



# Distinguishing hominin and brown hyena (*Parahyaena brunnea*) bone accumulations from the Middle Stone Age in South Africa

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## ABSTRACT

Brown hyenas (*Parahyaena brunnea*) are often implicated as either contributing to or scavenging faunal remains at archaeological sites in southern Africa. Various criteria have been established to distinguish between anthropogenic and brown hyena accumulations. Brown hyenas regularly feed on other carnivores. It is expected that such hyena assemblages will have a greater diversity of carnivore species, compared to accumulations of humans. We test this notion using anthropogenic accumulations dating to the Middle Stone Age from the Eastern and Western Cape of South Africa, as well as (nearly) contemporaneous fossil brown hyena accumulations from the same region, using a Carnivore Richness Index (CRI). This index measures the richness of carnivore taxa in samples against the richness of ungulate taxa. The results show that CRI values are generally low for faunas from layers and whole assemblages accumulated by hominins. The range is between 0.13 and 0.42 when all the layers are considered together as a whole for individual sites. For fossil brown hyena samples, the CRI values are consistently higher relative to hominin-induced samples with values ranging between 0.40 and 0.52. The results indicate that quantification using the CRI effectively discriminates layers and sites with higher probabilities of brown hyena activity from those of anthropogenic accumulations. Thus, if used in conjunction with other methods such as the carnivore-ungulate ratio, taphonomic modifications and the presence of juvenile hyena remains and coprolites, it will allow for better identification of the agents involved in the accumulation process.

## 1. Introduction

The Middle Stone Age (MSA) of southern Africa, dated between ca. 300,000 to 30,000 years ago, is an important period in the study of human evolution. It provides a crucial archaeological record regarding the origin of modern humans, and its complex behaviours (overview in Wadley, 2015). Humans were actively hunting a wide variety of prey (Badenhorst et al., 2022a), but there are often indications that multiple agents of accumulation, including brown hyenas (*Parahyaena brunnea*), contributed fauna to assemblages (e.g. Thompson, 2010; Thompson and Henshilwood, 2011). The other hyena species found in southern Africa during the late Pleistocene, the spotted hyena (*Crocuta crocuta*), are active hunters who sporadically accumulate bone remains (Brain, 1981). However, it is widely accepted that brown hyenas are actively accumulating skeletal remains of hunted and scavenged prey in dens, especially of other carnivore species (e.g. Skinner, 1976; Mills and Mills, 1977; 1978; Brain, 1981; Skinner and Van Aarde, 1991).

In the Eastern and Western Cape of South Africa, faunal assemblages

often contain chew marks and gastric etching attributed to carnivores in general. However, such assemblages often lack coprolites or juvenile hyena remains (e.g. Marean et al., 2000; Henshilwood et al., 2001; Thompson and Henshilwood, 2011; Badenhorst et al., 2016; Reynard and Henshilwood, 2019; Reynard, 2022; Ezeimo et al., 2024). In such cases, brown hyenas may have used these shelters transiently as temporary dens as feeding retreats or they scavenged bone following times of human occupation (Avery et al., 2008; Thompson, 2010; Thompson and Henshilwood, 2011; Val et al., 2014). For example, in dryer parts of southern Africa, brown hyenas resort to scavenging old carcasses as other predators disperse and fresh kills become less common (Owens and Owens, 1979). Moreover, brown hyena males are often nomadic and non-group living (Drea et al., 2018). Brown hyenas often use a variety of locations for feeding and breeding, either permanently or semi-permanently, including abandoned antbear holes, caves, rocky areas, crevices or thick bush cover (Skinner, 1976; Mills, 1982; Rautenbach, 1982). In cases where brown hyenas used shelters transiently, or scavenged bone remains following human occupation, the established

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criteria for recognising the role of brown hyenas have a lower visibility.

