especially during the summer months when temperatures can exceed 30°C. The influence of topography on faunal distribution in the Namib has been described by Coetzee.⁷

Perhaps the clearest indication of diversity can be obtained not through the calculation of summary statistics (e.g. Shannon-Wiener indices), but rather through visual inspection of the available data. Figure 2 illustrates changes in community composition and relative abundances of ungulate species along a gradient of primary production. The primary production estimates are based on rainfall data for localities in S.W.A. obtained from the Windhoek weather office (Mare, pers. comm.), using the relationship between mean annual rainfall and primary production established by Rutherford.⁴ The graphs in Fig. 2 represent the 'best fit' (obtained by visual inspection) for the data along a north-south gradient in primary production. Major

sources of uncertainty for these graphs include variability in primary production within each district, as well as the sampling method. Despite these uncertainties, the graphs can be considered to reflect general trends for the wide area under consideration (over 400 000 km²). It is apparent from these relationships that in regions of low primary production the species diversity is low, and small antelope (primarily springbok and klipspringer) are dominant. As one moves into regions of greater primary production, the relative abundances of springbok and klipspringer decrease while those of other species increase. These changes are accompanied by an increase in the number of species, including relatively large animals. In the northern regions where primary production is in excess of 3 000 kg/ha, the kudu is the dominant mammal.

Community composition naturally also depends on habitat. The predominant species in the southern and central regions of the country is the springbok, a grazer. The most important mammals in the north of the territory are primarily browsers and include kudu and giraffe.

Predictive value of modern relationships

Since it is not feasible to determine the catchment area from which archaeological faunal assemblages are derived, it is impossible to deduce the carrying capacity of a palaeo-environment on the basis of archaeological fauna. However, Thackeray⁸ has adopted an index which was considered to be an indirect estimate of carrying capacity in modern contexts, expressed in units that are independent of area. This index is termed the 'Mean ungulate bodymass' (M.U.B.), the mean mass of an ungulate in its community. (Carrying capacity is a theoretical concept which usually refers to the maximum number of individuals of a given species that can be supported in an area; it is used here to apply to populations of several species, and is considered to be a function of primary produc-

Table 1. Adult bodyweights of various species (in kg) used in the calculation of M.U.B.

<i>Madoqua</i> sp.	5
<i>Cephalophus</i> sp.	7
<i>Oreotragus</i> sp.	13
<i>Raphicerus</i> sp.	14
<i>Sylvicapra</i> sp.	16
<i>Ourebia ourebi</i>	17
<i>Pelea capreolus</i>	25
<i>Redunca fulvorufula</i>	25
<i>Antidorcas</i> sp.	35
<i>Ovis</i> sp.	35
<i>Phacochoerus</i>	50
<i>Aepyceros</i> sp.	52
<i>Potamochoerus</i> sp.	55
<i>Tragelaphus scriptus</i>	55
<i>Damaliscus</i> sp.	56
<i>Redunca arundinum</i>	75
<i>Tragelaphus angasi</i>	102
<i>Damaliscus lunatus</i>	137
<i>Alcelaphus caama</i>	139
<i>Connochaetes gnou</i>	170
<i>Bos</i> sp.	180
<i>Oryx</i> sp.	210
<i>Kobus</i> sp.	215
<i>Tragelaphus strepsiceros</i>	223
<i>Connochaetes taurinus</i>	240
<i>Hippotragus</i> sp.	261
<i>Equus zebra</i>	272
<i>Taurotragus oryx</i>	670
<i>Syncerus</i> sp.	800
<i>Equus capensis</i>	900
<i>Megalotragus</i> sp.	900
<i>Ceratotherium/Diceros</i>	1500
<i>Pelorovis</i> sp.	1800

Reproduced by Sabinet Gateway under licence granted by the Publisher (dated 2010).

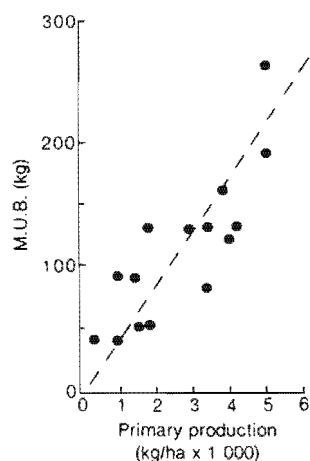


Fig. 3. Relationship between M.U.B. and primary production estimates based on rainfall data for 16 districts in S.W.A.

tion.) The index is calculated by determining the total mass of the ungulates, divided by the number of animals involved.

$$\text{M.U.B.} = \frac{\sum B_i n_i}{N} \quad (1)$$

where N is the total number of animals in the community; B_i is the mean adult mass of each species i (see Table 1); and n_i is the number of individuals of each species. (It should be noted that the M.U.B. index does not take the age and sex of the animals into account.)

The index correlates with primary production and the number of species in each community in South West Africa/Namibia (see Figs 3 and 4). The relationship between M.U.B. and primary production (P.P.) is given approximately as follows:

$$\text{P.P.} \approx 24 \times \text{M.U.B. kg/ha} \quad (2)$$

The formula does not necessarily apply where primary production is greater than 6 000 kg/ha, as is the case for subtropical regions north of S.W.A.

The relationship between M.U.B. and the number of species (N.S.P.) in each community is found by linear regression to be:

$$\log \text{M.U.B.} = (0.123 \times \text{N.S.P.}) + 0.66 \quad (r = .85) \quad (3)$$

This equation and the correlation coefficient were established using a presumed datum point (M.U.B. = 0, N.S.P. = 0) in addition to the datum points for the 16 districts given in Table 2.

