

Cave Usage by Multiple Taphonomic Agents: Issues towards Interpreting the Fossil Bearing Cave Deposits in South Africa

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Abstract The current use of caves in South Africa by three distinct collectors of faunal remains, leopard (*Pantherapardus*), brown hyaena (*Parahyaena brunnea*) and porcupine (*Hystrixafricaeaustralis*) as well as other species of taphonomic significance raises serious questions with regard to the interpretation of the hominin bearing caves. As part of study using multiple camera traps to monitor a number of caves in the Cradle of Humankind over a period of at least 20 months, we found that an individual cave may be used by no less than seven species. The results indicate that identifying a single collector or modifier from a fossil assemblage which may span thousands of years is not as straightforward as previously hypothesized.

Keywords: behavior, taphonomy, bone collecting, brown hyaena, warthog, honey badger, jackal, porcupine, leopard, cave usage

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1. Introduction

The interpretation of Plio-Pleistocene fossil cave deposits in relation to carnivore accumulations has been a point of contention amongst researchers for a number of years [1-19]. Carnivores and porcupines have been associated with the various members of Sterkfontein [3]. The site of Swartkrans was, at one time, thought to be the sole collection of leopards [3,9]. Other studies suggest that while leopards did play a role in the Swartkrans collections, other large bodied carnivores may have had a hand in the faunal assemblages [12]. The constant amongst the interpretations of palaeoanthropological fossil assemblages is the attempted identification of the collector, be they carnivore, hominin, rodent or avian. Little has been published on other potential mammalian taphonomic agents working on the faunal remains prior to fossilization.

Caves provide a multitude of amenities to animals including, but not limited to; a place to rear young [20], a place to cache food [9,21,22,23], a place to thermo-regulate [24,25], a hibernaculum [26], or use as a latrine [27]. Dolomite caves, which are very common in the Cradle of Humankind, Gauteng, South Africa, are often created in such a way to provide narrow openings and small corridors that are intermittently blocked by rock collapses [28], and reopened by erosion (McCarthy, pers. comm, 2011). Considering all the documented use of caves, it is important that we examine the cave systems

located in the Cradle of Humankind in order to determine how the modern fauna are making use of them today. Animals are often attributed to accumulations with only small amounts of evidence to imply their participation, such as tooth pit size [13]. There have been attempts to define criteria that identifies hyaena from hominid accumulations [5] and attempts to refine said criteria [11], although none of these have shown concretely that we can differentiate between these particular accumulators [22,29]. Here we discuss findings with regard to cave usage by multiple taphonomic agents. Caves were observed in the Cradle of Humankind, as various wild animals made use of said caves. The question is, considering we have evidence of at least four taphonomic agents (leopard (*Pantherapardus*), warthog (*Phacochoerus africanus*), porcupine (*Hystrixafricaeaustralis*), and honey badger (*Mellivoracapensis*)) appearing at the same cave within a short time period then how can we attribute, with any amount of certainty, the collections we find in the fossil record to a single taphonomic agent? The answer is that we cannot, especially when at least two of these agents have not been well studied as taphonomic agents.

2. Study Site

The study was conducted on the Malapa and John Nash Nature Reserves located within the Cradle of Humankind, which is located 45 km outside of Johannesburg, South Africa (Figure 1). These reserves are known for the fossil

sites of Gladysvale and Malapa [30,31]. The combined reserves comprise approximately 6730 hectares of privately owned land that gives a diversity of geology to examine. The geology is mainly dolomite, open bush,

rocky outcrops and also a rare tufa deposit. This geology provides a high number of cave systems for animals to utilize. Various aspects of the geology and karst systems on the reserve have been studied previously [9,28,31].