As indicated, MSA sites in the Eastern and Western Cape of South Africa have been instrumental in tracing the evolution of modern human behaviour by anatomically modern humans (e.g. Wadley, 2015; and references therein). As a result, an understanding of the role of different faunal accumulators of the faunal assemblages are crucial to delineate the behaviour of early modern humans. The Eastern and Western Cape provinces of South Africa yield numerous MSA sites (Fig. 1), which show a high probability of hominin accumulations. This is based on *inter alia*, the presence of cultural artefacts intermingled with animal remains, evidence for butchering and burning of bone remains, lack of hyena coprolites, and low incidences of carnivore chew marks. Moreover, a previous study established that these samples are large and thus useful for comparisons since small sample sizes often skew results (Badenhorst et al., 2022b). However, at some of these sites, such as Pinnacle Point and Blombos Cave (Reynard and Henshilwood 2017; 2019; Thompson, 2010; Thompson and Henshilwood 2011), there is evidence that carnivores, including hyenas, contributed some remains such as small bovids to the samples.

The same region also contains several faunal assemblages that were largely accumulated by brown hyenas. These sites date from the Middle to Late Pleistocene (about 781,000 to 11,000 years ago) and are thus broadly contemporaneous to the MSA assemblages. However, some sites, such as Duinefontein 2, have evidence of ephemeral hominin activity (Cruz-Uribe et al., 2003). The identification of brown hyenas as the main agent of accumulation is based on findings such as the presence of chew marks and hyena coprolites (Grine and Klein, 1993; Cruz-Uribe et al., 2003), the rich diversity of carnivore remains (Grine and Klein, 1993), especially the black-backed jackal (Klein, 1983) and a dominance of medium-sized bovids over smaller ones (Grine and Klein, 1993). All these MSA and hyena assemblages are located in the Cape Floristic Kingdom (Luyt et al., 2000) and thus the animals occurring in this region are relatively uniform (Skinner and Chimimba, 2005), making these samples suitable for comparison.

## 2. Recognising brown hyena assemblages

Bone assemblages from caves and shelters that have been accumulated by brown hyenas have certain characteristics (Palomares et al., 2022) such as chew marks (Blumenschine, 1988). The presence of juvenile hyena remains (Kuhn et al., 2010), hyena coprolites (Cruz-Uribe, 1991) and a lack of cultural artefacts (Scott and Klein, 1981) all indicate hyena activity. Moreover, a high ratio of carnivore vs. ungulate remains (based on either the Number of Identified Specimens [NISP] or the Minimum Number of Individuals [MNI]) is also indicative of hyena activity, since brown hyenas frequently prey on other carnivores (Mills

and Mills, 1977; Scott and Klein, 1981; De Ruiter et al., 2008; Kuhn et al., 2010; Fourvel et al., 2018). The great diversity of carnivore remains in faunal samples accumulated by brown hyenas has long been established (e.g. Scott and Klein, 1981; Pickering, 2002). For example, Kuhn et al. (2010,) suggested that a high MNI value of 30% or more carnivores, compared to ungulates, indicate brown hyena assemblages. Hominins consumed and interacted less frequently with carnivores (Scott and Klein, 1981; but see Val et al., 2020). While the dietary niches of hominins overlapped with those of brown hyenas, the former was able to regularly bring down large and potentially dangerous prey (e.g. Klein and Cruz-Uribe, 2000; Van Pletzen, 2000; Avery et al., 2008; Rector and Reed, 2010; Steele and Klein, 2013; Reynard et al., 2016; Van Pletzen-Vos et al., 2019; Reynard and Wurz, 2020; Ezeimo et al., 2024). Seal (*Arctocephalus pusillus*) remains accumulated by brown hyenas tend to have a higher representation of vertebrae and usually have a wider range of seal ages (Klein et al., 1999). In addition, the presence of jackals are also a signal of brown hyena activity (Klein et al., 1999).