The value of M.U.B. may also be predicted from mean annual rainfall and mean annual temperature. Using meteorological data provided by the weather office at Windhoek, a regression analysis gave the following relationship:

$$\text{M.U.B.} = (0.26 \times \text{M.A.R.}) + (1.05 \times \text{M.A.T.}) + 18.6, \quad (r = .79) \quad (4)$$

where M.A.R. refers to mean annual rainfall (mm) and M.A.T. is mean annual temperature (degrees Celsius).

An equation was obtained by which the number of ungulate species in a community could be predicted from climatic data:

$$\text{N.S.P.} = (0.008 \times \text{M.A.R.}) + (0.679 \times \text{M.A.T.}) - 5.30 \quad (r = .84) \quad (5)$$

This approach has potential application for archaeological investigations. Using independent estimates of rainfall and temperature (on the basis of palaeo-climatic techniques), M.U.B. and N.S.P. values can be predicted for a region in the vicinity of an archaeological site, and cautious comparisons made with the fauna in archaeological assemblages. This has value in assessing the extent to which environmental change contributed to the extinctions of fauna that occurred globally during the Terminal Pleistocene.

An attempt has also been made to establish a means of predicting the proportion of biomass represented by ungulates which are primarily either grazers (P.C.G.) or browsers (P.C.B.)

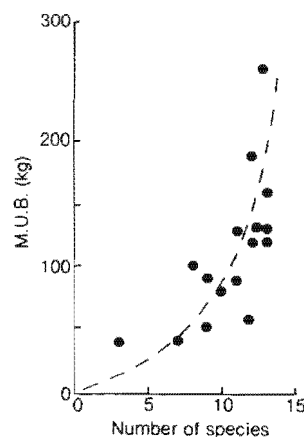


Fig. 4. Relationship between M.U.B. and N.S.P. values for modern faunal communities in S.W.A.

in a community, on the basis of mean annual rainfall and temperature. Multiple regression analyses gave the following relationships:

$$\text{P.C.G.} = (-0.08 \times \text{M.A.R.}) + (0.64 \times \text{M.A.T.}) + 42.8 \quad (r = .68) \quad (6)$$

$$\text{P.C.B.} = (0.04 \times \text{M.A.R.}) + (3.58 \times \text{M.A.T.}) - 46.0 \quad (r = .77) \quad (7)$$

The data on which these relationships are based are given in Table 2. These equations do not take mixed feeders into account, that is, those which browse and graze.

Statistics on modern faunal communities in S.W.A. do not necessarily apply to other regions with different faunal compositions, nor do they necessarily reflect 'stable' communities, and the influence of carnivore predation has not been taken into account. It is therefore necessary to extend this approach to other parts of Africa to derive relationships which might be of more general application.

Archaeological faunal assemblages

In the last decade there has been a dramatic improvement in the quality and quantity of archaeological research conducted in South Africa, and it is becoming possible to synthesise the data available to document changes in the distribution of fauna on

Table 2. Faunal indices for ungulate communities in South West Africa/Namibia. P.C.B. values refer to animals that are primarily browsers (giraffe, kudu, duiker and dik-dik), while P.C.G. values refer to animals that are primarily grazers (springbok, gemsbok, hartebeest and zebra).

	M.U.B. (kg)	N.S.P.	P.C.B.	P.C.G.	N	M.A.R. (mm)	M.A.T. (°C)
Tsumeb	256	12	38.4	1.7	11 150	531	22.2
Grootfontein	193	12	39.0	3.5	43 425	548	20.3
Outjo	163	13	47.3	18.0	37 370	409	21.1
Otjiworongo	125	13	57.9	26.4	47 720	455	20.7
Omaruru	134	11	59.1	24.8	27 120	298	22.5
Swakopmund	38	3	0	49.3	28	15	15.5
Karibib	131	13	49.6	27.3	22 000	205	22.5
Okahandja	134	13	53.6	34.4	35 810	375	20.2
Windhoek	116	12	49.8	32.2	72 140	370	19.3
Gobabis	81	10	46.8	43.9	74 240	369	19.5
Maltahöhe	87	11	24.1	36.1	24 170	168	20.4
Marienthal	48	12	20.3	75.3	41 980	192	21.4
Lüderitz	102	8	16.9	39.1	7 350	17	16.0
Bethanie	85	9	41.0	29.9	8 780	117	20.7
Keetmanshoop	49	9	32.7	59.2	21 440	143	20.7
Karasburg	44	7	28.1	51.1	14 970	120	19.9

the subcontinent during the last 130 000 years. Minimum numbers of individuals have been determined in most of the faunal analyses. This paper makes use of archaeological data from selected sites in Southern Africa, and applies several of the relationships described above.

Factors which are considered important in the interpretation of archaeological faunal data include the following: 1) the influence of preservational and other taphonomic biases (taphonomy refers to pre-depositional and post-depositional factors involved in the accumulation of material); 2) the influence of selective predation by human populations and/or carnivores; 3) the influence of climatic change on primary production and on the carrying capacity of the environment, resulting in changes in faunal community composition.

Several factors are therefore likely to have influenced the M.U.B. and N.S.P. values obtained from archaeological assemblages. For this reason the terms M.U.B._A and N.S.P._A are adopted to refer to the values obtained directly from the archaeological data, and should be distinguished from the terms M.U.B. and N.S.P., which refer to values determined solely by environmental factors for a given region at a certain time.

One problem is that one cannot assume that the relative abundances of faunal remains excavated at an archaeological site necessarily represent those in the original palaeo-community. This assumption has often been made but interpretations based on it must be considered with caution since many factors could have operated to bias the sample. For example, small animals may be under-represented owing to preservational factors; on the other hand, they may be relatively over-represented because the rate of turnover in the species may have been higher than that for larger animals. Smaller species may also be better represented at archaeological sites because small animals are more portable than large game. Large animals may have been butchered at the site of the kill and only parts of the animal carried to the 'base camp' site, as documented among modern Bushmen.⁹ The phenomenon of smaller fauna being over-represented due to portability has been termed the 'schlepp effect'¹⁰ and has been used to interpret several archaeological assemblages in Southern Africa.¹¹⁻¹³ It is therefore incorrect to assume that M.U.B._A and M.U.B. are equivalent in the vicinity of an archaeological site at particular times in the past.

