*Journal of Archaeological Science* (2000) **27,** 665–684
doi:10·1006/jasc.1999.0470, available online at http://www.idealibrary.com on IDEAL®

# Leopards as Taphonomic Agents in Dolomitic Caves—Implications for Bone Accumulations in the Hominid-bearing Deposits of South Africa

Darryl J. de Ruiter* and Lee R. Berger

*Palaeoanthropology Unit for Research and Exploration, Bernard Price Institute, University of Witwatersrand, Private Bag 3, Johannesburg 2050 South Africa*

(*Received 7 August 1998, revised manuscript accepted 31 May 1999*)

It has been hypothesised that leopards were significant contributors to the bone accumulations of the Plio-Pleistocene hominid-bearing caves of South Africa. Interpretations of leopard activity in these fossil caves were previously based upon reports of modern leopard behaviour in areas of southern Africa that were lacking in caves. In 1991 a leopard lair with an accompanying bone accumulation was discovered in a dolomitic cave on the John Nash Nature Reserve, South Africa. All of the bones in this cave could be unambiguously attributed to the activity of one individual leopard over a 1-year period. The resulting bone assemblage indicates that, when available, leopards will preferentially utilise the deep recesses of caves to the exclusion of trees when feeding, and that the size of prey leopards are capable of capturing, killing and transporting has previously been underestimated. The implications this may have for understanding the accumulation of fossils in the hominid-bearing caves of South Africa are that bones derived form leopards consuming prey in trees probably did not contribute significantly to the assemblages, and further that it is not necessary to invoke sabre-tooth cat involvement for the larger animals found in these assemblages. This modern cave probably represents a more appropriate model for the accumulation of bones in the fossil caves of the Sterkfontein Valley, and the assemblage is being continually monitored to view any and all taphonomic alterations that are occurring.

*Keywords:* TAPHONOMY, LEOPARD LAIR, BONE ACCUMULATION, FAUNAL ANALYSIS CARCASS DAMAGE AND DISINTEGRATION.

## Introduction

It has been recognised by palaeontologists that the methods by which bones in a fossil assemblage were collected have direct bearing on how representative those bones are of the faunal community in the external palaeo-environment (Behrensmeyer *et al.*, 1979). Studies of modern bone assemblages reveal that a number of potentially identifiable processes may have led to fossil bone accumulations. In southern Africa in particular, examinations of modern bone assemblages indicate that in cave situations carnivores, particularly leopards and hyaenas, and rodents, such as porcupines, are the most significant non-human accumulators of large bone assemblages (Hughes, 1954*a*, *b*, 1961; Klein, 1975; Brain, 1981, 1993; Maguire, 1976; Scott & Klein, 1981; Newman, 1993). Modern taphonomic studies have further resulted in the recognition that in the South African Plio-Pleistocene fossil-bearing cave sites, leopards and possibly sabre-tooth cats may have been the most important accumulating agents of early hominid bones in dolomitic cave assemblages (Brain, 1981, 1993; Vrba, 1975, 1976).

The behaviour of leopards has been documented in many areas of Africa, and their habit of protecting kills by storing them in trees is well known (Pienaar, 1969; Schaller, 1972; Brain, 1981; LeRoux & Skinner, 1989; Mills, 1990). However, the majority of studies that have examined this aspect of leopard behaviour have done so in areas where caves are rare or absent (Turnbull-Kemp, 1967; Pienaar, 1969; Schaller, 1972; Smith, 1977; Busse, 1980; Brain, 1981; Mills, 1990). Only a few studies have examined leopard activity in caves (Simons, 1966; Brain, 1981; Sutcliffe, 1973). Studies of leopard behaviour in dolomitic regions are lacking, and thus the activities of leopards in the presence of dolomitic caves are not well understood. Since leopards are hypothesised to be such important bone accumulating agents in the fossil bearing dolomitic caves of South Africa, the actions of these carnivores in a similar geomorphological setting as the hominids are found in is significant.

The tree stashing behaviour of leopards has been used as a model to account for the deposition of bones in some of the fossil caves of South Africa (Brain, 1968, 1969, 1970, 1974, 1981, 1993). The discovery and examination by the authors of a modern leopard lair in

---

*For correspondence. E-mail: 055daryl@chiron.wits.ac.za

0305–4403/99/080665+20 $35.00/0

a dolomitic cave on the John Nash Nature Reserve, near Johannesburg, provides an alternate model for the deposition of fossils in dolomitic caves in South Africa. The bone accumulation formed in this cave was the consequence of a leopard dragging complete carcasses into the cave itself, and the resultant bone assemblage reflects the behavioural patterning of that leopard. This is in contrast to the model of leopards consuming prey in trees growing in cave entrances, and randomly dropping bones into the cave from those trees. It is possible that the spatial distribution of bones within some South African Plio-Pleistocene caves may reflect the feeding behaviour of leopards that dragged entire carcasses into the caves.

It has also been hypothesised that sabre-tooth cats may have contributed a significant proportion of the material in the faunal assemblages of the South African fossil caves (Brain, 1981, 1993; Vrba 1975, 1976), since many of these prey animals were considered too large to have been captured and dragged to the vicinity of the caves by leopards. Based on the size of carcasses located within the cave analysed in this study, it is apparent that the abilities of leopards to kill and cache large animals has been underestimated. While it is possible that sabre-tooth cats contributed to the fossil assemblages in South Africa, it is not necessary to invoke their involvement.

## Study Site

The cave featured in this paper has been designated WU/BA-001, and was examined as part of an ongoing research program of modern and fossil bone accumulations in southern Africa. WU/BA-001 is located on the John Nash Nature Reserve, a private game reserve approximately 45 km north of Johannesburg, South Africa. Parts of the approximately 9500 hectare John Nash Nature Reserve have previously been referred to as the Jack Scott Nature Reserve, or Uitkomst (see Brain, 1981), since this area was studied prior to 1966 when the current owner amalgamated several farms into the present large reserve. Today, the reserve has a particularly rich and varied population of indigenous and introduced antelope, and an abundance of carnivores. Approximately 12 species of antelope are found within the fenced reserve area, as well as several other large mammal taxa (Table 1). The most abundant species are blesbok (*Damaliscus dorcas*) and impala (*Aepyceros melampus*). Tree cover in the area is sparse in the highlands, with most of the trees growing in the entrances of caves, or at least near to caves. There are, however, large areas of dense riverine bush and woodland.

The reserve is fortunate in having within its borders numerous dolomitic caves of varying sizes, including the Gladysvale early hominid site (Berger *et al.*, 1993). The larger caves within the reserve have been previously mapped and described by Martini & Keyser (1989). Depending on size and location, these dolomitic caves are utilised to varying degrees by animals for shelter, lairs, or feeding places. One cave, referred to by Brain (1981) as being on Uitkomst farm, has been recognised since 1955 as a breeding and feeding lair for brown hyaenas (*Hyaena brunnea*) and the authors have visited several active brown hyaena lairs within 5 km of WU/BA-001. Approximately 10 km to the west of the reserve is a large colony of Cape Vultures (*Gyps coprotheres*). Vultures are among the most active of scavengers in the area. The presence of other scavengers in the vicinity of leopards has been postulated as the driving force behind leopard food caching in trees (Brain, 1981; Skinner & Smithers, 1990).

## The Leopard Lair

In September 1991 Joe DeBeer, a game manager on the John Nash Nature Reserve, showed one of the authors (LRB) WU/BA-001, a small, partially mined cave within the boundaries of the reserve that had been used by a leopard (*Panthera pardus*) as a living and feeding lair for nearly a year. The leopard, a large female weighing nearly 50 kg, had regrettably been culled some time earlier due to her prolific feeding habits and subsequent impact on the local antelope population. Although the cave system used by the leopard is small, the two chambers preserve the largely complete remains of no less than eight medium- and large-sized antelopes as well as the mummified skin and skeleton of a caracal (*Felis caracal*) and the skulls of two porcupines (*Hystrix africaeaustralis*). Other skeletal remains are buried in the sediments of the cave, but were most probably not deposited as a result of the activity of the leopard in question here.

WU/BA-001 has been visited on a few occasions since its initial discovery, and the state of the carcasses has been continuously monitored. In the intervening 7 years (between 1991 and 1998), changes are evident in some of the carcasses. These changes are related to the position of bones, as well as their degree of disintegration. Table 2 provides details of these skeletons and their varying states of preservation as recorded in September 1991, immediately after their discovery, as well as in August 1998, during the most recent visit to the cave.

WU/BA-001 is located in an extremely rugged area of the reserve, approximately 1·5 km southwest of the Gladysvale fossil cave, on the northeast facing slope of a large, grass covered hill. The primary rock which forms the hills in the area of the lair are gray colored dolomitic limestones of the Eccles Formation. The presence of loose boulders and outcrops of dolomite gives the terrain a very broken appearance. The lair is easily recognised by the presence of a several large wild olive trees (*Olea capensis*) growing out of the entrance. Geomorphologically, the lair is part of a system of caves that have at least three entrances further down

*Table 1. Large mammals commonly found in the John Nash Nature Reserve*

| | |
|---|---|
| Bovidae | |
| | Blesbok (*Damaliscus dorcas*) |
| | Impala (*Aepyceros melampus*) |
| | Mountain reedbok (*Redunca fulvorufula*) |
| | Kudu (*Tragelaphus strepsiceros*) |
| | Eland (*Taurotragus oryx*) |
| | Gemsbok (*Oryx gazella*) |
| | Springbok (*Antidorcas marsupialis*) |
| | Red hartebeest (*Alcelaphus buselaphus*) |
| | Waterbok (*Kobus ellipsiprymnus*) |
| | Blue wildebeest (*Connochaetes taurinus*) |
| | Steenbok (*Raphicerus campestris*) |
| | Klipspringer (*Oreotragus oreotragus*) |
| Equidae | |
| | Burchell's zebra (*Equus burchelli*) |
| Giraffidae | |
| | Giraffe (*Giraffa camelopardalis*) |
| Primates | |
| | Chacma baboon (*Papio cynocephalus*) |
| | Vervet monkey (*Cercopithecus aethiops*) |
| | Galago (*Galago moholi*) |
| Carnivora | |
| | Leopard (*Panthera pardus*) |
| | Brown hyaena (*Hyaena brunnea*) |
| | Black backed jackal (*Canis mesomelas*) |
| | Civet cat (*Civettictis civetta*) |
| | Caracal (*Felis caracal*) |
| Rodentia | |
| | Porcupine (*Hystrix africaeaustralis*) |

slope, although there is presently no open connection between the leopard lair and these lower chambers.

The lair has two main chambers and a number of small, blind side tunnels (Figure 1). The smaller Upper Chamber is roughly rectangular in shape, approximately 10 × 12 m, and about 3 m in height. The floor is strewn with small rocks and fist-sized chunks of dolomite that originate from turn-of-the-century lime mining activities in the cave (H. Norton, pers. comm.). The floor of the Upper Chamber slopes northward, downwards from Entrance 1, at approximately 25 degrees. At the far northern wall in the "bottom" area of the chamber there is an approximately $1 m^2$ opening (Passage 1, Figure 1) that gives access to the lower chamber.