These criteria are beneficial when multiple lines of evidence are used when applied to archaeological and fossil assemblages (Pickering, 2002; Kuhn et al., 2010). However, the criteria have limitations. The size of the tooth marks (Pobiner, 2008) overlaps between different carnivore taxa (Delaney-Rivera et al., 2009). While the frequency of chew marks is high in bone collections of modern dens of brown hyenas (often 50 % or more, Kuhn et al., 2010), for fossil samples however, this frequency is often quite low (e.g. Cruz-Uribe, 1991; Stynder, 1997), due to factors such as variable damage that are difficult to distinguish from other sources, as well as poor surface preservation (Cruz-Uribe, 1991). Thus, while a high representation of chew marks are indicative of hyena activity, a low frequency does not necessarily imply low carnivore activity (Cruz-Uribe, 1991). For example, at the Late Holocene hyena accumulation of Deelpan (Free State province, South Africa), only 2% of the fauna showed chew marks (Scott and Klein, 1981). Moreover, the frequency of chew marks left by brown hyenas is influenced by various factors, including the size of the prey, bone density, length of fragments, the size of clans and the time spent to access a carcass (Faith 2007, Fourvel et al., 2015).

Using faunal ratios such as the carnivore-ungulate ratio to distinguish samples accumulated by hominins and carnivores have long been employed in Africa (e.g. Cruz-Uribe, 1991; Kuhn et al., 2010), the Levant and Europe (e.g. Rabinovich et al., 2004; Dusseldorp, 2013; Orbach and Yeshurun, 2021). While the carnivore-ungulate ratio is useful for samples that were quantified using the same method, such as NISP or MNI, comparing results quantified using different methods is more problematic (ie, NISP vs. MNI, see Badenhorst et al., 2021). Often, like in the case of many MSA sites from the Eastern and Western Cape in South Africa, the Cape fur seal (*Arctocephalus pusillus*) make up a substantial

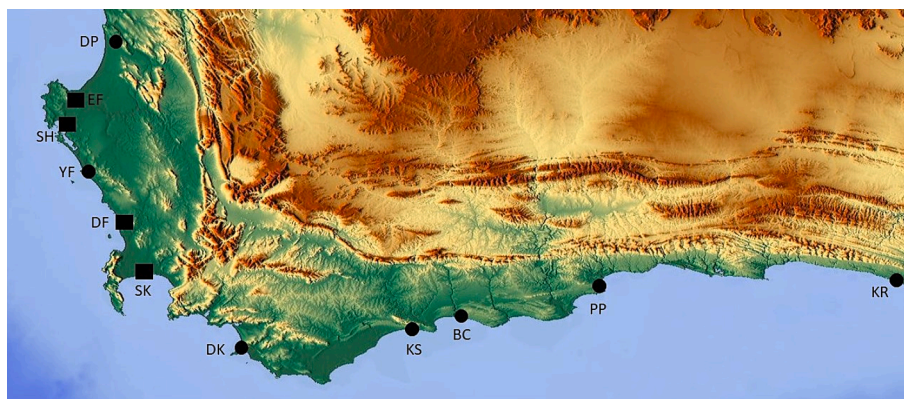


**Fig. 1.** Hominin and archaeological hyena samples from the Eastern and Western Cape of South Africa used to calculate the CRI. The hominin accumulations (circles on map): BB Blombos Cave, DK Die Kelders, DP Diepkloof Shelter, KD Klipdrift Shelter, KR Klasies River Mouth, PP Pinnacle Point (also a hyena sample), YF Ysterfontein. The hyena accumulations (squares on map): DF Duinefontein, EF Elandsfontein Bone Circle, SH Hoedjiespunt and Sea Harvest, PP Pinnacle Point, SK Swartklip.