Another sampling problem concerns the uncertainty as to whether N.S.P._A = N.S.P. If the assemblages have accumulated over long periods of time, it is probable that more species are represented than actually existed at any one time. Other possible reasons why N.S.P._A and N.S.P. may not be equivalent include selective predation by the agents of accumulation, portability of differently sized animals, as well as habitat variation and differences in the size of home ranges of certain species in the vicinity of the site. It is therefore impossible to have any strict control over the assumption that N.S.P._A = N.S.P. However, with care given to the selection of samples from relatively short and equal time intervals, the probability that N.S.P._A = N.S.P. for particular time periods is increased.

The application of diversity indices (such as Shannon-Wiener or Simpson's C indices) to archaeological faunal assemblages seems inadvisable since we cannot be sure to what extent these indices reflect the diversity of the original palaeo-communities. Despite these difficulties in quantifying diversity, it should be possible to make qualitative statements as to whether one particular taxonomic group becomes common, rare, or absent in the archaeological record. For example, in the case of the southern Cape, there seems to be a widespread decrease in the relative abundance of alcelaphines during the Terminal Pleistocene, presumably associated with the decline in temperature and availability of grassland; accompanying this was a decline in the number of relatively large ungulates, with at least six species becoming extinct.²

New approaches

This section describes new approaches in faunal analysis, involving 1) the use of an equation obtained from a recent taphonomic analysis aimed at correcting a systematic (and therefore predictable) preservational bias against small fauna, and 2) the use of the M.U.B.-N.S.P. relationship obtained from modern faunal communities.

Behrensmeier *et al.*¹⁴ undertook a survey of carcasses in Amboseli National Park, Kenya, where modern census data on ungulates were available. The results of this survey indicated that smaller fauna were under-represented, perhaps due to fragmentation caused by such factors as natural weathering, trampling, and the combined influences of carnivore and scavenger activity. An equation has therefore been derived by which this bias can be corrected, based on the ratio of 'observed' to 'expected' carcasses (taking turnover rates among living populations into account), in relation to body size, as follows:

$$\log(\text{FS}/\text{FE}) = (0.59 \log X) - 1.2 \quad (r = 0.9) \quad (8)$$

where FS refers to the frequency of occurrence of a species in an actual sample, and FE is the expected frequency of occurrence of the same species whose mean adult body weight is X (kg). (Note: the equation was published incorrectly in the original paper;¹⁴ an erratum notice is due to appear in a future issue of *Palaeobiology*.)

The equation can be applied to archaeological faunal data to obtain M.U.B._K values, which are calculated from 'corrected' estimates (FE) of numbers of individuals of a particular species represented in each archaeological assemblage.

The relationship between M.U.B. and N.S.P. established from modern faunal communities (Equation 3) provides a further useful approach for interpreting their archaeological counterparts, in terms of which the observed M.U.B._A and M.U.B._K values may be interpreted. These values may also be compared to 'expected' M.U.B. values for a given region at a certain time (M.U.B._E), where M.U.B._E estimates are obtained on the basis of predictive relationships such as Equations (3) and (4). For example, if it can be shown that the hypothesis

$$H_1: \text{M.U.B.}_K = \text{M.U.B.}_E$$

can be accepted, while a second hypothesis

$$H_2: \text{M.U.B.}_A = \text{M.U.B.}_E,$$

can be rejected, then we may infer that the taphonomic equation does in fact correct for a systematic preservational bias. Secondly, we may infer that there is some similarity between the composition of 'taphonomically corrected' archaeological assemblages and that of the palaeo-community. Thirdly, we may conclude that predation was essentially opportunistic in the sense that animals available in the vicinity of the archaeological sites were hunted and brought to the sites in close proportion to their natural abundances in the original palaeo-communities.

If on the other hand the M.U.B._K results do not come close to the 'expected' M.U.B._E values, and if it is also assumed that the M.U.B._K values take systematic preservational factors into account, then we may make other inferences regarding selective predation. If M.U.B._K > M.U.B._E we may infer that relatively large species were selected for and brought to the site. Alternatively, if M.U.B._K < M.U.B._E we may infer that relatively small fauna were selected.

These inferences cannot be confirmed by any strict statistical approach; their degree of certainty is assumed to be dependent upon the similarity between M.U.B._E and M.U.B._K values.

A cautionary note should be given with regard to the use of statistical tests to substantiate or refute hypotheses about archaeological data. Inferences based on the acceptance of H_1 may still be erroneous owing to factors over which there is no control. However, conclusions may be strengthened if consistent M.U.B._K values are obtained for several closely contemporaneous assemblages from one or more sites in the same biome.

Examples from the southern Cape

Examples are drawn from analyses of faunal remains from three archaeological sites in the southern Cape: Boomplaas,¹⁵ Nelson Bay,¹⁶ and Klasies River Mouth caves.¹¹ The assemblages accumulated within time periods referred to here as Upper Pleistocene (c. 130 000 – c. 20 000 B.P.); Terminal Pleistocene (c. 20 000 – 10 000 B.P.); 'Early Holocene' (10 000 – 5 000 B.P.) and 'Late Holocene' (5 000 B.P. – Present). Estimates for the mean adult body weights of ungulates used in the calculations of M.U.B._A and M.U.B._K are given in Table 1. Elephant and hippopotamus were not included in the M.U.B._A calculations. For the purpose of comparison with the faunal assemblages from Boomplaas, the assemblages from Klasies River Mouth and Nelson Bay were considered as a single sequence. There is, however, a discontinuity lasting more than 10 000 years between the Upper Pleistocene assemblages from Klasies River Mouth and those of the Terminal Pleistocene from Nelson Bay cave, but the two sites are situated within the Cape ecozone,¹⁷ and are relatively close to each other.