The area of the Lower Chamber is approximately 8 × 18 m (Figure 1). One may enter this chamber either through Passage 1 from the Upper Chamber, or directly from the Entrance area via Entrance 2. However, gaining access by Entrance 2 involves climbing down the large western talus slope which angles downward in places as much as 35 degrees and requires one to traverse loose rocks, organic debris and boulders. The most likely entrance by which animals gain access is therefore through Passage 1, via the Upper Chamber.

Following Brain's (1981) analysis of the position of bones accumulated at the Quartzberg Leopard Feeding Lair, we have divided the cave chambers into three zones: the light, the twilight and the dark (Figure 1). The light zone comprises mainly the entrance area of the cave and the areas of the Upper Chamber and the first few meters of the talus slope beneath Entrance 1. The twilight zone includes the remainder of the Upper Chamber and a second talus slope down to about 3 m from Entrance 2 as well as the area in the immediate vicinity of Passage 1; this area consists of a raised shelf of dolomite. The dark zone comprises the remainder of the Lower Chamber.

The contours of the cave wall, as well as all skeletal material, were mapped using a Leica T1010™ theodolite with a Disto™ GSI lasermeter attachment in 1998, allowing accuracy to within approximately 0·5 cm. Subsequent visits to the cave will repeat the mapping procedure for each bone to determine if any movement of the materials is evident. The relative positions of each of the bones and of bone clusters are mapped in Figure 1 for reference in discussions of individual carcasses below.

## Observations

### *The light zone*

The entrance area is a relatively large, tree-filled fissure that gives access to the two chambers of the cave (Figure 1). Seven large wild olive trees dominate the entrance area. The floor of the entrance area is littered with organic material in the form of leaves and branches, the majority of which originate from the trees. There is a small talus slope comprising topsoil and several dolomite blocks against the southern wall of the entrance area. This material has evidently been derived from debris washing into the entrance area from the surface during rainstorms. Organic material in the entrance area appears to rot rapidly due to exposure to the elements. No bones are visible in the entrance area.

### *The twilight zone*

In the western part of the Upper Chamber there is most of the skeleton of an adult male blesbok (Individual 1) (Table 2). The skeleton had been separated into two parts. The more northerly situated remains comprised the head and horns, with the mandibles still attached and encased in skin in 1991 (Figure 2(a)). The second set of remains (Figure 3(a)) were located about 1·5 m downslope form the head and horns. These comprised both forelimbs, both scapulae, a few ribs and at least four cervical vertebrae, the articulated hind limbs and pelvis, a few lumbar and thoracic vertebrae, and several rib fragments. The second set of remains was held together by cartilage and desiccated skin. A few isolated bone splinters, fragments of vertebrae, and ribs that are apparently part of this carcass were scattered amongst the rocks and floor debris of the Upper Chamber.

*Table 2. Remains and state of preservation of individual animals within the leopard lair in 1991 and again in 1998*

| Individual | Gender | Species | Remains in 1991 | Remains in 1998 |
|---|---|---|---|---|
| 1 | Male | *Damaliscus dorcas* | cranium, mandible, all teeth, both forelimbs with humeral heads missing, both hind limbs, pelvis with ilia chewed, sternum with six rib ends attached and chewed superiorly; most of skin present | bones still present but moved from original positions; most of skin on thorax, forelimbs & skull has disintegrated, allowing for extensive scattering; pelvis and hindlimbs have lost skin, but remain articulated |
| 2 | Female | *Felis caracal* | complete and articulated; covered by skin | some skin has disintegrated, skull has deteriorated, some teeth are falling out |
| 3 | Female | *Damaliscus dorcas* | cranium, mandible, all teeth, horns chewed to bases; skeleton complete except right femur missing; all ribs damaged near sternal ends; pelvis and hindlimbs displaced slightly downslope; covered by skin | very little change apparent; skin partially deteriorated on underside, some scattering noted, but mostly intact; becoming buried under rocks falling through passage 1 |
| 4 | Male | *Redunca fulvorufula* | complete except ribs chewed near sternal ends; vertebral column, pelvis and hind limbs articulated but displaced downslope approximately 1 m; right horn partially chewed at tip; front hooves chewed away; carcasse covered by skin | articulated hind limbs have migrated approx. 0·5 m further downslope, but remain encased in skin; very little alteration otherwise apparent |
| 5 | Female | *Redunca fulvorufula* | cranium, both forelimbs and scapulae, both hind limbs with fractured left tibia, disarticulated thoracic vertebrae; little skin, some cartilage present; mixed with Ind. 6 extensive carnivore damage on limbs | further deterioration of skin evident, allowing for increased mixing of bones with Ind. 6; some bones have fallen over ledge, creating a widely scattered carcasse |
| 6 | Female | *Raphicerus campestris* | eight disarticulated thoracic vertebrae, right humerus, radius and femur, left radius, metacarpal, plus numerous rib fragments among rocks; almost no skin present; bones mixed with those of Ind. 5 | advanced mixing apparent with Ind. 5; also, destruction of bones evident, probably as a result of rockfalls through passage 1; some bones are becoming buried by these fallen rocks |
| 7 | Male | *Damaliscus dorcas* | cranium, mandible, all teeth; both forelimbs, humeral heads missing; both hindlimbs; four cervical vertebrae, four thoracic vertebrae; partially covered in skin, strip attaching head and thorax; appears "eaten out" of skin | some deterioration of skin evident: strip attaching cranium to thorax completely disintegrated; little other alteration apparent; no movement evident, and deterioration of bones at same stage as 1991 |
| 8 | Male | *Damaliscus dorcas* | cranium, mandible, all teeth, both forelimbs, head of right humerus missing, both hindlimbs vertebrae present but scattered, rib fragments scattered, vertebrae, ribs and pelvis chewed; almost completely skeletonised | little alteration evident; those few vertebrae & ribs previously articulated have collapsed in on themselves; borer moth larvae activity more prevalent; little other alteration apparent and no further scattering noted |
| 9 | Female | *Taurotragus oryx* | complete, articulated skeleton, cranium and mandible; back left phalanges missing; chewing damage evident in neck area, as well as on distal parts of ribs; almost completely covered in skin | most of the skin has disintegrated, leaving the bones exposed; very little movement of these bones has occurred; carcasse occasionally submerged during rainy season as water pools in bottom of cave; effects of submergence not known at this time |
| 10 | Indet. | *Hystrix africaeaustralis* | cranium and mandible; no skin evident | missing from cave, fate unknown |
| 11 | Indet. | *Hystrix africaeaustralis* | cranium and mandible; no skin evident | missing from cave, fate unknown |
| 12 | Indet. | Bovid class II | buried and unknown in 1991 | series of articulated vertebrae, pelvis; probably accumulated prior to leopard discussed here |
| 13 | Indet. | Bovid class II | buried and unknown in 1991 | pelvis; probably accumulated prior to leopard discussed here |
| 14 | Indet. | *Hystrix africaeaustralis* | buried and unknown in 1991 | pelvis; probably accumulated prior to leopard discussed here |
| 15 | Indet. | *Procavia capensis* | buried and unknown in 1991 | cranium and mandible exhibiting damage consistent with leopard consumption; probably accumulated prior to leopard discussed here |

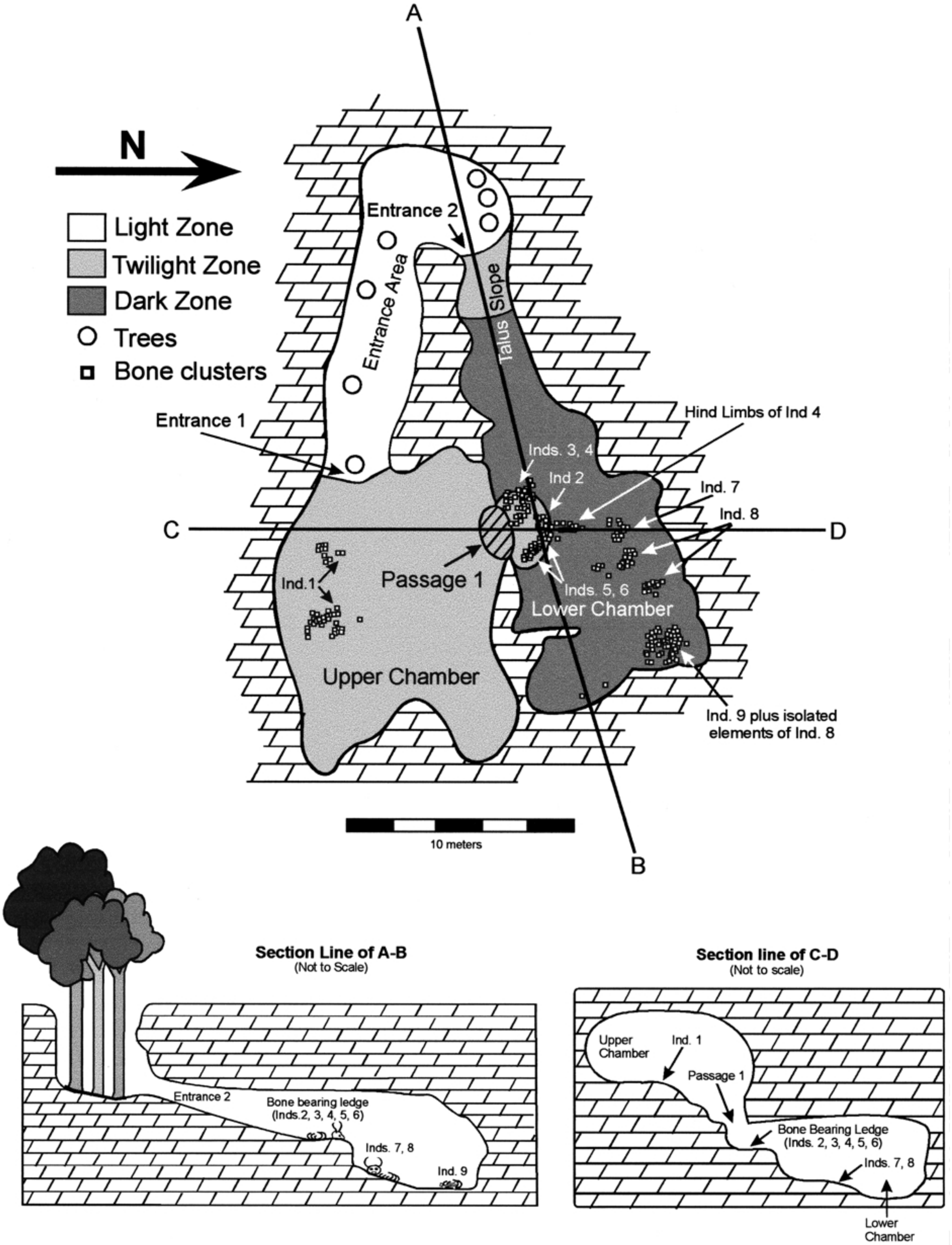

Figure 1. WU/BA-001 leopard lair in plan view. Section plans are not to scale.