proportion of the fauna (e.g. Klein, 1976; Grine and Klein, 1993; Klein and Cruz-Urbe, 2000; Van Pletzen, 2000; Avery et al., 2008; Rector and Reed, 2010; Badenhorst et al., 2016; Reynard and Wurz, 2020). In such cases, the use of the carnivore-ungulate ratio can potentially mask the role of other agents of accumulation (for this reason, Badenhorst et al., 2021 excluded seals from their carnivore – ungulate calculations). Where samples are quantified using MNI to infer brown hyena accumulations (Kuhn et al., 2010), a myriad of factors complicate such results. MNI is not an actual number (Perkins, 1973:369) but merely an ‘at least’ amount of animals responsible for a sample (Plug and Plug, 1990). Potentially, each bone comes from a different individual, unless it can be proven otherwise (Perkins, 1973:367). There is no consensus on how to calculate MNI which makes comparisons between assemblages difficult (Klein and Cruz-Urbe, 1984:26–28). The scale at which MNI is calculated (layer, phases or entire samples) will result in vastly different MNI’s (Casteel, 1977:126; Grayson, 1984:29; Plug and Plug, 1990:53).

### 3. Brown hyena prey

Today, brown hyenas are restricted to southern Africa (Skinner and Chimimba, 2005). However, their past distribution was much wider, including eastern Africa during the Pleistocene (Werdelin and Barthelme, 1997), and spanning as far north as Spain during the Upper Pliocene (Arribas et al., 2003). Brown hyenas likely evolved from the Pliocene form *P. howelli* in eastern Africa (Werdelin and Lewis, 2020), and today, they typically live in small social groups of varying sizes (Mills, 1984). Brown hyenas direct their hunting efforts towards medium and smaller animals including carnivores such as Cape fur seals, bat-eared foxes (*Otocyon megalotis*), aardwolf (*Proteles cristata*), African wildcats (*Felis lybica*), honey badgers (*Mellivora capensis*) and striped polecat (*Ictonyx striatus*). Prey is obtained through active hunting, competition for subsequent kills around carcasses, and during scavenging (Mills, 1990). While brown hyenas have a diverse diet throughout the subcontinent, they tend to focus on consuming abundant prey in their surrounding habitat (Mills, 1990; Burgener and Gusset, 2003; Maude, 2005; Slatter and Muller, 2014). For example, along the Namib coast, the diet of brown hyenas is more restricted, and consist mostly of seals (Siegfried, 1984; Mills, 1990; Skinner and Van Aarde, 1991; Kuhn et al., 2008).

The main competitor of brown hyenas is black-backed jackals (*Lupulella mesomelas*). These jackals often occur in high density. The former often chase away jackals from kills, and are often alert to the activities of jackals, whom they also readily kill and consume (Mills, 1990). An abundance of fossil jackal remains in faunal samples is often an indicator of hyena activity, reflecting the frequent interaction between brown hyenas and jackals at carcasses, with slow or daring jackals often falling prey to brown hyenas (Skinner and Van Aarde, 1991; Klein et al., 1999). The diets of brown hyenas and jackals overlap, as in the Central Kalahari Desert, where they both scavenge during the wet season and hunt small animals during the dry season (Owens and Owens, 1978). Remains of various carnivore taxa are often common in brown hyena dens (e.g. Brain, 1981), an aspect we investigate here.

In this paper, we present a new approach to distinguish brown hyena from hominin assemblages, using the richness of carnivores and ungulates in samples. This method is especially useful for making comparisons between samples where faunas were quantified using different

methods (e.g. NISP vs. MNI), in those samples that were not quantified at all, where samples are dominated by seals, or where detailed taphonomic analyses are still to be undertaken. In all, multiple lines of evidence are required to investigate the agent(s) of accumulation. Our approach is based on the presence and absence of taxa in samples. While the presence (or absence) of a taxon in a sample is related to aspects such as actual presence (through hunting or scavenging by hominins and hyenas), sample size, transport, butchery, post-depositional removal and identification limitations, our datasets used in this study provide robust results, and is confirmed by statistical tests. There are few modern faunal samples accumulated by brown hyenas in the Eastern and Western Cape of South Africa (but see Slater and Muller, 2014). However, since brown hyenas feed on prey found in an area, and modern nature conservation areas do not often reflect past animal diversity, we did not include them. The wider application of this new method, for example to Plio-Pleistocene sites in the Cradle of Humankind in South Africa (e.g. Brain, 1981; Val et al., 2014; Fourvel et al., 2018), is beyond the scope of the current paper.