The faunal samples obtained from these sites are among the largest yet obtained from single sites in Southern Africa for the periods under consideration. A difficulty was encountered in the lack of control over sample sizes; an attempt has been made to standardize these by restricting each assemblage to approximately 40 individuals. This is not entirely satisfactory since minimum numbers of individuals were determined for natural, culture-stratigraphic or arbitrary units whose dimensions were varied, and some units may have accumulated over greater periods of time than others. It was occasionally necessary to combine units into a single assemblage, and in other cases the number of individuals in a unit was already greater than 40. *

Figure 5 shows the distribution of these and several other sites in relation to actual evapotranspiration,¹⁸ which has been shown by Rosenzweig¹⁹ to be a good predictor of primary productivity. M.U.B._A, 'taphonomically corrected' M.U.B._K, 'expected' M.U.B._E and N.S.P._A values for the assemblages from the three sites are given in Table 3. In the absence of adequate palaeoclimatic data, M.U.B. estimates have been obtained from Equation (3) on the basis of N.S.P._A values. It is emphasized that the examples are given here primarily to illustrate the procedure outlined above. Inferences based on the comparisons between M.U.B._A, M.U.B._K and M.U.B._E values, on the assumption that N.S.P._A ≈ N.S.P., may be tested when more reliable M.U.B._E estimates become available.

These data are used to test hypotheses H_1 and H_2 , which can be expressed alternatively by:

$$H_1: M.U.B._E/M.U.B._K = 1.$$

$$H_2: M.U.B._E/M.U.B._A = 1.$$

The hypotheses were tested on the basis of Student's t -statistic, computed by the formulae

$$t_x = \frac{\bar{X} - \mu}{\sigma_x/\sqrt{N}} \quad \text{and} \quad t_y = \frac{\bar{Y} - \mu}{\sigma_y/\sqrt{N}}$$

where \bar{X} is the mean value of M.U.B._E/M.U.B._A and \bar{Y} is the mean value of M.U.B._E/M.U.B._K for each data set; $\mu = 1$, the hypothesized mean value for X and Y ; σ and N refer respectively to the standard deviation and number of observations for each data set.

Hypothesis H_2 can be rejected in the case of the Boomplaas sequence ($t_x = 10.49$; $P < 0.05$; d.f. = 10) as well as for the Klasies-Nelson Bay sequence ($t_x = 9.28$; $P < 0.05$; d.f. = 24). Table 3 shows that M.U.B._A values are consistently greater than M.U.B._E values, from which one may infer that large ungulates are over-represented in the archaeological assemblages. Figures 6a and 7a show that the M.U.B._A data do not correspond closely with the expected relationship between M.U.B. and N.S.P. based on modern faunal communities, which implies that the

Table 3. Archaeological data for Upper Pleistocene (UP), Terminal Pleistocene (TP), Early Holocene (EH) and Late Holocene (LH) assemblages. N.S.P._A refers to number of species in each assemblage, N is the sample size and NE is the number of individuals expected on the basis of the taphonomic correcting equation. Alpha-numeric symbols refer to assemblages arranged in chronological order from Klasies River Mouth cave ($K_1 - K_{11}$); Nelson Bay Cave ($N_1 - N_{14}$); Boomplaas Cave ($B_1 - B_{11}$); Apollo 11 cave and other sites in southern South West Africa ($S_1 - S_3$); and Elands Bay Cave ($E_1 - E_4$).

	M.U.B. _A (kg)	M.U.B. _K (kg)	M.U.B. _E (kg)	N.S.P. _A	N	NE	Period	Years B.P.
K1	378	114	59	9	27	36	UP	? 130 000
K2	653	259	182	13	98	75	UP	
K3	574	147	316	15	91	110	UP	
K4	497	148	426	16	114	130	UP	
K5	560	199	240	14	83	77	UP	
K6	544	199	44	8	53	49	UP	
K7	482	149	78	10	46	51	UP	
K8	482	204	78	10	30	26	UP	
K9	430	202	78	10	32	29	UP	
K10	540	227	44	8	19	15	UP	? 30 000
K11	215	51	44	8	36	77	LH	
<hr/>								
N1	298	104	240	14	33	43	TP	18 000
N2	265	96	426	16	45	59	TP	
N3	253	94	240	14	24	32	TP	
N4	243	79	138	12	31	47	TP	
N5	135	52	78	10	25	46	TP	
N6	199	75	78	10	38	58	TP	9 000
N7	140	44	44	8	27	56	EH	
N8	84	30	44	8	81	202	EH	
N9	181	54	33	7	36	70	EH	
N10	121	37	44	8	47	109	EH	5 000
N11	203	51	44	8	33	67	LH	
N12	177	41	25	6	37	86	LH	
N13	169	48	33	7	42	85	LH	2 000
N14	214	54	44	8	48	95	LH	
<hr/>								
B1	85	45	19	5	26	50	UP	? 130 000
B2	370	149	44	8	23	24	UP	
B3	319	116	78	10	20	24	UP	
B4	383	191	182	13	55	46	TP	20 000
B5	282	134	138	12	61	64	TP	
B6	159	74	59	9	32	48	TP	12 000
B7	88	32	44	8	41	101	EH	
B8	133	44	102	11	40	85	EH	8 000
B9	67	29	33	7	23	57	EH	
B10	79	31	44	8	28	67	LH	2 000
B11	101	37	44	8	39	85	LH	
<hr/>								
S1	140	38	25	6	24	56	UP	40 000
S2	181	58	25	6	13	24	UP	40 000
S3	89	38	33	7	39	85	EH, LH	
<hr/>								
E1	164	34	59	9	34	89	TP	11 000
E2	137	26	33	7	47	136	EH	
E3	32	19	25	6	24	71	LH	3 500
E4	61	22	25	6	23	67	LH	3 500

M.U.B._A values do not correspond directly to the M.U.B. values for the palaeo-communities, and that the relative abundances of the archaeological faunas have probably been affected by preservational biases against small ungulates, and by other, uncertain factors.