As of 1998, the skin adhering to the skull had disintegrated, leaving it completely defleshed (Figure 2(b)). The cranium had been moved from lying on its right side to resting upside-down on its horns and snout. The mandibles had been moved out of anatomical position, and the right mandible had been flipped

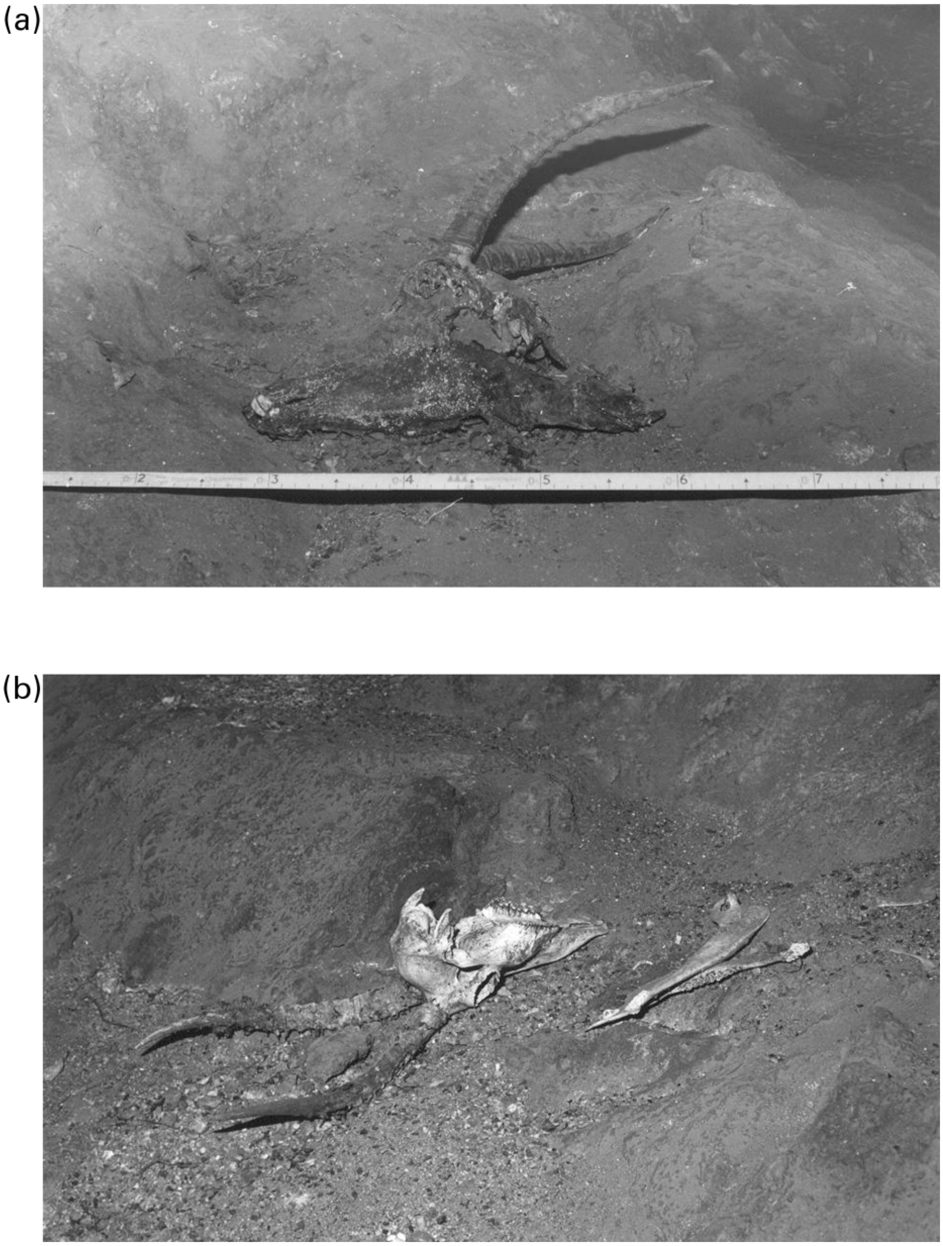

Figure 2. (a) Individual 1 in 1991: adult male blesbok skull still encased in skin with mandibles articulated. (b) Individual 1 in 1998: skin completely disintegrated. Note the disturbed provenience, probably a result of human activity.

over. Although the agent responsible for moving these pieces is not known with certainty, it is possible that humans moved them while examining them in the intervening 7 years. The forelimbs and scapulae have also been moved, and are also now almost completely defleshed (Figure 3(b)). Extensive scattering of these bones has taken place, though the agent of their dispersal is unknown. The hind limbs and pelvis have not suffered as much skin loss, and as such have remained articulated. They remain in the almost same location as they were found in 1991, though the entire mass has gravitationally migrated slightly downslope towards the north.

In the twilight zone of the Lower Chamber immediately below Passage 1 is the largest concentration of animal remains in the cave. No less than five individuals are identifiable in an area approximately 3·0 × 1·5 m in size. This region of bone concentration is on a raised ledge that sits about 1·5 m above the sloping floor of the Lower Chamber (Figure 1). The relative positions of the individual skeletons are presented in Figure 1. The individuals comprise a female caracal (Individual 2), a female blesbok (Individual 3), a male mountain reedbok (*Reduncа fulvorufula*—Individual 4), a female mountain reedbok (Individual 5) and a steenbok (*Raphicerus campestris*—Individual 6).

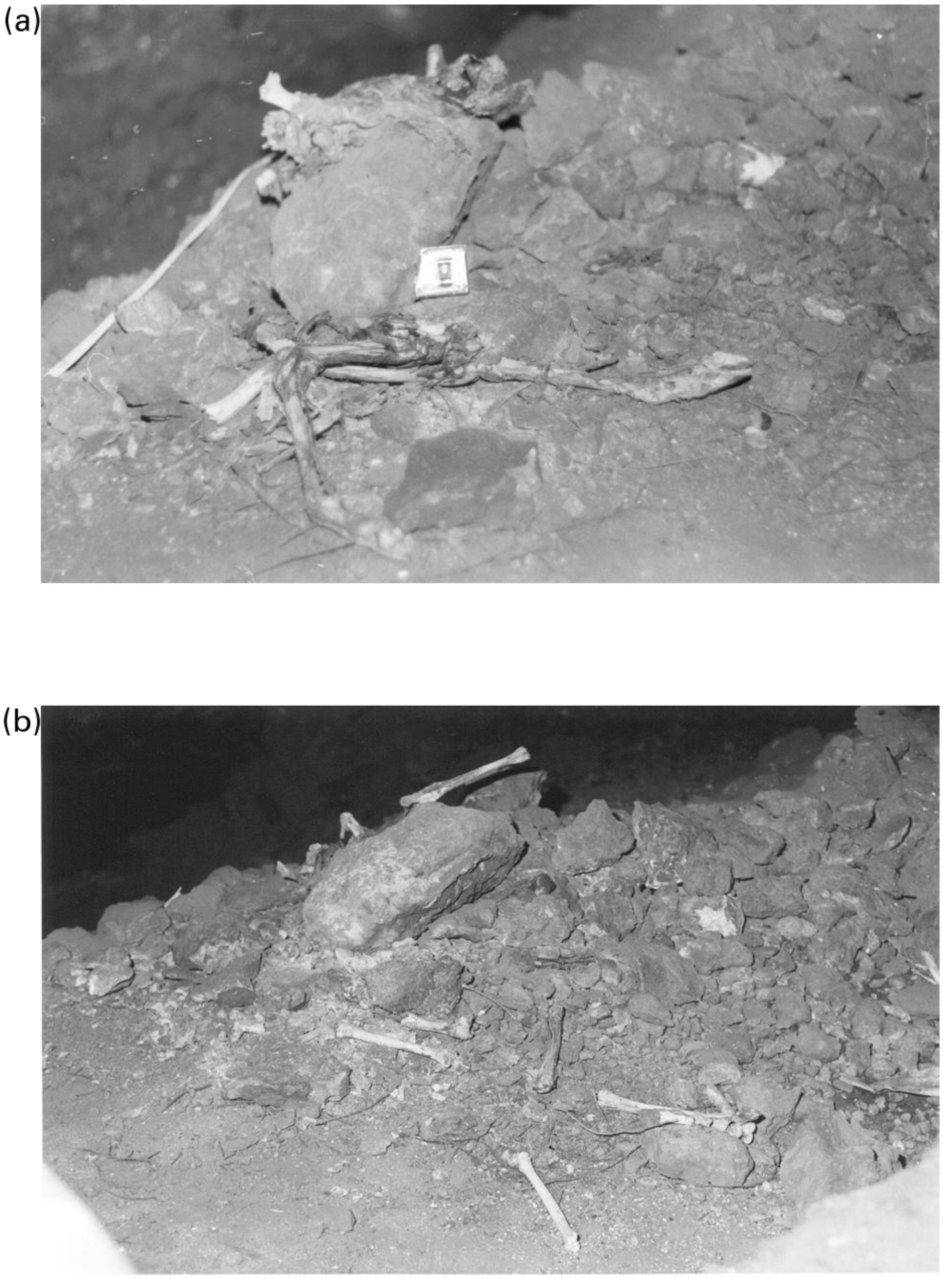

Figure 3. (a) Individual 1 in 1991: adult male blesbok post-cranial skeleton partially encased in skin. (b) Individual 1 in 1998: note almost complete disintegration of skin and scattering of bones.

The caracal is one of the most complete specimens, with the carcass having suffered very little external damage (Figure 4(a)). The apparent cause of death is indicated by four large puncture marks in the neck. Little if any of the caracal had been eaten by the leopard, but the animal may have been disemboweled as there was a large slit in its belly. All of the skin of the caracal was present in 1991, but most of the hair had fallen out. The overall condition of preservation might be best described as natural mummification.