Palaeoecological reconstruction of the Eastern and Western Cape indicates less aridity during the Pleistocene than today, with a higher water table and an extended range of wet habitats (Faith et al., 2020). Despite a wider distribution during the Pleistocene (Avery, 2019), many of the carnivore taxa from the hominin and brown hyena samples do not occur in the Cape Floristic Region in recent times largely due to advancing development in the area (Skinner and Chimimba, 2005). A previous study found that the carnivore-ungulate ratio from sites in this region was unaffected by glacial and interglacial episodes during the Pleistocene (Badenhorst et al., 2021). Thus, we do not consider changes in climatic conditions as a major driver of patterns as we discuss in this paper.

### 4. Material and method

The MSA sites with low probabilities of carnivore activity in the Eastern and Western Cape of South Africa include Blombos Cave (Henshilwood et al., 2001; Badenhorst et al., 2016; Reynard and Henshilwood, 2019), Die Kelders (Klein and Cruz-Urbe, 2000), Diepkloof Shelter (Steele and Klein, 2013), Klasies River Mouth (Klein, 1976a; Van Pletzen, 2000; Van Pletzen-Vos et al., 2019; Reynard and Wurz, 2020; Ezeimo et al., 2024), Klipdrift Shelter (Reynard et al., 2016), Pinnacle Point PP13B (Rector and Reed, 2010) and Ysterfontein (Avery et al., 2008).

The fossil brown hyena samples include Duinefontein 2 (Klein, 1976b; Cruz-Urbe et al., 2003), Elandsfontein Bone Circle (Klein, 1983), Hoedjiespunt 1 (Stynder, 1997), Pinnacle Point PP30 (Rector and Reed, 2010), Sea Harvest (Grine and Klein, 1993) and Swartklip 1 (Klein, 1975; 1983; Klein et al., 2007).

We calculate a Carnivore Richness Index (CRI), which measures the richness of carnivores against ungulates, using only mutually exclusive species for computing the carnivore and ungulate NTAXA. We included seals in our calculations as brown hyenas often prey on these animals (Siegfried, 1984; Kuhn et al., 2010). The number of taxa (NTAXA) in a faunal assemblage refers to species richness, or the minimum number of identified taxa in a sample (Lyman, 2015). The ratio is calculated in the following manner:

$$\text{Carnivore Richness Index (CRI)} = \frac{\text{Carnivore NTAXA}}{\text{Carnivore NTAXA} + \text{Ungulate NTAXA}}$$

**Table 1**

CRI values for hominin-induced samples per individual layers (only layers with 10 or more carnivore + ungulate NTAXA).