In contrast, H_1 can be accepted for the Boomplaas sequence; a strongly significant result is obtained ($t_y = 0.30$; $P > 0.25$; d.f. = 10). The close agreement between the 'taphonomically corrected' M.U.B._K values and the expected relationship for most

of the assemblages, is apparent in Fig. 6b. These statistics and observations imply that a systematic preservational bias against small ungulates may indeed be accounted for by the taphonomic equation. Furthermore, selective predation may be discounted on the basis of the correspondence between M.U.B._K and M.U.B._E values, although some degree of selective predation cannot be discounted.

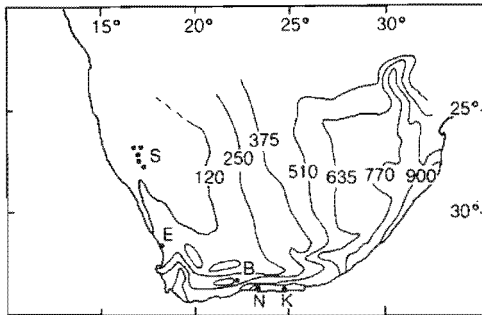


Fig. 5. Distribution of archaeological sites relative to evapotranspiration contours (in mm) based on Schulze.¹⁸ B, Boomplaas Cave; K, Klasies River Mouth Cave; N, Nelson Bay Cave; E, Elands Bay Cave; S, Apollo 11 Cave and other sites.

If preservation and selective predation are largely accounted for in the M.U.B._K data for Boomplaas, the temporal variation (Fig. 8) in the M.U.B._K values remains to be explained. This perhaps arises from climatic changes. Since M.U.B._K ≈ M.U.B._E, the decrease in M.U.B._K values during and since the Terminal Pleistocene can be seen to represent a decrease in primary production, leading to a decrease in carrying capacity of the environment. This may have been a significant factor in contributing to the extinction of *Equus capensis*, *Pelorovis antiquus* and *Megalotragus priscus*, whose last recorded occurrence at Boomplaas is documented c. 12 000 B.P. Barclay²⁰ has shown on theoretical grounds that the probability of extinction is increased by a decrease in carrying capacity.

Analysing the Klasies-Nelson Bay sequence in its entirety, hypothesis H₁ is also accepted ($t_f = 1.31$; $P > 0.10$; d.f. = 24), from which it may be inferred that the taphonomic equation corrects for a systematic preservational bias (Figs 7a and 7b should be compared). However, on analysing part of the Klasies-Nelson Bay sequence, it is noted that a closely contemporaneous group of Upper Pleistocene assemblages (presumably dating to a period c. 80 000–40 000 B.P., referred to in Table 3 as K₆, K₇, K₈, K₉ and K₁₀) have M.U.B._K values which are significantly greater than the M.U.B._E values ($t_f =$

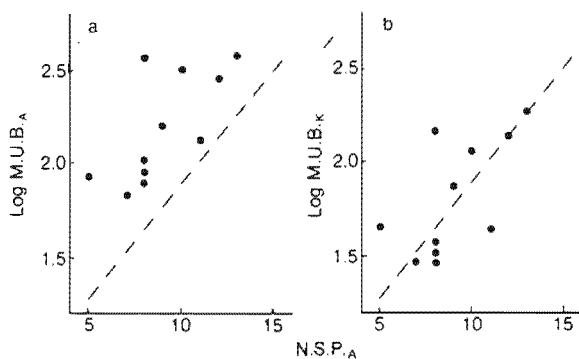


Fig. 6. Summary statistics for Boomplaas Cave assemblages. (a) Log M.U.B._A relative to N.S.P._A compared to (b) log M.U.B._K values, showing a closer agreement with the M.U.B.-N.S.P. relationship obtained for modern ungulate communities (dotted line).

8.68; $P < 0.05$; d.f. = 4). Figure 9 indicates the discrepancy in the M.U.B._K values of this group from the expected relationship between M.U.B. and N.S.P. This observation could be interpreted in terms of selective predation on relatively large ungulates. In contrast to the K₆-K₁₀ data, the Terminal Pleistocene assemblages (N₁-N₆) are characterized by M.U.B._K values which are less than the expected M.U.B._E values, although the differences are not statistically significant ($t_f = 1.73$; $P > 0.05$; d.f. = 5). These assemblages include three extinct species (*Pelorovis antiquus*, *Megalotragus priscus* and *Antidorcas australis*) as well as a locally extinct hartebeest, *Damaliscus niro/dorcas*, which are last recorded at Nelson Bay Cave c. 12 000 B.P.

Inferences based on the significantly greater values of M.U.B._K relative to M.U.B._E in the K₆-K₁₀ Upper Pleistocene sequence, suggest that the process of extinction could have begun before the Terminal Pleistocene, as a result of selective predation on large ungulates; the agents of predation are likely to have included both carnivores and Middle Stone Age peoples. This adds a different perspective to the suggestion that the megafaunal extinctions in the Terminal Pleistocene are largely attributable to improved technical competence among Later Stone Age peoples.²

Populations of relatively large fauna generally take longer to rebuild after a decline in numbers following environmental perturbations. They may therefore be particularly susceptible to extinction at the hands of a variety of predators, not only human. It is not possible to distinguish clearly the agencies of predation, although suggestions have been given on how this distinction may be made.^{21,22} Age distributions obtained for several ungulates represented in the Upper Pleistocene and Terminal Pleistocene assemblages from Klasies River Mouth and Nelson Bay Caves,²³ show a pattern similar to mortality data for the modern buffalo,²⁴ in which juveniles as well as old individuals are well represented in the absence of prime adults. Intensive predation on young ungulates, at a time when carrying capacity was decreasing and when the intrinsic rate of increase of a species was declining, could have contributed to the extinctions which occurred in the Terminal Pleistocene.