By 1998, some of the skin of the caracal had disintegrated, but not to the extent that bones were being lost (Figure 4(b)). The skull, however, had suffered deterioration, and some of the teeth had come loose. One of the canines had fallen completely out, and ended up about 1 m downslope. The carcass itself appears to be moving closer to the edge of the ledge, and may soon fall over. The force responsible for this movement is probably a combination of human and hyrax (*Procavia capensis*) activity in the cave, as well as

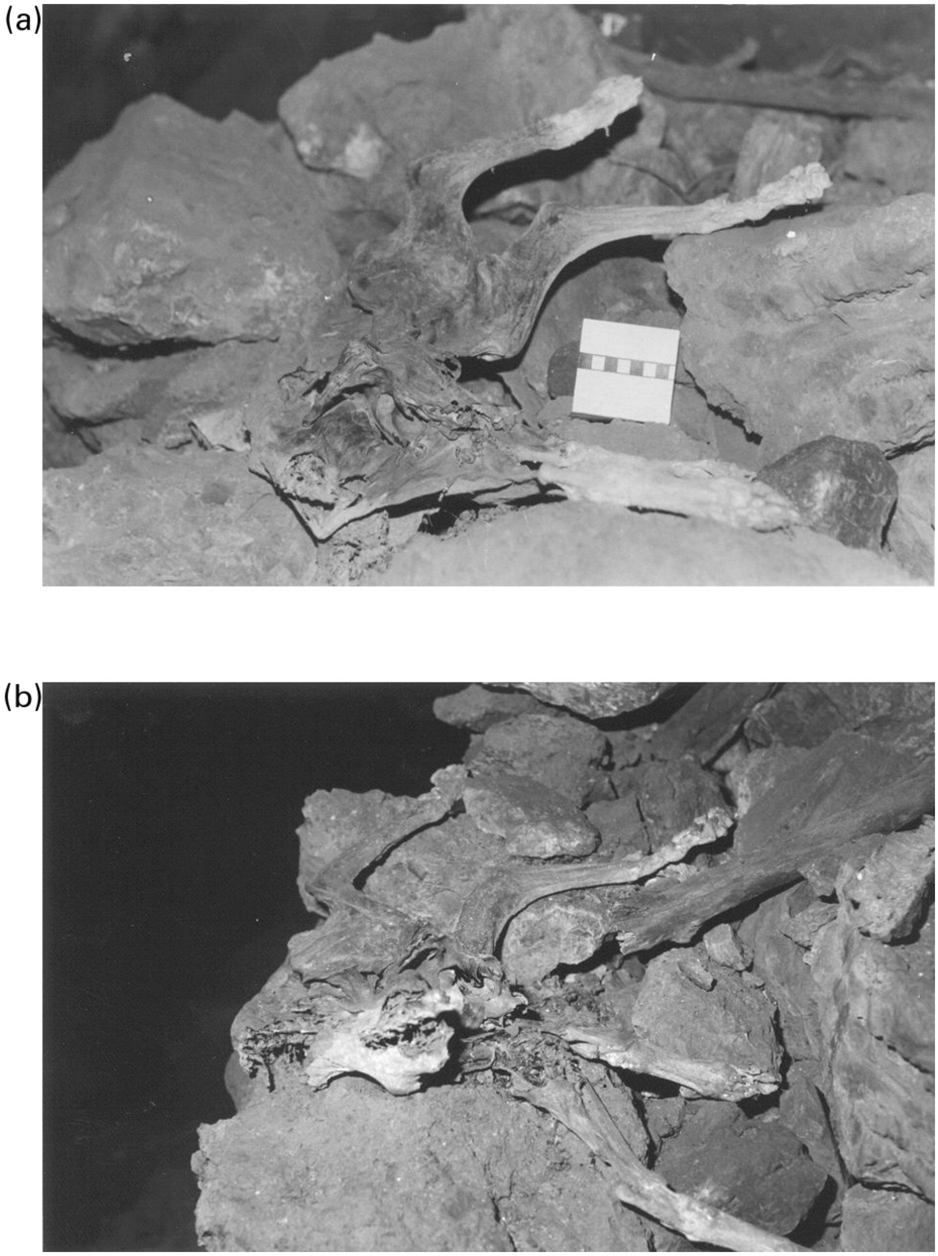

Figure 4. (a) Individual 2 in 1991: adult female caracal, almost completely encased in skin. (b) Individual 2 in 1998: very little deterioration is apparent; exogenous wood may have aided in moving carcass towards edge of ledge.

exogenous material falling into the chamber through Passage 1. Upon entering the Lower Chamber via Passage 1, one must use extreme caution to avoid disturbing the remains of the caracal. This is not always possible in this difficult to negotiate passage, and occasional accidental missteps occur, moving the carcass. Also, several large deposits of recent hyrax droppings are now evident in the cave, indicating the presence of hyraxes.

Since no other agent of dispersion can be identified, we can only assume that it is the activity of humans and hyraxes causing movement of many of the bones. Humans (aside from scientists) no longer enter the cave, but prior to approximately 1995 people visiting the Nature Reserve would occasionally enter the cave to look at the carcasses collected inside. Scientists also cause inadvertent disturbance to the material when entering the cave to examine the carcasses, which is why excursions to the cave are now so strictly limited. There is no evidence of recent porcupine activity in the cave. None of the bones have been gnawed by any type of rodent (as far as can be seen), no porcupine quills have been found, and no porcupine faeces is visible.

Individuals 3 and 4, where visible, were mostly intact form the thorax to the head (Figure 5(a)). For the most part, these specimens showed a similar state of

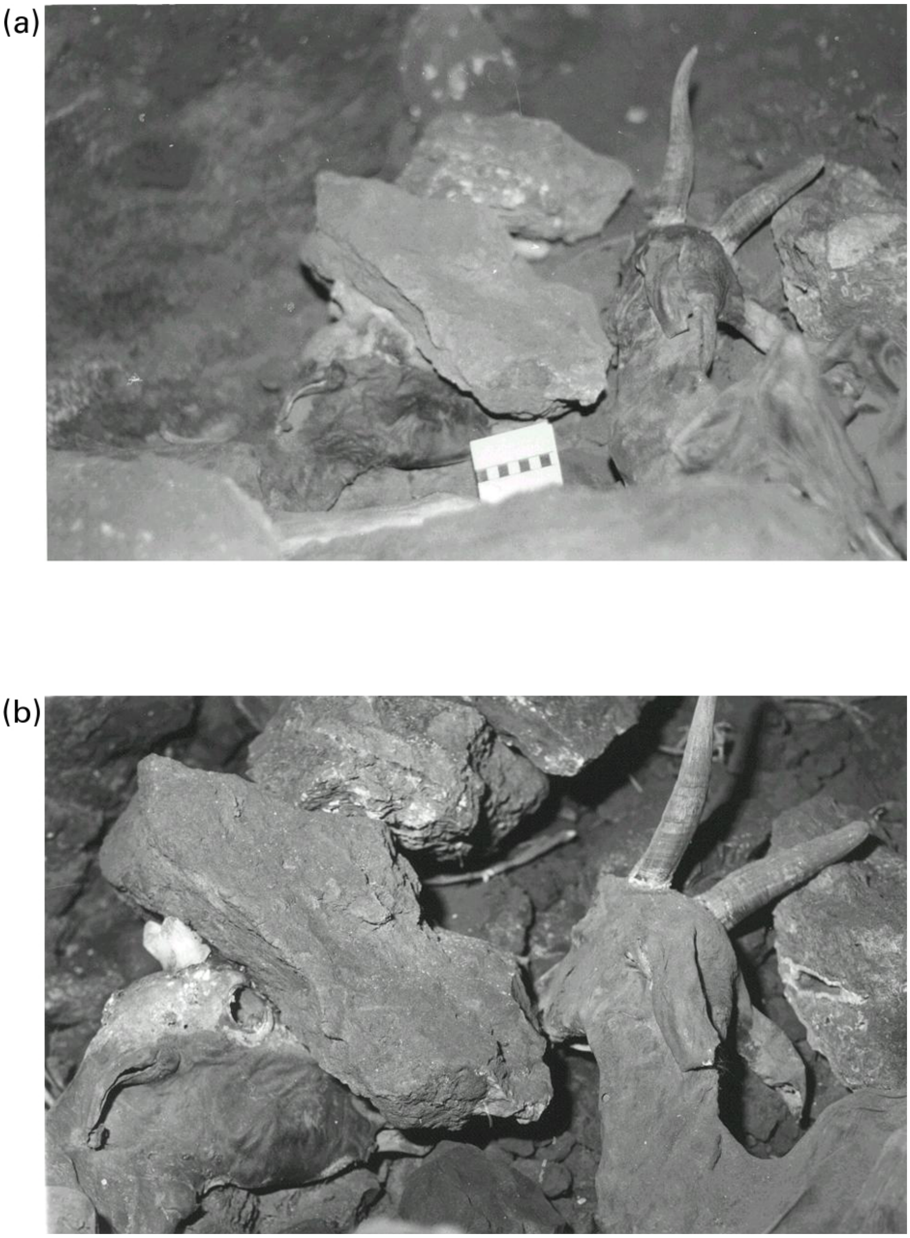

Figure 5. (a) Individual 3 (left) in 1991: adult female blesbok. Individual 4 (right): adult male mountain reedbok. (b) Individuals 3 and 4 in 1998. Note that very little alteration is apparent. On the underside (not visible in photos) some deterioration of skin and consequent slight movement of bones has occurred, probably as a result of water action in the cave.

preservation to the caracal. The hind limbs of Individual 3, a female blesbok, had been detached and lay a few decimetres south of the head, and the right femur could not be located. Both horns had been chewed almost to the bases. Individual 4, a mountain reedbok, had the tip of the right horn chewed. Its hindlimbs and pelvis were disarticulated from the head and thorax and lay about 0·5 m below the ledge on the edge of the talus slope. Its forelimbs were complete with the exception of the hooves which had been chewed away. Dolomite, breccia boulders and loose rock have fallen through Passage 1 from the Upper Chamber resulting in the partial burial of both specimens.

These carcasses have suffered very little alteration over 7 years (Figure 5(b)). It appears that most of the skin has remained intact, and very little degradation of bones is evident. It is probable that the presence of skin has prevented scattering, and the burial of these specimens by loose boulders had facilitated their survival. The only movement apparent can be seen in the pelvis and hindlimbs of Individual 4, which have migrated a further 0·5 m downslope. This movement is probably

Figure 6. Individual 5 in 1998: male mountain reedbok cranium and skeleton mixed with Individual 6, a female steenbok. These remains are being buried by material falling through Passage 1, and much disturbance is evident.

Figure 7. Talus slope leading from Entrance 2 to the lower chamber of WU/BA-001. View looking up the slope towards the entrance, facing west.

a result of hyrax as well as human activity in the cave. The substrate upon which these bones rest is highly unstable, comprised of small chunks of dolomite.