| Site                   | Layer         | Age (Kya) | NTAXA Carnivores | NTAXA Ungulates | CRI  |
|------------------------|---------------|-----------|------------------|-----------------|------|
| Blombos                | BBC M1        | 75        | 7                | 11              | 0.39 |
| Blombos                | BBC M2        | 81        | 8                | 10              | 0.44 |
| Blombos                | BBC M3        | 98        | 8                | 13              | 0.38 |
| Die Kelders 1          | MSA 4/5       | 65        | 10               | 16              | 0.38 |
| Die Kelders 1          | MSA 6         | 65        | 11               | 16              | 0.41 |
| Die Kelders 1          | MSA 7         | 65        | 4                | 9               | 0.31 |
| Die Kelders 1          | MSA 8         | 65        | 2                | 11              | 0.15 |
| Die Kelders 1          | MSA 9         | 65        | 3                | 7               | 0.30 |
| Die Kelders 1          | MSA 12        | 65        | 3                | 10              | 0.23 |
| Die Kelders 1          | MSA 14        | 65        | 5                | 11              | 0.31 |
| Diepkloof              | Post HP       | 6         | 6                | 11              | 0.35 |
| Diepkloof              | Late HP       | 52        | 7                | 11              | 0.39 |
| Diepkloof              | Inter HP      | 75        | 6                | 11              | 0.35 |
| Diepkloof              | Early HP      | 107       | 3                | 8               | 0.27 |
| Diepkloof              | Still Bay     | 73        | 4                | 6               | 0.40 |
| Klasies River Cave 1A  | LBS + RBS     | 110       | 1                | 13              | 0.07 |
| Klasies River Cave 1A  | SAS Base      | 126       | 3                | 15              | 0.17 |
| Klasies River Cave 1A  | SAS middle    | 90        | 1                | 14              | 0.07 |
| Klasies River Cave 1A  | Upper         | 65        | 3                | 15              | 0.17 |
| Klasies River Cave 1A  | 1A MSA III    | 50        | 2                | 13              | 0.13 |
| Klasies River Cave 1A  | 1A HP         | 65        | 1                | 11              | 0.08 |
| Klasies River Cave 1A  | 1 & 1A        | 93        | 1                | 12              | 0.08 |
| Klasies River Cave 1A  | MSA II U      | 101       | 3                | 14              | 0.18 |
| Klasies River Cave 1A  | 1/1A/AA43/Z44 | 108       | 1                | 12              | 0.08 |
| Klasies River Cave 1A  | MSA II L      | 108       | 1                | 12              | 0.08 |
| Klasies River Cave 1A  | 1/1A/AA43/Z44 | 108       | 1                | 12              | 0.08 |
| Klasies River Cave 1A  | MSA I         | 115       | 2                | 10              | 0.17 |
| Klasies River Cave 1B  | RS            | 115       | 2                | 10              | 0.17 |
| Klipdrift              | PBA/PBB       | 59        | 2                | 10              | 0.17 |
| Pinnacle Cave 13B West | LBG Sand      | 114       | 2                | 10              | 0.17 |
| Ysterfontein 1         | Upper         | 129       | 5                | 8               | 0.38 |
| Ysterfontein 2         | Middle        | 121       | 6                | 7               | 0.46 |
| Ysterfontein 3         | Lower         | 132       | 3                | 7               | 0.30 |

**Table 2**

CRI values for hominin-induced samples, combined for each site, and including all layers.

| Site                        | NTAXA Carnivores | NTAXA Ungulates | CRI  |
|-----------------------------|------------------|-----------------|------|
| Blombos                     | 10               | 14              | 0.42 |
| Ysterfontein                | 6                | 9               | 0.40 |
| Klipdrift                   | 4                | 15              | 0.21 |
| Pinnacle Point              | 2                | 14              | 0.13 |
| Diepkloof                   | 10               | 14              | 0.42 |
| Klasies River Cave 1 and 1A | 3                | 19              | 0.14 |
| Klasies River Cave 1A       | 3                | 5               | 0.38 |
| Klasies River Cave 1B       | 2                | 10              | 0.17 |
| Die Kelders                 | 13               | 20              | 0.39 |

Using the CRI, the values can only range between 0 and 1. It is expected that hyena samples will have CRI values closer to 1, and anthropogenic accumulations will have values closer to 0. We calculated the CRI per layer, as well as for the entire faunal sample from the different sites. We only included samples with 10 or more carnivore + ungulate NTAXA for the calculations, as small samples may skew the results. We used an unpaired Mann-Whitney *U* test to investigate differences between the samples.