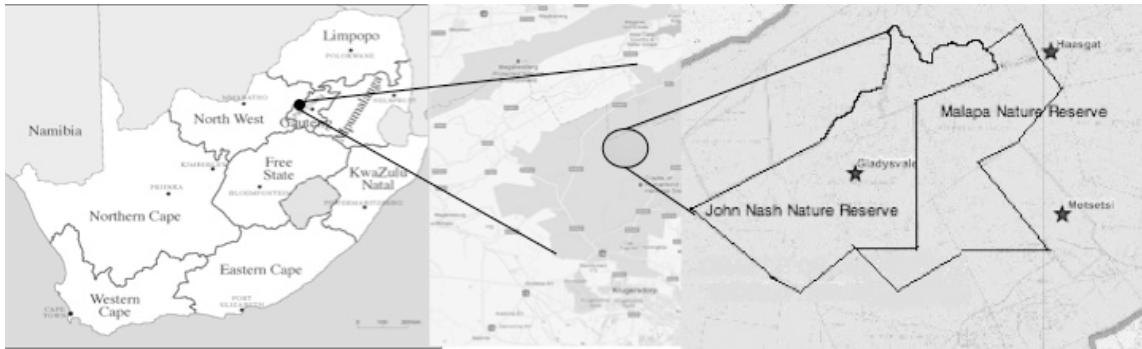


Figure 1. Map showing location of Malapa and John Nash Nature Reserves within the Cradle of Humankind, South Africa

Transitioning between the Carletonville Dolomite Grasslands and the Moot Plain Bushveld the reserves consist of grasslands, Backenveld vegetation and wetlands [32]. The combined reserves support a wide variety of free ranging wildlife, including, but not limited to, sable (*Hippotragus niger*), blue wildebeest (*Connochaetes taurinus*), kudu (*Tragelaphus strepsiceros*), impala (*Aepyceros melampus*), blesbok (*Damaliscus pygargus phillipsi*), eland (*Taurotragus oryx*), mountain reedbeek (*Redunca fulvorufula*), chacama baboon (*Papio hamadryas ursinus*), vervet monkey (*Chlorocebus pygerythrus*), zebra (*Equus quagga*), giraffe (*Giraffa camelopardalis*), warthog (*Phacochoerus africanus*), brown hyaena (*Hyaena brunnea*), leopard (*Panthera pardus*), black-backed jackal (*Canis mesomelas*), caracal (*Caracal caracal*), serval (*Leptailurus serval*), African clawless otter (*Aonyx capensis*), honey badger (*Mellivora capensis*), slender mongoose (*Galerella sanguinea*), porcupine (*Hystrix africae australis*) and both species of genet (*Genetta genetta* & *Genetta tigrina*) [33]. Of particular interest are species cited in the palaeoanthropological literature as having a direct impact upon fossil

assemblages. Namely these include the leopard, hyaena and porcupine [3,5,9,11,13,21,22,29,34,35].

3. Materials and Methods

Twelve motion sensor trail cameras (either Moultrie[®], Bushnell[®] or Lynx Optics[®]) were set up at varying locations on the nature reserves and were checked at 20-30 day intervals. The motion sensor was set to take three time-lapsed photos when movement is detected. With this we were able to monitor the various caves and subsequent usage with minimal disturbance to the wildlife. The cameras have been placed taking into account locations suggested by individuals who work at the reserve and have seen particular animals, as well as by tracking spoor when possible. Most locations were chosen from witness reports as the geology at the nature reserves makes the terrain difficult for tracking spoor. Photos were time and date stamped, as well as recorded ambient temperatures.



Plate 1. Uitkomst Cave with evidence of porcupine as well as brown hyaena and warthog in the cave

4. Results

Over the course of this study we observed four caves being used by taphonomic agents (Table 1), one of which

has what appears to have at least two separate entrances. This particular cave, known as Uitkomst Cave, is a Late Iron Age site. This cave has a cavern entrance on one side and at least one entrance located within a rock collapse. Brown hyaena and warthog were recorded at this cave, as well as a large amount of porcupine quills and scat (Plate 1). The second cave, referred to as Porcupine Cave, is a dolomitic cave and has had brown hyaena, large-spotted genet, black-backed jackal, Chacma baboon, warthog, porcupines and porcupets documented entering/exiting the cave. See examples on Plate 2. This cave is not a cavern entrance, but rather is a long and narrow fissure cave with

a smaller entrance. These two caves were formed in dolomite, by a karst system that is part of the Transvaal Supergroup [27], and have a different type of geology to the tufa caves. The next two caves are formed within the same tufa formation on the Malapa Nature Reserve and are referred to as the Upper Tufa Cave and the Lower Tufa Cave. The Upper Tufa Cave is the most active cave with at least seven different animals seen at the entrance including: leopard, warthog, porcupine, Chacma baboon, vervet monkey, honey badger and kudu (See Plate 3). The Lower Tufa Cave is the least active with only three animals seen at the cave: kudu, sable, and warthog.