Individuals 5 and 6 were identifiable only from their broken skull and mandibles (Individual 5) and parts of the post-cranial skeletons (Individual 6) which lay on the raised shelf in the Lower Chamber below Passage 1 (Figure 6). Individual 5 is a female mountain reedbok, and Individual 6 a female steenbok. In 1991, numerous small bone fragments and broken limb bones were visible among the boulders which were found on the floor of the shelf, and these are presumably the mixed

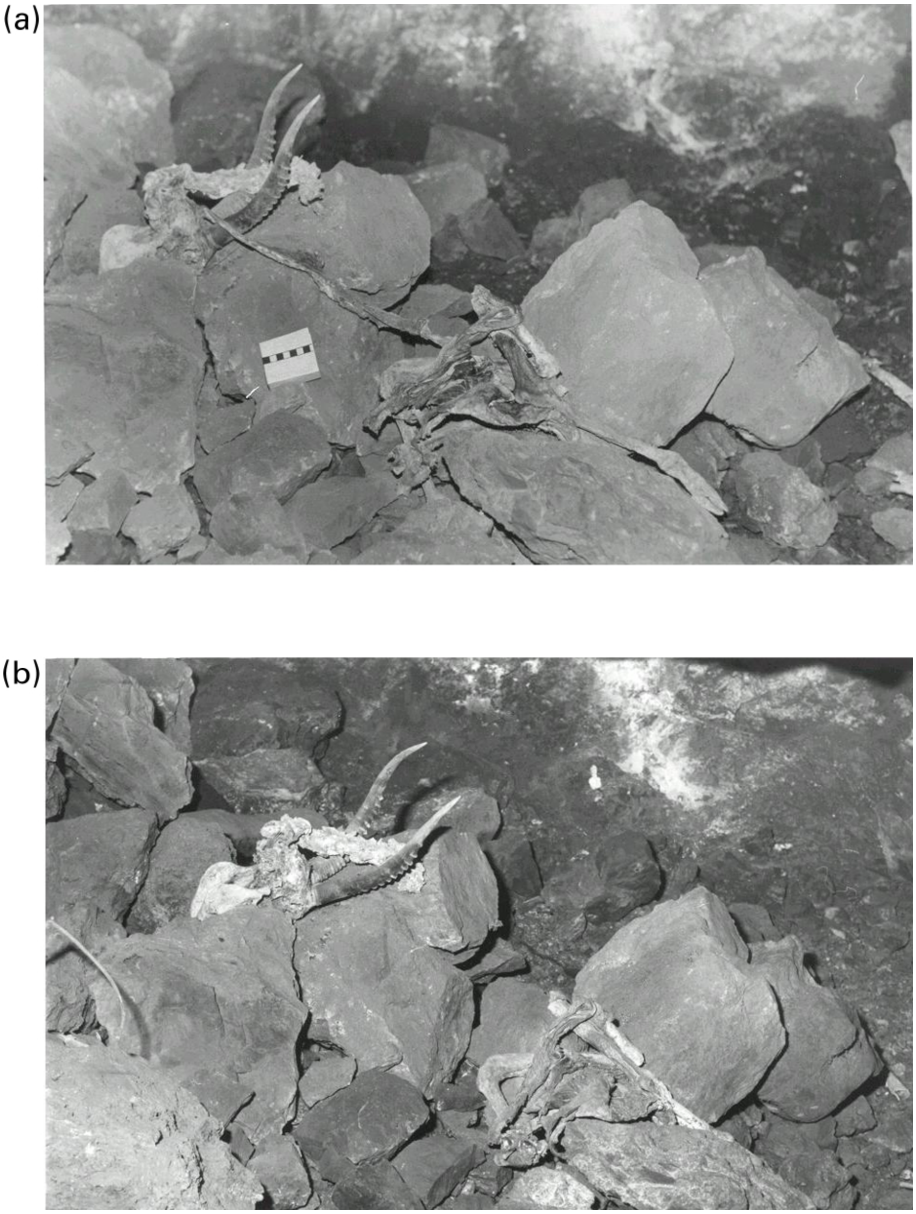

Figure 8. (a) Individual 7 in 1991: juvenile–adult male blesbok. Note the strip of skin attaching the cranium to the thorax. Note also the four limbs held together by strips of skin, providing an ''eaten out'' appearance. (b) Individual 7 in 1998: strip of skin joining cranium and thorax has disintegrated; otherwise little alteration apparent.

remains of these two individuals. The front limbs and approximately one-third of the thorax of Individual 5 were partially articulated by cartilage. The hindlimbs were also partially covered by skin, but had fallen over the ledge and come to rest in the dark zone of the cave at the base of the ledge. Although originally covered in dried skin, it was still possible to view extensive carnivore damage on the distal parts of all Individual 5's limbs. The associated humerus also had the proximal end chewed away and the left scapula exhibited chewing along the superior margin. Individual 6 was represented by some vertebrae, ribs, and fore-limb elements. Its bones were thoroughly mixed with those of Individual 5, but were still identifiable based on their smaller size and the distinctive anatomy of the steenbok.

It appeared that most of the skeletal elements were still present in 1998, but the authors were unable to examine these fragments more closely without disturbing their context. It is difficult to establish what damage is due to the rocks that fall through Passage 1 from the Upper Chamber and what damage was originally caused by the leopard's feeding activities. Some of the skin of the mountain reedbok has deteriorated over the years, and further mixing of the bones of these two

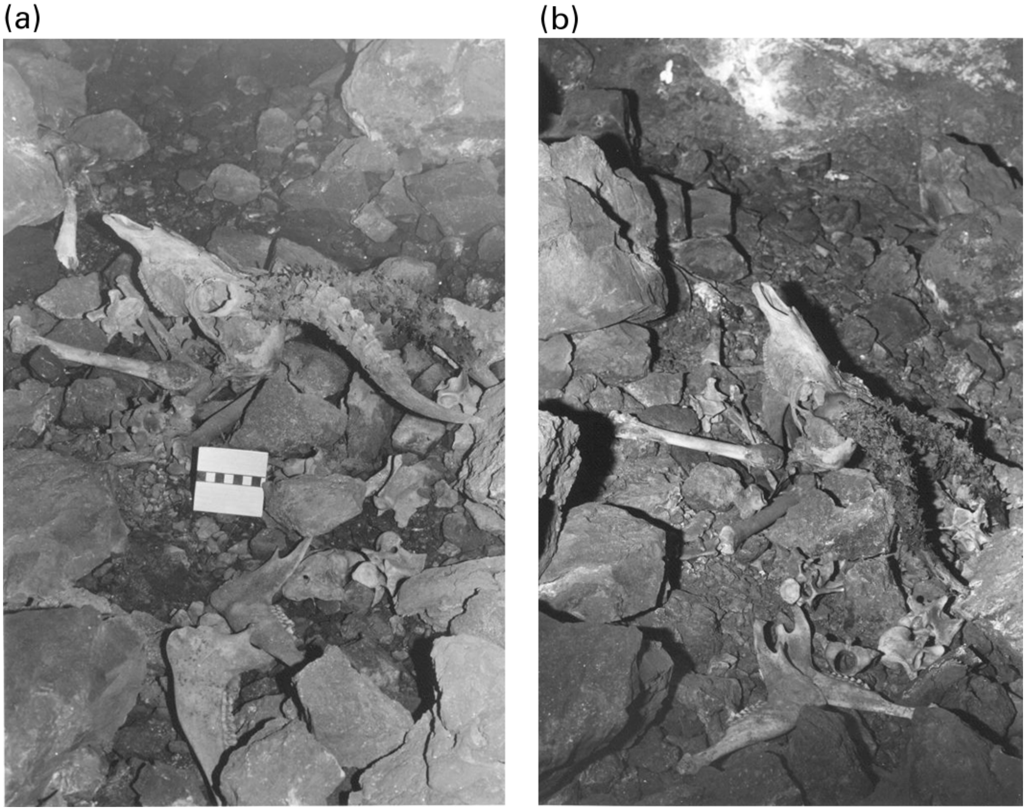

Figure 9. (a) Individual 8 in 1991: adult male blesbok almost completely skeletonised. It has been extensively scattered, probably as a result of Individual 9 being dragged over it. (b) Individual 8 in 1998; some movement of mandibles is evident, probably as a result of human activity. Note the increased borer moth activity long after skeletonisation.

individuals was noted. Many of the bones of these specimens have continued to break apart, due apparently to natural deterioration, while others, particularly those well down among the boulders, are being buried by smaller debris that falls through Passage 1. Hyrax activity is probably responsible for movement of the bones, since the carcasses are in a difficult to reach spot, generally away from the footfalls of larger mammals. Burial appears to provide a measure of protection from further damage and deterioration.

The Twilight zone at Entrance 2 comprises the upper one-third of the talus slope leading into the cave from this second entrance. There is a considerable amount of organic material all over the surface of the slope which has fallen from this second entrance area. There is no bone visible on the upper part of the talus slope. The whole talus slope is composed of loose rocks and rubble, the surface of which is extremely unstable (Figure 7). For this reason, we find it unlikely that the leopard used Entrance 2 as anything but an emergency exit from the lower chamber.

### *The dark zone*

The dark zone comprises the remainder of the Lower Chamber (Figure 1). This zone contained the remains of at least three antelopes and two porcupines. The antelope remains include one juvenile-adult male blesbok, one adult male blesbok (Individuals 7 and 8, respectively), and an adult female eland (*Taurotragus oryx*) (Individual 9). The two porcupines were both juvenile and were represented only by skulls (Individuals 10 and 11).

Approximately 2 m up-slope (south) of the northernmost wall of the cave, nearly in the centre of the Lower Chamber, is the upper part of the rib cage, the scapulae, fore-limbs, hind-limbs, cranium and mandible of a juvenile-adult male blesbok (Individual 7, Figure 8(a)). In 1991, the thorax was held together by sinews of desiccated skin and muscle tissue, and the first four vertebrae were attached to the cranium by sinews. A long strand of skin attached the thorax to the back of the cranium. This carcass exhibited what Brain (1981) has described as an "eaten out" appearance, with the four limbs held together by strands skin. The majority of the thorax and abdominal contents had been consumed by the leopard. In the intervening years, very little alteration of this carcass has occurred (Figure 8(b)). By 1998, the strip of skin connecting the skull and thorax had disintegrated completely, and some further defleshing was apparent. However, the bones all basically lie in their original positions.