**Table 3**

Carnivore taxa present in hominin-induced samples. BC = Blombos Cave, YF = Ysterfontein, KL = Klipdrift Shelter, PP = Pinnacle Point, DK = Diepkloof, KR = Klasies River, KD = Die Kelders per NISP/MNI. All layers included for all sites. In some cases, MNI's are not available, and are indicated by a dash.

| Taxa                                                                   | BC    | YF     | KL  | PP  | DK   | KR    | KD      |
|------------------------------------------------------------------------|-------|--------|-----|-----|------|-------|---------|
| <b>HYAENIDAE</b>                                                       |       |        |     |     |      |       |         |
| <i>Parahyaena brunnea</i> (brown hyena)                                |       |        | 1/- |     |      | 11/-  | 9/4     |
| Hyaenid general (hyaena)                                               | 2/-   | 5/3    |     |     | 8/1  |       |         |
| <b>FELIDAE</b>                                                         |       |        |     |     |      |       |         |
| <i>Panthera leo</i> (lion)                                             |       |        |     |     |      |       | 1/1     |
| <i>Panthera pardus</i> (leopard)                                       |       |        |     |     | 13/2 | 3/-   |         |
| <i>Felis silvestris</i> (wildcat)                                      | 24/-  | 7/3    |     |     | 68/5 |       | 24/5    |
| cf. <i>Felis silvestris</i> (possibly wildcat)                         | 1/-   |        |     |     |      |       |         |
| <i>Felis</i> sp.                                                       | 1/-   |        |     | 1/1 |      |       |         |
| <i>Caracal caracal</i> /<br><i>Leptailurus serval</i> (caracal/serval) | 3/-   | 13/4   | 2/- |     | 50/3 |       | 13/3    |
| <b>VIVERRIDAE</b>                                                      |       |        |     |     |      |       |         |
| <i>Genetta</i> sp. (genet)                                             | 8/-   |        |     |     | 2/1  |       | 9/4     |
| Viverridae general (mongoose)                                          |       |        |     |     |      |       | 1/1     |
| <b>HERPESTIDAE</b>                                                     |       |        |     |     |      |       |         |
| <i>Herpestes ichneumon</i> (Egyptian mongoose)                         |       |        |     |     |      |       | 9/2     |
| <i>Herpestes pulverulentus</i> (Cape gray mongoose)                    | 20/-  |        |     |     | 13/2 |       | 225/15  |
| <i>Atilax paludinosus</i> (Water mongoose)                             |       |        |     |     |      |       | 2/2     |
| <i>Herpestes</i> sp. (mongoose)                                        | 8/-   |        | 1/- |     |      |       |         |
| <b>CANIDAE</b>                                                         |       |        |     |     |      |       |         |
| <i>Lupulella mesomelas</i> (black-backed jackal)                       | 2/-   | 1/1    |     |     | 13/2 |       | 10/3    |
| <i>Lycan pictus</i> (wild dog)                                         |       |        |     |     |      |       | 1/1     |
| <i>Vulpes chama</i> (Cape fox)                                         | 5/-   |        |     |     | 1/1  |       |         |
| Canid                                                                  | 1/-   |        |     |     |      |       |         |
| <b>MUSTELIDAE</b>                                                      |       |        |     |     |      |       |         |
| <i>Aonyx capensis</i> (clawless otter)                                 | 1/-   |        |     |     |      | 6/-   |         |
| <i>Ictonyx striatus</i> (striped polecat)                              | 8/-   |        |     |     |      |       | 8/2     |
| <i>Mellivora capensis</i> (honey badger)                               | 2/-   | 4/3    |     |     | 1/1  |       | 98/7    |
| <b>OTARIIDAE</b>                                                       |       |        |     |     |      |       |         |
| <i>Arctocephalus pusillus</i> (Cape fur seal)                          | 281/- | 205/15 |     | 2/2 | 3/1  | 376/- | 1329/35 |
| cf. <i>Arctocephalus pusillus</i> (possibly Cape fur seal)             | 3/-   |        |     |     |      |       |         |
| <i>Arctocephalus</i> cf. <i>pusillus</i> (possibly Cape fur seal)      | 21/-  |        | 2/- |     |      |       |         |
| <i>Arctocephalus</i> sp. (seal)                                        |       |        |     |     |      | 460/- |         |