Figures 8 and 9 show the temporal variation in M.U.B._K and N.S.P._A values for the Boomplaas and Klasies-Nelson-Bay sequences. Both series display similar trends: relatively low M.U.B._K values were obtained for the earliest Upper Pleistocene assemblages (here called B₁ and K₁); M.U.B._K values increased during later stages of the Upper Pleistocene, and decreased from the Terminal Pleistocene into the Holocene. It is suggested that these broad trends were governed mainly by environmental factors as they affected primary production.

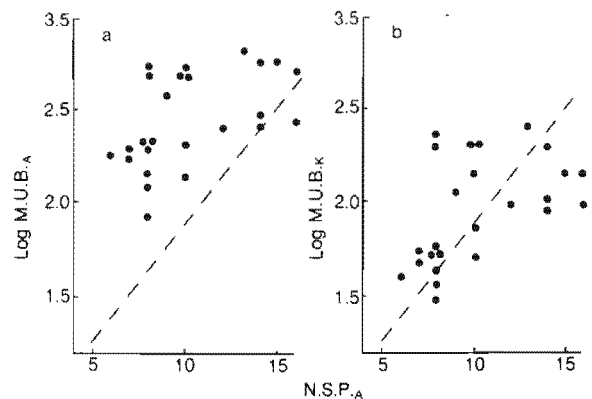


Fig. 7. Summary statistics for Klasies River Mouth Cave and Nelson Bay Cave assemblages. (a) Log M.U.B._A relative to N.S.P._A, compared to (b) log M.U.B._K values, showing a closer agreement with the M.U.B.-N.S.P. relationship obtained for modern ungulate communities (dotted line).

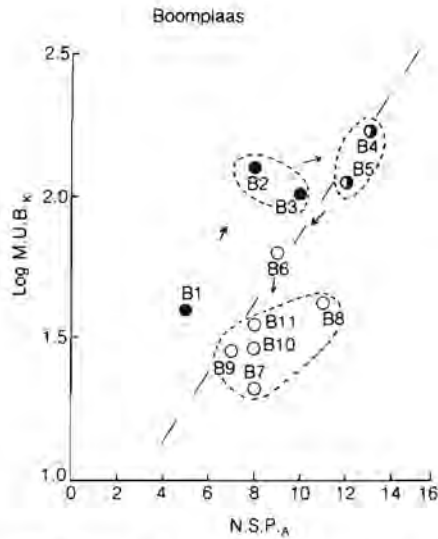


Fig. 8. Changes in M.U.B._K and N.S.P._A values for Upper Pleistocene (●), Terminal Pleistocene (◐) and Holocene (○) assemblages from Boomploas Cave, showing the apparent trajectories through time, relative to the 'expected' relationship (dashed line) based on modern faunal communities in S.W.A. Alpha-numeric symbols refer to assemblages from the site, numbered in chronological order corresponding to the symbols listed in Table 3.

Examples from the Namib Desert and western Cape

We consider here analyses of faunal remains from several sites in the Karoo-Namaqualian ecozone,¹⁷ which are characterized by low primary production and a low species diversity, in the south-western part of the subcontinent. These sites include Apollo 11 and several others in southern South West Africa/Namibia,¹² and Elands Bay,²⁵ situated in the western Cape, South Africa (Fig. 5). Apollo 11 provides faunal assemblages from the Upper Pleistocene, Terminal Pleistocene and Holocene. Holocene assemblages from several small sites in southern S.W.A. have been combined with those from the same period from Apollo 11. Elands Bay provides material from the Terminal Pleistocene and Holocene. All these assemblages are small relative to those from the southern Cape, and, notably in the case of the Upper Pleistocene deposits at Apollo 11, have accumulated over relatively long periods of time. (These small samples may be due in part to the low primary production in this region, which supports relatively small numbers of ungulates per unit area, which in turn limits the size of local human populations and other agents of accumulation.) These

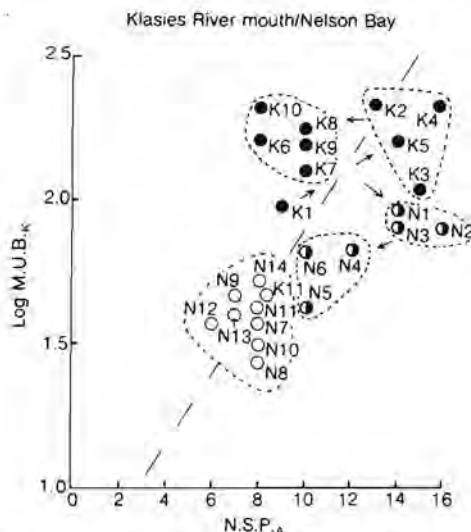


Fig. 9. Changes in M.U.B._K and N.S.F._A values for assemblages from Klasies River Mouth Cave and Nelson Bay Cave. Symbols as in Fig. 8.

assemblages therefore call for particular caution when drawing inferences based on summary statistics (Table 3).

Taking the assemblages from this region collectively, it is apparent that the M.U.B._K values agree more closely with the M.U.B._A values than with the M.U.B._A information. In contrast to the M.U.B._A results shown in Fig. 10a, Fig. 10b shows a closer agreement between the M.U.B._K data and the 'expected' M.U.B.-N.S.P. relationship. Hypothesis H_1 can be accepted ($t_y = 0.62$; $P > 0.25$; d.f. = 6) and hypothesis H_2 rejected ($t_x = 3.51$; $P < 0.05$; d.f. = 6). These observations suggest that the taphonomic equation (Equation 8) again appears to correct for a preservational bias against small fauna.