Plate 2. Examples of warthog and porcupine entering Porcupine Cave



Plate 3. Examples of leopard, porcupine, warthog and honey badger at Upper Tufa Cave

Table 1. Cave usage by species

Animal ACTION	Lower Tufa	Porcupine	Uitkomst	Upper Tufa	Grand Total
Warthog	14	29	20	33	96
ENTER	6	18		16	40
EXIT	7	11		11	29
GUARD	1			5	6
INSIDE			20		20
LOITER				1	1
Vervet monkey				5	5
LOITER				5	5
Sable	2				2
LOITER	2				2
Porcupine		15		3	18
ENTER		7		1	8
EXIT		8		2	10
Leopard				1	1
LOITER/ENTER				1	1
Large-spotted genet		1			1
EXIT		1			1
Kudu	1			3	4
LOITER	1			3	4
Jackal		2			2
ENTER		2			2
Honey badger				2	2
LOITER				2	2
Chacma baboon		3		2	5
INSIDE		2			2
LOITER				2	2
ABOVE		1			1
Brown hyaena		1	1		2
ENTER		1			1
INSIDE			1		1
Grand Total	17	51	21	49	138

Table 1 indicates each time a species is entering, exiting, inside of or loitering near the entrance of a cave.

5. Discussion

The animals discussed henceforth both affect bones and use caves in different ways, with special attention paid to four of the animals that we have observed at cave entrances thus far. Some animals that we are looking at are known collectors of bone, the porcupine for example is a well-known collector and modifier of bone [2,3,5,23,36,37,38,39,40], as are hyaenas [1,3,5,11,12,13,14,17,21,22,23,29,38,41,42,43,44], leopards [3,9] and suids [45], although hyaenas and porcupines tend to collect larger amounts of bones.

The hyaena and porcupine prefer different kinds of bones, hyaenas prefer greasy bones, such as pelvis, vertebrae and ribs, for nutritional value (if meat is not available) [6,18,46,47], while porcupines prefer drier bones to hone their teeth or possibly due to osteophagia [3,48,49,50]. The porcupine will often collect dry bones to prevent botulism [36] that have been left behind by the hyaenas and other carnivores and thus derive a fitness benefit. While porcupine accumulations are easy to determine based on gnaw marks [2,3,5] and a high percentage of gnaw marks [2,3] hyaena accumulations appear to change dramatically depending on environmental conditions at time of collection [22].

In addition to bone collecting it is also important to examine the way that animals “use” the bones. Felids often deflesh their prey [10,13,51], while hyaenas will deflesh and crush the bones, occasionally digesting bone as well [11]. This is interesting because as hyaenas are more often scavengers than leopards their ability to crush bones allows them to reach nutrients that are stored in the bone, including grease and marrow. Suids have also been

observed as taphonomic agents by reference [52] in Spain and by reference [45] in Borneo, with corroborating evidence of suids in Africa acting on remains. Although warthogs are not often considered taphonomic agents osteophagia has been observed on 11 occasions by tame warthog in Uganda [53], and reference [54] has witnessed warthogs going after carcasses and with bone fragments in faeces. The evidence for honey badgers [55] as taphonomic agents is less conclusive because of the lack of published work, regarding taphonomy, on this species. Badgers are hunters and scavengers and known for their capability of scavenging large prey [37,56,57,58]. While studies have been done on European badgers (*Melesmeles*) and North American badgers (*Taxideataxus*) [56,57,59,60] where bone gnawing was documented, little is known about the honey badgers affect upon bones. Reference [56] discusses the breaking down of a sheep (*Ovisaries*) carcass by captive European badgers and reference [58] furthermore suggests lambs being killed by badgers. Reference [55] discuss the analysis of faecal matter of a honey badger to determine its food sources, implying that honey badgers does in fact consume skeletal elements (as indicated by the ability to determine prey remains from faeces) and as such is a potential taphonomic agent. However most research on the honey badger has been conducted by Begg [61,62] and is based mainly in the Kalahari of South Africa. Reference [63] states that honey badgers often eat the entirety of their prey with the exception being larger prey, such as the springhares (*Pedetescaensis*) and black-backed jackals, and larger prey was often eaten in underground burrows making it difficult to observe.