Just below the forelimbs of Individual 7 is the cranium, mandible, upper limbs, thorax, pelvis and

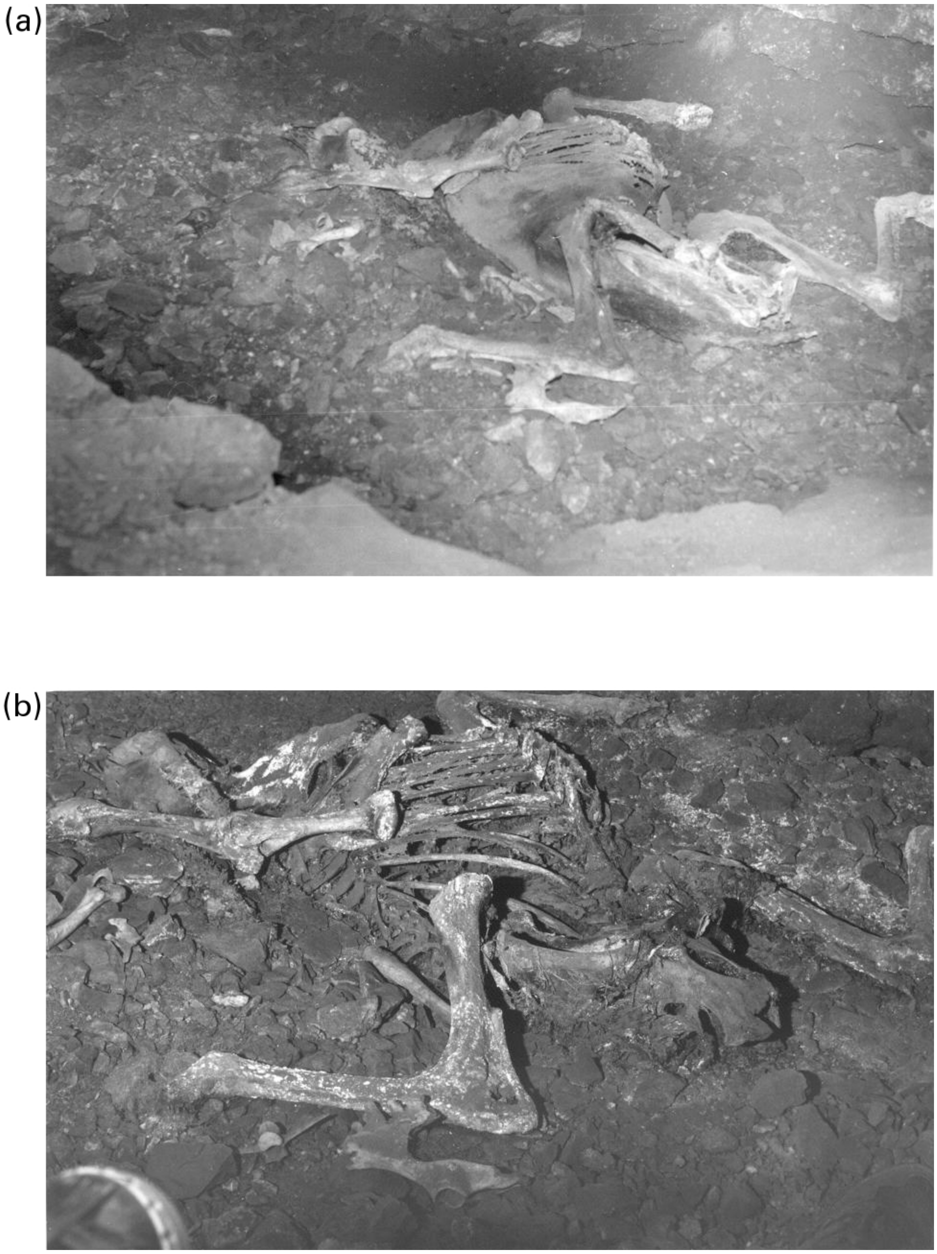

Figure 10. (a) Individual 9 in 1991: adult female eland still mostly encased in skin. (b) Individual 9 in 1998: most of the skin has disintegrated, except for the limbs. Note the pelvis, humerus, vertebrae, and other bones of Individual 8 in close proximity. Whitened patches on skin are some form of fungal growth.

hind limbs of a large, adult male blesbok (Individual 8, Figure 9(a)). This individual was already almost completely skeletonised in 1991, and pieces of bone from the carcass were found among the rocks and debris on the floor within a 1 m radius of the skull. There was also a scattering of vertebrae and other bones down the slope beneath this carcass, and they were presumably derived from this individual. It would appear that this carcass became skeletonised and subsequently another carcass, most probably Individual 9, was dragged over it, scattering the bones downslope. Some of the vertebrae and ribs were still held together by skin. Several of the vertebrae and ribs showed extensive carnivore damage, particularly along the transverse processes of the vertebrae and the distal margins of the rib cage. One ilium had also been chewed. The horn casings and hooves of this individual had been extensively attacked by the larvae of borer moths (Figure 9(a)).

As of 1998, little alteration was apparent with this individual, aside from increased borer moth larvae activity (Figure 9(b)). Otherwise, the distribution of bones, most likely the result of the leopard's activity in this cave, has remained virtually unchanged in the

Figure 11. Several wild olive trees (*Olea capensis*) growing in the entrance area of WU/BA-001. No bones were located in the catchment area underneath these trees.

years since they were first strewn about the cave. The mandibles have been moved, probably by humans in the cave, since the right mandible which previously sat partially under the left mandible has been flipped over and now rests atop the left mandible. The only other alteration can be seen in the thoracic cage which was initially held together by desiccated skin. This skin has subsequently disintegrated, and the ribs have collapsed inwards on themselves.

The most striking animal remains in the dark zone are the complete, mummified remains of an adult female eland that lay in the far northeastern corner of the cave (Individual 9, Figure 10(a)). No visible part of the eland had been eaten in 1991, with the exception that the internal organs appeared to have been removed. Tooth puncture marks were visible along the neck line from just below the skull to the brisket. There was extensive damage to the skin in the neck area, possibly a result of being dragged, and there was some apparent chewing damage to the distal parts of all the visible ribs. The eland was lying on its side with the fore- and hind-limbs twisted back and out of anatomical position. Borer moth larvae had attacked the horns and hooves. A number of bones, probably derived from Individual 8 are also located near to the eland, most likely as a result of the eland being dragged over Individual 8.

By 1998, most of the skin of this animal had subsequently deteriorated, exposing most of the bones, except for the limb segments. Nonetheless, very little movement of these bones occurred. Water pools in the bottom of this cave in the rainy season, partially submerging the carcass. It is probable that the presence of this pooled water has aided the decomposition of this individual, but what long-term effects such immersion will have are unknown at this time.

Figure 12. Adult Burchell's zebra skeleton located in WU/BA-002. Carcass has been totally defleshed.

Figure 13. Recently uncovered skeletal remains underneath Individual 3 (compare with Plate 4). Water activity in the cave probably excavated these remains.

*Table 3. Age breakdown of leopard kills of large mammals in the Kruger National Park during the period February 1966 to January 1968 (data from Pienaar, 1969)*

| Species | Adult | Juvenile | Infant | Indet. |
|---|---|---|---|---|
| Waterbok (*Kobus ellipsiprymnus*) | 2 | 11 | 7 | 1 |
| Blue Wildebeest (*Connochaetes taurinus*) | 1 | 1 | 4 | 3 |
| Kudu (*Tragelaphus strepsiceros*) | 2 | 6 | 9 | 2 |
| Cape Buffalo (*Syncerus caffer*) | 0 | 1 | 2 | 0 |
| Burchell's Zebra (*Equus burchelli*) | 0 | 0 | 4 | 3 |
| Impala (*Aepyceros melampus*) | 600 | 76 | 57 | 58 |

Certainly it has aided in the deterioration of the skin, but how it will affect the bones remains to be seen.

The two juvenile porcupines (Individuals 10 and 11) were represented in 1991 only by two undamaged skulls which appeared to be of the same age. The most recent visit to the cave failed to relocate these skulls, and their fate is unknown.

WU/BA-001 is unique in that the entire accumulation discussed here can be attributed to one single leopard over a 1-year period. All specimens discussed were collected by this one animal, and therefore form a known, coherent assemblage of bones. However, within the same cave, recent water activity has revealed previously unknown skeletal remains of at least four other animals in the cave which were probably not the result of the activity of this one known leopard (Table 2). These include two class II bovids, a porcupine, and a hyrax, which were previously buried in sediment immediately underneath the cranium of Individual 3 (Figure 13). The presence of these bones indicates that this cave has been used previously, most probably by a feeding carnivore, and the possibility exists that many more specimens lie buried in the cave. However, in the interests of this important taphonomic study, no attempt will be made to excavate any other remains, since the prime concern of the study is the bone accumulation of a known carnivorous agent in a specified amount of time.

*Table 4. Large bodied felids in the South African Plio-Pleistocene fossil bearing caves. Data taken from Brain (1981) and Turner (1987, 1993)*

| | *Homotherium* | Megantereon | Dinofelis | Panthera pardus | Panthera leo | Acinonyx jubatus |
|---|---|---|---|---|---|---|
| Sterkfontein Member 4 | X | X | X | X | X | – |
| Sterkfontein Member 5 | X | X | – | X* | X | – |
| Swartkrans Member 1 (HR) | – | X | X | X | – | – |
| Swartkrans Member 1 (LB) | – | – | – | X | X | – |
| Swartkrans Member 2 | – | – | – | X | – | – |
| Swartkrans Member 3 | – | X | – | X | – | X |
| Kromdraai B | – | X | X | X | – | – |

**Panthera cf. pardus* has recently been identified in Sterkfontein Member 5 (T. Pickering, pers. comm.).

*Table 5. Species lists from leopard lairs in southern Africa*

| | | *Sites* | | |
|---|---|---|---|---|
| *Prey species* | Portsmut* | Hakos* | Quartzberg* | John Nash |
| Chacma baboon (*Papio cynocephalus*) | 1 (20) | 1 (1) | 1 (3) | |
| Leopard (*Panthera pardus*) | 1 (50) | 2 (26) | | |
| Wild dog (*Lycaon pictus*) | | 1 (39) | | |
| Caracal (*Felis caracal*) | | | | 1 |
| Blesbok (*Damaliscus dorcas*) | | | | 4 |
| Steebok (*Raphicerus campestris*) | | | 1 (3) | 1 |
| Klipspringer (*Oreotragus oreotragus*) | 2 (26) | 1 (4) | 4 (38) | |
| Gemsbok (*Oryx gazella*) | | 1 (1) | 1 (3) | |
| Kudu (*Tragelaphus strepsiceros*) | | 2 (8) | | |
| Eland (*Taurotragus oryx*) | | | | 1 |
| Mountain Reedbok (*Redunca fulvorufula*) | | | | 2 |
| Ovicaprid | | 1 (4) | | |
| Domestic cow (*Bos* sp.) | | 1 (7) | 1 (1) | |
| Class II bovid | 2 (10) | 1 (7) | | |
| Class III bovid | 1 (2) | 6 (96) | | |
| Zebra (*Equus zebra*) | 2 (13) | 2 (6) | 1 (1) | |
| Hyrax (*Procavia capensis*) | 4 (15) | 2 (4) | 6 (15) | |
| Porcupine (*Hystrix africaeaustralis*) | | | | 2 |
| Chelonia indet. | 1 (11) | 1 (6) | | |

*Portsmut, Hakos and Quartzberg data taken from Brain, 1981; numbers indicate minimum numbers of individuals (MNI), parentheses indicate number of identified specimens (NISP).

It would appear that the presence of desiccated skin on many of these carcasses has aided in their survival. The bones of those animals still possessing skin are those which tend to be the least scattered. In contrast, those carcasses which were defleshed to a greater degree are also those which are more widely scattered. The gradual burial of some of these carcasses by blocks of dolomite also seems to afford a measure of protection, both against scattering and against deterioration (providing the block did not damage the bones when it initially fell). Although all these carcasses described here were probably collected over a period of less than 1 year, they seem to represent numerous different stages of deterioration. Further, this deterioration does not appear to be mitigated so much by time as by the location of the carcass in the cave.