The equation would appear to compensate for the high degree of fragmentation which can be expected as a result of low rates of accumulation in this region of low primary production. Analysis of a bone sample from Apollo 11 indicated intense fragmentation.¹² Undiagnostic bone flakes (representing 69.9% of the total sample) measured less than 2.5 cm in mean length, while identifiable fragments (only 8.5% of the total sample) measured less than 3.5 cm in mean length.

These desert sites would be expected to be characterized by a small number of species and low M.U.B. values. Despite the sampling uncertainties, it is apparent that these assemblages include a small number of species as well as low M.U.B._K values compared with regions of higher primary production.

Ecological and evolutionary implications

The above examples are given primarily to indicate how certain summary statistics can assist archaeological interpretations. These cases can also be useful in substantiating ecological theory concerning the dynamics of community evolution. The climatic changes which occurred on the African subcontinent towards the end of the Upper Pleistocene (involving changes in rainfall, temperature and increased seasonality) are likely to have induced major perturbations in faunal communities. Stuckenber²⁶ has pointed out that little is known about the effects of temperature on past ecosystems in Southern Africa. Archaeological faunal assemblages provide a means of contributing to our understanding of the nature of palaeo-ecological changes.

The decrease in M.U.B._A and M.U.B._K values during and since the Terminal Pleistocene in the southern Cape reflects an apparent increase in the relative abundance of small ungulates. Since M.U.B._K ≈ M.U.B._E in the examples given above, the observed decrease in M.U.B._K values may reflect a real increase in the relative abundances of small fauna in the palaeo-communities during this period. This is relevant in terms of r and K selection theory because relatively small animals, which have a greater capacity for reproduction than large animals, are more capable of recovery from an environmental perturbation.³⁰

That at least five ungulate species became extinct during the Terminal Pleistocene in the southern Cape, a region of relatively high primary production, contrasts with the observation that apparently only one extinct species, *Equus capensis*, is known from the Terminal Pleistocene assemblages of Elands Bay and Apollo 11 caves. Why should only one species have become extinct? Possible reasons include the following: 1) In a desert biome, the population density of a prey species may reach critically low levels, thus limiting the population size of predator species and ensuring the preservation of the prey. By contrast, in regions characterized by relatively high primary production and high species diversity, and subjected to a major environmental perturbation involving a decrease in carrying capacity, predators may have several prey species to which to turn; predation pressure may become intense as a result of a relatively large number of predator species, whose numbers may increase at the expense of declining prey species. 2) The nature of ecological changes in response to a global decrease in temperature during the

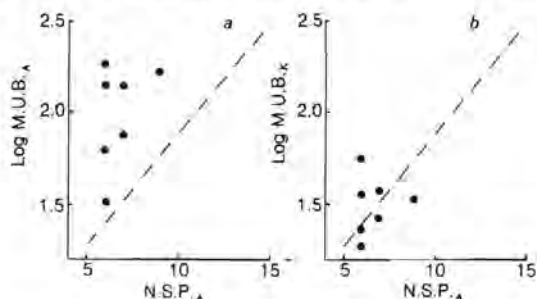


Fig. 10. Summary statistics for Elands Bay Cave, Apollo 11 Cave and other assemblages in southern S.W.A. (a) Log M.U.B._A relative to N.S.P._A, compared to (b) log M.U.B._K values, showing a closer agreement with the M.U.B.-N.S.P. relationship obtained for modern ungulate communities (dashed line).

Terminal Pleistocene will not have been the same in all biomes. Indeed, while a reduction in temperature is likely to have reduced primary productivity in temperate, subtropical or tropical biomes, it will have increased in a desert biome owing to a decrease in evaporation rate.²⁷ In the case of the southern Namib and western Cape, an increase in rainfall is believed to have occurred during the Terminal Pleistocene in response to a northward shift of the stable Atlantic anticyclone system.²⁸ It is therefore probable that ungulate communities were not adversely affected by climatic change, at least for part of the Terminal Pleistocene in those regions where primary productivity increased in response to higher rainfall. Aridification would have occurred in response to a southward return of the anticyclone system, and to increasing temperatures towards the beginning of the Holocene. The last recorded occurrence of *E. capensis* at Apollo 11 is documented c. 14 000 B.P.,¹² whereas the corresponding date for Elands Bay, further south, is c. 10 000 B.P.,²⁵ a difference in time compatible with the palaeo-climatic reconstructions. This does not discount the possibility that predation may have contributed towards its extinction in both areas.

Conclusions

Three factors have been considered as important in influencing M.U.B._A values for archaeological faunal assemblages: 1) preservational biases against relatively small fauna; 2) environmental factors, notably rainfall and temperature; and 3) predation by human hunters, carnivores and scavengers. Preservational biases may be taken into account by the calculation of M.U.B._K values on the basis of the taphonomic equation, the applicability of which has been substantiated in general terms in this paper. A problem remains in distinguishing the extent to which environmental factors and predation contribute to M.U.B._K values. Since the behavioural component is difficult to quantify, especially where a number of predators were involved, efforts should be made to obtain palaeo-climatic data to enable estimation of the environmental component of M.U.B._K values; residual values may be cautiously interpreted in terms of behaviour. This approach may permit determination of the extent to which environmental factors contributed to Terminal Pleistocene extinctions.

The modern ecological relationships given in this paper are suitable for modelling changes in palaeo-environments; research is continuing in this direction. Detailed palaeo-environmental data are clearly essential, and additional information from modern ecosystems throughout Africa is necessary to substantiate and improve the ecological relationships given here.