The behaviour of leopards, porcupines and hyaenas using caves is a well-documented occurrence

[2,3,9,13,20,21,22,23,38,40,64,65]. Jackals [16,23], warthogs [3,20,23] and honey badgers have also been documented as cave users [55,59,62,66]. Brown hyaena, striped hyaena (*Hyaenahyaena*) and leopard are known to cache and transport food back to their maternity dens, which leads to the relatively large bone accumulations found in the dens of these species [5,9,21,22,67,68,69,70]. Brown hyaenas are not known to be effective hunters and depend heavily on scavenged remains from other animals prey, often relying on their ability to smell a carcass up to 14 km away [70]. The brown hyaena and jackal are known to compete for food and occasionally derive fitness benefits by stealing food from one another [69,71,72]. According to reference [69], despite their mutual competition for food and thievery in the open veld, jackals are not known to scavenge from hyaena food caches, while reference [23] have seen signs of jackal occupation in hyaena dens of the Masai Mara National reserve, Kenya. Jackals share prey with animals that are frequent cave users and known taphonomic agents such as the brown and spotted hyaenas [23,69,71,72,73]. It is of note that during research in Namibia in 2005 a pair of jackals, with pups, briefly occupied a known brown hyaena den, and the pups were observed gnawing on bones previously collected by the brown hyaenas (Observed by BK).

6. Conclusion

This study has given us insight into cave usage by a variety of animals in the Cradle of Humankind. As most of the fossil sites in the Cradle of Humankind span thousands, if not millions of years, to say that an entire fossil assemblage is the result of an individual species would be remiss. To date we have recorded seven potential taphonomic species at the same cave in a short time period. Two of the seven species are known taphonomic agents (leopard and porcupine) and the other two are potential taphonomic agents based upon studies on similar, captive or tame species (honey badger and warthog) with the remaining three being Chacma baboon, vervet monkey and kudu. If the two potential agents are indeed bone modifiers than we have four bone modifying agents at one cave in the period of one month.

Even when using previously published data [2,4,5,11,13,29] to identify the producer(s) of faunal accumulations it is possible other agents have also been in contact with the accumulation. Reference [39] reports "that several specimens show overlapping marks from numerous agents (e.g., punctate depressions & porcupine gnawing), demonstrating that multiple accumulators acted upon individual specimens" [[39] p. 1109] in regards to specimens recovered from Plovers Lake, in the Cradle of Humankind, South Africa. Although hyaenas act on bones quite aggressively, marks previously made by other agents can still be seen [10] therefore it is vital to look thoroughly at any hyaena assemblages for marks that may belong to another agent. To complicate the issue even more it has also been shown that the different species of hyaena over varying geographical and environmental conditions leave behind different taphonomic signatures [22,42].

There has been a great deal of discussion surrounding the abundance of certain animal remains as evidence of specific taphonomic agents acting on an accumulation

[2,3,5,11,21,38,39,64], but this data is not conclusive [22,29]. We have observed that many animals eat/hunt based on what is available to them, for example on the west coast of Namibia brown hyaenas are known to favour the Cape fur seal (*Arctocephalus pusillus pusillus*) [38,65,72,73]. So to say that an abundance of skeletal remains of the Cape fur seal implies brown hyaena is not the same as saying that a lack Cape fur seal skeletal elements in a given accumulation means it is not brown hyaena. Brown hyaena accumulations are typically reflective of the environment because they scavenge from the kills of many different species [69], except on the coast where there is an abundance of Cape fur seals and lack of other large predators, thus the brown hyaena becomes the apex predator, while with other predators this may not be the case. For example it is possible that there were many hyraxes but they may not be present in an accumulation produced by an agent that does not favour hyrax. "The literature reflects a great rift between estimates of leopard predation based on observed kills and carcass remains versus actual leopard diet as determined by scat analysis" Reference [38 p. 5]. We must take this into consideration as we examine faunal accumulations, including looking at fossil faunal remains in cave sites where from death to fossilization there could have been many different agents using that particular cave, whether they modified one bone or one hundred. Consequently the animals in this study have different approaches to how they may affect animal carcasses and it is very possible for them all to act on the same set of bones. Under these circumstances it would be very difficult to pin point which taphonomic agents were responsible for a fossil accumulation that spans thousands, if not hundreds of thousands, of years. Lastly we will mention that although we may be able to identify the primary collecting and/or modifying agent that does not mean that it is the only taphonomic agent, as it is probable that other species have entered the cave and gnawed on the accumulation that had been left by the initial accumulator. It is imperative to consider all of these factors when assessing an accumulation.

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Competing Interests

The authors have no competing interests be they financial or otherwise.

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