The leopard in question here had been viewed entering the cave, although she was never seen actually transporting a carcass. Nonetheless, the likelihood of another agent being responsible for the carcasses in the cave is small. The two entrances to the cave are steep and difficult to negotiate. Antelope would be very unlikely to attempt to enter the cave, since there is nothing of interest for them inside the cave (e.g. no mirabilite such as in the caves on Mt Elgon in Kenya). The cave is on the side of a hill, and is clearly visible; in other words, antelope would not be likely to fall into the cave accidentally, as in a natural death trap situation. Even if an antelope should fall into the cave, it would not reach the deepest recesses of the caves where the carcasses are located. Rather, it would be found in the Entrance Area of the cave, and as of yet no bones have been recovered from the Entrance Area. Although water pools in the bottom of the cave, there is no evidence of rapid water flow into the cave as would be seen had the carcasses been washed into the cave in a flood situation. The location of the cave on the side of a hill, over 3 km from the nearest river, also argues against water activity being an accumulating agent of bones in this cave.

Instead, there is a good deal of evidence that a leopard was the sole accumulating agent. Most of the carcasses are located in the Lower Chamber (Figure 1), more than 8 m from either of the entrances. It appears as though the eland (Individual 9) had been dragged over Individual 8, scattering its remains. The eland could not have passed through Entrance 2 or Passage 1 alive, since it would simply too large to fit. The only way it could have entered the cave was dead, with its limbs flaccid and in close proximity to its body, as would happen while being dragged.

The eland (Individual 9) showed tooth punctures along its neck, consistent with having been dragged, as well as removal of its internal organs, a characteristic leopard behaviour (Brain, 1981). The caracal (Individual 2) as well had been disemboweled, and it too showed tooth puncture marks along its neck. One of the blesboks in the Dark Zone (Individual 7) exhibited a characteristic "eaten out" appearance, again typical of leopard feeding (Brain, 1981). Also, most of the carcasses have been chewed by a large carnivore in a manner suggestive of leopard feeding (Brain, 1981). Individuals 3, 4, 5, 7, 8, and 9 all show tooth damage from the activity consistent with leopard activity, mostly confined to distal limb segments, ribs and horn cores, but occasionally to vertebrae, pelves, and some long bones. More detailed examination of the carnivore damaged bones was not possible without disturbing the context of the material, and therefore was not attempted. Further work will be directed at studying the damage inflicted by the leopard at a later date.

## Discussion

### *Leopards in trees*

Brain (1968, 1969, 1970, 1974, 1981) hypothesised that a significant contributing factor to some of the large bone accumulations in the Plio-Pleistocene dolomitic caves of the Transvaal was leopards utilising the trees that frequently grow from the entrances of these caves as private feeding retreats and food storage locations. The peculiar leopard behaviour of storing carcasses by stashing them in trees has been documented in many areas of southern Africa (Turnbull-Kemp, 1967; Pienaar, 1969; Brain, 1981; Mills, 1990; Skinner & Smithers, 1990; Estes, 1991). In contrast, the utilisation of caves as caches or feeding retreats has been noted as exceptional behaviour in Kenya (Simons, 1966), Tanzania (Sutcliffe, 1973), and Namibia (Brain, 1981). The storage of prey in trees and caves is usually considered a behavioural defence against hyaenas, lions, vultures and other scavengers taking the leopard's kill, though tree caching is considered to be more prevalent. By 1981, Brain had altered his earlier hypothesis to include leopard activities both in trees and in caves, and more recently (Brain, 1993) he again supported the idea of leopards depositing bones in Plio-Pleistocene caves both from trees and inside caves. However, most discussions of the accumulation of sites such as Sterkfontein and Swartkrans have focused on leopards in trees as a major source of bones.

In most areas where leopards were examined, the consumption of a kill stored in a tree would follow a typical pattern (after Brain, 1981). After a carcass had been dragged into a tree, a leopard would repeatedly return to that carcass to feed, sometimes for days, until it had either been consumed, or the leopard lost interest. During the process of consumption, parts of the prey animal would fall from the tree. The hypothetical situation in the fossil caves held that these falling bones would come to rest either in the cave itself, or in the catchment area of the cave, where they might eventually be brought in to the cave by water action or perhaps even porcupines (Brain, 1981). The result of this episodic deposition of bones would be that the ultimate fossil assemblage would represent numerous bony elements from a variety of different individuals scattered about the cave in an unpatterned spatial distribution.

The area of the John Nash Nature Reserve offers a unique opportunity to observe the behavior of leopards in the presence of dolomitic caves to determine if it fits Brain's earlier model. It would appear, in contrast to the "leopard in the tree" hypothesis, that leopards preferentially utilise the deep recesses of the caves themselves rather than overhanging trees. All of the carcasses attributed to the leopard in WU/BA-001 were deposited within the cave itself, and none could be ascribed to a kill which had been dragged into a tree, despite the fact that there are several large trees growing in the entrance of this cave (Figure 11).

This conclusion is supported by other caves in the area as well. Approximately 1 km to the south of WU/BA-001 another leopard lair was discovered, designated WU/BA-002. Located within the deepest recesses of this cave, in a blind side tunnel excavated by miners many years ago, was the virtually complete skeleton of an adult zebra (*Equus burchelli*) (Figure 12), an animal that would have weighed approximately 300 kg when alive (Skinner & Smithers, 1990). It is highly unlikely that the zebra accidentally fell into the cave, since the cave is quite visible, and there is nothing inside to attract a zebra to such a potentially dangerous place. The tunnel marking the zebra's final resting place is approximately 1·2 m in height, and 4 m in length. Zebras stand approximately 1·4 m at the shoulder (Skinner & Smithers, 1990), so had the zebra been alive when it entered the cave, it could not possibly fit into this small tunnel, unless it crawled in on its belly, a behaviour inconsistent with known zebra activities. The skeleton was totally defleshed, but owing to the extreme difficulty in gaining access to this carcass, we were unable to assess what, if any, damage had been done to the carcass by the presumed leopard collector. No other large carnivore (i.e. non-leopard) lair we have entered has displayed the complete, articulated skeletal remains from so large an animal.

Hyaena dens, as reported by Brain (1981) and Klein (1975), are characterised by highly fragmented bones and highly scattered carcasses or carcass elements, a conclusion we support based on the hyaena dens we have located in the John Nash Nature Reserve and surrounding area.

The conclusion reached based on WU/BA-001 is that in the presence of dolomitic caves, leopards will preferentially utilise the deep recesses of the cave itself, rather than overhanging trees, for the storage and private consumption of kills. This conclusion agrees with Brain's (1993) revised model for the deposition of hominid bones in the caves of the Sterkfontein Valley. This behaviour is also probably not restricted to dolomitic caves alone. The caves studied by Brain (1981), Simons (1966) and Sutcliffe (1973) were non-dolomitic, and yet housed numerous skeletal remains attributed to leopard activity. The implication for the hominid fossil caves of South Africa is that the distribution pattern of fossils should be viewed as a key to the feeding behaviour and activity pattern of an animal within the cave. Unless other taphonomic agents are in evidence, the presence of numerous articulated skeletons might be explained by the actions of felids, even in the absence of chewing marks, since these marks do not appear abundant on the bones in WU/BA-001. Finally, one should not underestimate the collecting capabilities of a single animal over a relatively short period of time.

### *Leopard killing capacity*

Although reports indicate that occasionally they do take large prey, leopards are thought to concentrate mainly on animals smaller than their own body size (Pienaar, 1969). In an exhaustive study of predation patterns in Kruger National Park during the periods 1936–1946 and 1954–1966, Pienaar (1969) noted that leopards killed numerous large animals. Table 3 shows that most of these larger animals were represented by juvenile or infant individuals weighing much less than the adult form (during the period February 1966–January 1968). Two adult waterbok (*Kobus ellipsiprymnus*) of unknown sex were taken; adult male waterboks weigh as much as 270 kg, while adult females are somewhat smaller and lighter (Skinner and Smithers, 1990). An adult wildebeest (*Connochaetes taurinus*), if male, would have weighed 250 kg, or 180 kg if female. Two adult Kudu (*Tragelaphus strepsiceros*) taken also fall into this similar weight category, with males weighing 250 kg, and females 200 kg. The largest buffalo (*Syncerus caffer*) taken was a juvenile of unknown size.

In spite of the leopards preference for relatively smaller prey animals, for example the large majority of Impala taken in Kruger (Table 3), larger prey are not as rare as may be thought. The adult female eland found in WU/BA-001 may represent the largest documented leopard kill in southern Africa. This animal, when alive would have weighed between 350 and 450 kg (Skinner & Smithers, 1990). The ability of leopards to kill and cache prey many times their own body weight would imply that perhaps we need not invoke the activity of sabre-tooth cats in the accumulation of the assemblages of bones found in the hominid bearing caves of South Africa.

### *The possible role of sabre-tooth cats*

The role of sabre-tooth and false sabre-tooth cats in the accumulation of the hominid fossil deposits has been discussed for a number of years. Vrba (1975, 1976) speculated that many of the prey animals found in the hominid fossil caves, particularly the bovids, were too large to have been caught and killed by leopards, and that therefore a larger culprit was required. She implicated sabre-tooth cats as the agent responsible, a conclusion Brain (1981, 1993) supported. Based on the size of some of the carcasses found in WU/BA-001 and other nearby caves (e.g. WU/BA-002), it would appear that leopards are capable of killing and transporting much heavier loads than was previously thought possible. The necessity of sabre-tooth and false sabre-tooth cats as collecting agents might thus fall away.

Numerous large carnivores have been found in the Plio-Pleistocene hominid bearing caves of South Africa. Table 4 lists the large-bodied fossil felids found in the various members of the caves of the Sterkfontein Valley. The presence of sabre-tooth cats appears to be rather sporadic. The genus *Megantereon* can be found in Sterkfontein Members 4 and 5, as well as Swartkrans Member 3 and Kromdraai A. Unfortunately, most of the specimens are not identifiable to the species level. *Megantereon gracile* is found in Sterkfontein Member 4, and *Megantereon cultridens* in Swartkrans Member 3. *Magnetron sp.* can be found in Sterkfontein Member 5, Swartkrans Member 1 (Hanging Remnant), and Kromdraai B. Swartkrans Member 1 (Lower Bank) and Member 2 are lacking in *Megantereon* altogether. *Homotherium* is found in Kromdraai A and Bolt's Farm, and Sterkfontein Members 4 and 5. The false sabre-tooth, *Dinofelis barlowi*, fossils are located in Sterkfontein Member 4, while indeterminate *Dinofelis sp.* specimens are found in Swartkrans Member 1 (Hanging Remnant) and Kromdraai B.