It is hoped that the procedures outlined in this paper will be adopted wherever else Terminal Pleistocene extinctions are known to have occurred, and thus will lead to more satisfactory conclusions than the assertion that 'overkill' due to intensive human predation *must* have been the cause of these extinctions.²⁹

I am grateful to D. R. Pilbeam, A. Richard, A. K. Behrens-meyer and H. V. Merrick (Yale University) and T. Shaw (Cambridge University) for their encouragement and assistance in the preparation of the manuscript. R. R. Inskip permitted my using unpublished faunal data from the Late Pleistocene deposits at Nelson Bay Cave, analysed by R. G. Klein. This work has been supported by a CSIR grant, a Yale University Fellowship and a Harry Crossley Bursary administered by the University of Cape Town.

Received 29 May; accepted 14 December 1979.

- Joubert, E. and Mostert, P. K. N. (1975). Distribution patterns and status of some mammals in South West Africa. *Madoqua*, **9**, 5-45.
- Klein, R. G. (1974). A provisional statement on Terminal Pleistocene mammalian extinctions in the Cape Biotic Zone (southern Cape Province, South Africa). *S.Afr. archaeol. Soc. Goodwin Ser.*, **2**, 39-45.
- Giess, W. (1971). A preliminary vegetation map of South West Africa. *Dinteria*, **4**, 5-114.
- Walter, H. (1939). Grassland, Savanne und Busch der arideren Teile Afrikas in ihrer ökologischen Bedingtheit. *Jb. wiss. Bot.*, **80**, 750-860.
- Nel, J. A. J. (1975). Faunal distributions—species density and ecological diversity of South African mammal communities. *S.Afr. J. Sci.*, **71**, 168-171.
- Simpson, C. G. (1964). Species densities of North American Recent mammals. *Syst. Zool.*, **13**, 57-73.
- Coetzee, C. G. (1969). The distribution of mammals in the Namib desert and adjoining inland escarpment. *Sci. Pap. Namib Desert Res. Stn.*, **4**, 23-36.
- Thackeray, J. F. (1977). *Towards a clarification of the extent to which environmental change contributed to Terminal Pleistocene extinctions in Southern Africa*. MSc thesis, University of Cape Town.
- Yellen, J. E. (1978). Cultural patterning in faunal remains: evidence from the 'Kung Bushmen. In *Experimental Archaeology*, edit. D. Ingersoll, J. Yellen and J. MacDonald. Columbia University Press, New York.
- Perkins, D. and Daly, P. (1968). A hunter's village in Neolithic Turkey. *Sci. Am.*, **219**, 97-106.
- Klein, R. G. (1976). The mammalian fauna of the Klasies River Mouth sites, southern Cape Province, South Africa. *S.Afr. archaeol. Bull.*, **31**, 75-99.
- Thackeray, J. F. (1979). An analysis of faunal remains from archaeological sites in southern South West Africa (Namibia). *S.Afr. archaeol. Bull.*, **34**, 18-33.
- Klein, R. G. (1977). The mammalian fauna from the Middle and Later Stone Age (Later Pleistocene) levels of Border Cave, Natal Province, South Africa. *S.Afr. archaeol. Bull.*, **32**, 14-28.
- Behrens-meyer, A. K., Western, D. and Dechant, D. E. (1979). New perspectives in palaeoecology from a Recent bone assemblage. *Palaeobiol.*, **5**, 12-21.
- Klein, R. G. (1978). A preliminary report on the larger mammals from the Boomplaas Stone Age Cave site, Cango Valley, Oudshoorn District, South Africa. *S.Afr. archaeol. Bull.*, **33**, 66-75.
- Klein, R. G. (1972). The Late Quaternary mammalian fauna of Nelson Bay cave (Cape Province, South Africa): its implications for megafaunal extinctions and environmental and cultural change. *Quat. Res. (N.Y.)*, **2**, 135-142.
- Devred, in De Vos, A. (1975). *Africa, the Devastated Continent?* Junk, The Hague.
- Schulze, B. R. (1958). The climate of South Africa according to Thornthwaite's rational classification. *S.Afr. geog. J.*, **XI**, 31-53.
- Rosenzweig, M. L. (1968). Net primary productivity of terrestrial communities: prediction from climatological data. *Amer. Nat.*, **102**, 67-74.
- Barclay, H. (1975). Population strategies and random environments. *Can. J. Zool.*, **53**, 160-165.
- Vrba, E. (1974). *The fossil Bovidae of Sterkfontein, Swartkrans and Kromdraai*. PhD thesis, University of Cape Town.
- Klein, R. G. (1975). Palaeo-anthropological implications of the non-archaeological bone assemblage from Swartklip I, South-Western Cape Province, South Africa. *Quat. Res. (N.Y.)*, **5**, 275-288.
- Klein, R. G. (1978). Stone Age predation on large African bovids. *J. archaeol. Sci.*, **5**, 195-217.
- Sinclair, A. R. E. (1977). *The African Buffalo*. University of Chicago Press, Chicago.
- Parkington, J. E. (1976). *Follow the San: an analysis of seasonality in the prehistory of the south-western Cape*. PhD thesis, Cambridge University.
- Stuckenberg, B. R. (1969). Effective temperature as an ecological factor in Southern Africa. *Zool. Afr.*, **4**, 145-197.
- Cooper, C. F. et al. (1974). In *Proc. 3rd Conf. Climatic Impact Assessment Program*, Cambridge, Mass., U.S. Dept. Transportation, 550-562.
- Van Zinderen Bakker, E. M. (1975). The origin and palaeo-environment of the Namib Desert biome. *J. Biogeog.*, **2**, 65-73.
- Martin, P. S. (1967). Pleistocene overkill. In *Pleistocene Extinctions: the search for a cause*, edit. P. S. Martin and H. S. Wright. Yale University Press, New Haven.
- Pianka, E. R. (1974). *Evolutionary Biology*. Harper and Rowe, New York.