Although the absence of evidence cannot be held as evidence of absence, the likelihood that leopards, and not sabre-tooth cats, collected the large bovids in these assemblages, perhaps with the aid of hyaenas which are also prevalent in these fossil assemblages, appears to be strong. The necessity of sabre-tooth and false sabre-tooth cats as agents of collection is not compelling. The only carnivore consistently found in each member of every site is *Panthera pardus*, the leopard. While it is certainly possible that cave or tree frequenting behaviour marked some or all species of the genera *Homotherium, Megantereon* and *Dinofelis*, the more parsimonious explanation would appear to be that some other large felid was responsible for the felid derived bones. Since leopards are consistently found in the palaeoenvironment represented by each site member, they may be a more viable alternative source of bones than sabre-tooth cats. For instance, sabre-tooth or perhaps false sabre-tooth cats have been implicated as a possible source of bones in the Swartkrans Member 1 Lower Bank assemblage, and perhaps the Swartkrans Member 2 assemblage, yet there are no remains of any sabre-tooth or false sabre-tooth cats in either of these members. Leopards are found in both assemblages; in fact, leopards are the only felid found in Swartkrans Member 2, while leopards and lions (*Panthera leo*) are both found in the Lower Bank of Member 1. While the presence or absence of various carnivore remains in an assemblage does not mean that they can or cannot be considered to be collecting agents, it seems more probable that the leopards found ubiquitously in all assemblages were responsible for the bones, rather than the variably represented sabre-tooth and false sabre-tooth cats.

### *Variable behaviour of individual leopards*

Lam (1992) cautioned against underestimating the variability which may be possible in carnivore derived bone accumulations. Although specifically referring to spotted hyaenas, Lam's warning serves for leopards as well. Leopards tend to be quite catholic in their behaviours, a trait which carries over to their prey preferences. When no large prey are available, leopards are quite capable of subsisting on much smaller animals. Their ability to survive on virtually any form of carnivorous diet is probably what allows leopards to survive in areas long after other large bodied carnivores have been forced to move, usually in the face of human encroachment.

Table 5 lists the fauna recovered from three other leopard derived assemblages in southern Africa, compared to the John Nash lair. As can be seen, no taxon is shared by all four assemblages, and in fact, the WU/BA-001 assemblage shares only one species with one other site; *Raphicerus campestris* is found in both WU/BA-001 and the Quartzberg lair. Aside from this one species, WU/BA-001 houses a unique assemblage. While most likely only indicating the opportunistic behaviour of leopards in general, as well as the differences in local environments and fauna between the four sites, the differences in faunal content serve to emphasize the importance that these local environments, and individual leopard feeding habits, may have on the species present within a bone assemblage. The ultimate appearance and makeup of a faunal assemblage, particularly one collected by a leopard in this case, will be a result of the prevailing local conditions, as well as the individual idiosyncratic behaviour of the leopard itself.

### *Characteristics of leopard-derived assemblages*

Using WU/BA-001 as a model, a number of characteristics may be indicative of leopard derived assemblages. The animals in the cave are represented by relatively complete skeletons, or at least articulated remains. Chewing damage is mostly restricted to distal limb segments, rib ends and horn cores, and occasionally to vertebral processes, proximal humeri and pelves, although even this is limited in WU/BA-001. These bones, however, do tend to have low structural density (Lyman, 1994), probably mitigating their consumption by leopards. There is often little chewing damage apparent on the long bones, particularly on the long bones of the larger carcasses. Most elements of the carcass are present, and fracturing damage is rare. Also, despite the presence of brown hyaenas within the John Nash Nature Reserve, these bones have suffered no further carnivore ravaging beyond that inflicted by the leopard itself.

## Conclusions

The John Nash Nature Reserve provides what appears to us to be an appropriate model for the accumulation of felid derived remains in the Plio-Pleistocene hominid fossil caves of South Africa. In the presence of dolomitic caves, it would appear that leopards will preferentially utilise the deep recesses of the caves themselves for food caching and feeding retreats, rather than trees overhanging the cave entrances. The resultant faunal assemblages will thus reflect the patterned behaviour of these carnivores, rather than spatially unpatterned debris falling from trees. The implication of this interpretation may be that such analytical tools as minimum numbers of individuals (MNI) and minimum numbers of elements (MNE) are appropriate in the analysis of the faunal accumulations in cave assemblages. The individual appears to be the proper unit of analysis in assemblages collected by leopards, as opposed to the minimum number of animal units (MAU) and its body part unit of analysis recommended for use in human derived assemblages (Binford, 1978, 1981).

Although it is possible that sabre-tooth cats frequented the fossil caves of the Sterkfontein Valley during the Plio-Pleistocene, and perhaps deposited carcasses within the caves, it is not necessary to invoke their involvement based on large prey sizes alone. It would appear that when required, leopards are quite capable of capturing, killing and transporting extremely large carcasses, many times their own body weight. The hypothesised intra-cave behaviour of sabre-tooth and false sabre-tooth cats was based on the assumption that many of the carcasses in the hominid fossil caves were too large to be leopard accumulated. This wide-ranging hypothesis regarding the potential behaviour of a multitude of species and genera of sabre-tooth cats may not be a requirement when analysing the Sterkfontein Valley assemblages.

We must also use caution when attributing new faunal assemblages to a certain carnivorous agent. The contents of a given faunal assemblage may be quite distinct from another assemblage collected by the same type of agent. Lam (1992) has noted that hyaena derived assemblages are much more variable than had previously been assumed. In this instance, it must also be concluded that leopard accumulations may indicate the opportunistic behaviour of leopards in general, as well as the differences in local environments and fauna. Assemblages may reflect, not so much the collecting agent, but perhaps the prevailing local conditions in terms of environment and animal community.

## Acknowledgements

This research was funded by the Palaeo-Anthropology Scientific Trust and the National Geographic Society. Special thanks are due the John Nash family for unlimited access to the Reserve. Travis Pickering aided in photographing the material inside the cave, as well as providing information on the faunal material from Sterkfontein Member 5. Colin Menter and Chris "Zonk" Carlson helped with the mapping of the cave. We would also like to thank Jeff McKee for early work on this paper as well as aid with the photographs. Bob Brain provided critical comments and helpful insight on cave assemblages. An earlier version of this paper was presented at the Dual Congress 1998 in Sun City, South Africa.

## References

Behrensmeyer, A. K., Western, D. & Dechant Boaz, D. E. (1979). New perspectives in vertebrate paleoecology from a recent bone assemblage. *Paleobiology* **5,** 12–21.

Berger, L. R., Keyser, A. W. & Tobias, P. V. (1993). Brief communication: Gladysvale: first early hominid site discovered in South Africa since 1948. *American Journal of Physical Anthropology* **92,** 107–111.

Binford, L. R. (1978). *Nunamiut Ethnoarchaeology*. New York: Academic Press.

Binford, L. R. (1981). *Bones: Ancient Men and Modern Myths*. New York: Academic Press.

Brain, C. K. (1968). Who killed the Swartkrans ape-men? *South African Museums Association Bulletin* **9,** 127–139.

Brain, C. K. (1969). The probable role of leopards as predators of the Swartkrans australopithecines. *South African Archaeological Bulletin* **24,** 170–171.

Brain, C. K. (1970). New finds at the Swartkrans Australopithecine site. *Nature* **225,** 1112–1119.

Brain, C. K. (1974). A hominid skull's revealing holes. *Natural History* **83,** 44–45.

Brain, C. K. (1981). *The Hunters or the Hunted?* Chicago: University of Chicago Press.

Brain, C. K. (1993). A taphonomic overview of the Swartkrans fossil assemblages. In (C. K. Brain, Ed.) *Swartkrans, a Cave's Chronicle of Early Man*. Pretoria, Transvaal Museum Monographs **8,** 258–264.

Busse, C. (1980). Leopard and lion predation upon chacma baboons living in the Moremi Wildlife Reserve. *Botswana Notes and Records* **12,** 15–21.

Estes, R. D. (1991). *The Behavior Guide to African Mammals*. Berkeley: The University of California Press.

Hughes, A. R. (1954*a*). Hyaenas versus australopithecines as agents of bone accumulations. *American Journal of Physical Anthropology* **12,** 467–486.

Hughes, A. R. (1954b). Habits of hyaenas. *South African Journal of Science* **51,** 156–158.

Hughes, A. R. (1961). Further notes on the habits of hyaenas and bone gathering by porcupines. *Zoological Society South African News Bulletin* **3,** 35–37.

Klein, R. G. (1975). Palaeo-anthropological implications of the non-archaeological bone assemblage from Swartklip 1, south-western Cape Province, South Africa. *Quaternary Research* **5,** 275–288.

Lam, Y. (1992). Variability in the behavior of spotted hyaenas as taphonomic agents. *Journal of Archaeological Science* **19,** 389–406.

Le Roux, P. G. & Skinner, J. D. (1989). A note on the ecology of the leopard (*Panthera pardus* Linneaus) in the Londolozi Game Reserve, South Africa. *African Journal of Ecology* **27,** 167–171.

Lyman, R. L. (1994). *Vertebrate Taphonomy*. Cambridge: Cambridge University Press.

Maguire, J. (1976). *A Taxonomic and Ecological Study of the Living and Fossil Hystricidae, with Particular Reference to Southern Africa*. Ph.D. Thesis. University of the Witwatersrand.

Martini, J. E. J. & Keyser, A. W. (1989). The caves of the John Nash Game Reserve in the Krugersdorp area. *Bulletin of the South African Speleological Association* **30,** 39–45.

Mills, M. G. L. (1990). *Kalahari Hyaenas: The Comparative Ecology of Two Species*. London: Unwin-Hyman.

Newman, R. (1993). The incidence of damage marks on Swartkrans fossil bones from the 1979–1986 excavations. In (C. K. Brain, Ed.) *Swartkrans, a Cave's Chronicle of Early Man*. Pretoria, Transvaal Museum Monographs **8,** 217–228.

Pienaar, U. de V. (1969). Predator-prey relationships amongst the larger mammals of the Kruger National Park. *Koedoe* **12,** 108–176.

Schaller, G. B. (1972). *The Serengeti Lion: A Study in Predator–Prey Relations*. Chicago: University of Chicago Press.

Scott, L. & Klein, R. G. (1981). A hyena-accumulated bone assemblage from the late Holocene deposits at Deelpan, Orange Free State. *Annals of the South African Museum* **86,** 217–227.

Simons, J. W. (1966). The presence of leopard and a study of the food debris in the leopard lairs of the Mount Suswa caves, Kenya. *Bulletin of the Cave Exploration Group of East Africa* **1,** 51–69.

Skinner, J. D. and Smithers, R. H. N. (1990). *The Mammals of the Southern African Subregion*. Pretoria: University of Pretoria Press.

Smith, M. R. (1977). Movement patterns and feeding behavior of Leopard in the Rhodes Matapos National Park, Rhodesia. *Arnoldia Rhodesia* **8,** 1–16.

Sutcliffe, A. J. (1973). Caves of the east African Rift Valley. *Transactions of the Cave Research Group of Great Britain* **15,** 41–65.

Turnbull-Kemp, P. (1967). *The Leopard*. Cape Town: Howard-Timmins.

Vrba, E. (1975). Some evidence of the chronology and palaeoecology of Sterkfontein, Swartkrans and Kromdraai from the fossil Bovidae. *Nature* **254,** 301–304.

Vrba, E. (1976). *The Fossil Bovidae of Sterkfontein, Swartkrans and Kromdraai*. Pretoria, Transvaal Museum Memoir No. 21.