## 5. Results

The CRI values are generally low for hominin-induced samples from the individual layers (Table 1), ranging between 0.07 and 0.46. The values remain low when the entire samples are considered (Table 2), ranging between 0.13 and 0.42. The overall richness of carnivore taxa in these hominin-induced samples is low (NTAXA = 16), and common taxa include Cape fur seal, caracal/serval (*Caracal/Leptailurus*), African wildcat, black-backed jackal, honey badger, brown hyena, genet

**Table 4**

CRI values for fossil hyena samples.

| Site                      | Layer     | Age (Kya) | NTAXA Carnivores | NTAXA Ungulates | CRI  |
|---------------------------|-----------|-----------|------------------|-----------------|------|
| Duinefontein 2            | Horizon 2 |           | 8                | 12              | 0.4  |
| Duinefontein 2            | Horizon 3 |           | 5                | 7               | 0.42 |
| Elandsfontein Bone Circle |           |           | 7                | 10              | 0.41 |
| Hoedjiespunt              |           |           | 18               | 16              | 0.52 |
| Pinnacle Cave PP30        | PP30      | 151       | 12               | 17              | 0.41 |
| Sea Harvest               | All       | 65        | 18               | 18              | 0.5  |
| Swartklip                 |           |           | 13               | 13              | 0.5  |

(*Genetta sp.*) and Cape grey mongoose (*Galerella pulverulenta*, Table 3). It is possible that slightly higher CRI values, such as at Blombos Cave coupled with the presence of hyenas and jackals may indicate sporadic hyena activity (see Thompson and Henshilwood, 2011; Badenhorst et al., 2016; Reynard and Henshilwood, 2019). However, the possibility that these and other carnivores were actively hunted by hominins cannot be excluded.

The fossil hyena samples have higher CRI values compared to hominin-induced samples (Table 4), ranging between 0.4 and 0.52. The original data were reported per site (and not per individual layer), except for Duinefontein 2. The fossil hyena samples contain a higher diversity of carnivore taxa (NTAXA = 24) compared to the hominin-induced samples, and the most common species include black-backed jackals, caracals, wildcats, Egyptian mongooses (*Herpestes ichneumon*), brown hyenas, striped polecats, hunting dogs (*Lycaon pictus*), honey badgers, lions, leopards (*Panthera pardus*) and Cape foxes (*Vulpes chama*, Table 5).

In summary, the CRI values are low for samples accumulated by hominins, and highest for the fossil brown hyena samples (Table 6, Fig. 2). The CRI values can be used to distinguish between hominin (by layers or overall) and brown hyena samples (Table 7). The distinction between human and hyena samples using the CRI is further supported when compared to carnivore chew marks (Fig. 3) and carnivore-ungulate ratios (Fig. 4, Badenhorst et al., 2021; Ezeimo et al., 2024).

## 6. Discussion and conclusion

It is recognised that the dating of the archaeological samples used in this study is relative, and the exact time of accumulation in days, weeks, months, years or decades is completely unknown. Moreover, aspects such as sample size, faunal preservation, identification limitations, retrieval and excavation decisions can influence the results. Some fossil brown hyena samples used in this study also display evidence for hominin activities such as at Duinefontein (Cruz-Urbe et al., 2003) and porcupine activity at Hoedjiespunt (Stynder, 1997) and Sea Harvest (Grine and Klein, 1993). Some of these factors could have contributed to the (relative) fluctuations in the CRI values. However, it does not seem like the possibility of other, secondary agents of accumulations affected the CRI values significantly, as is indicated by the statistical confirmation that the CRI is valuable as an additional method to distinguish between these types of samples. The variability of the CRI values in the hominin samples, coupled with the occurrence of hyenas, jackals and a variety of other carnivores, may indicate periodic occupation and use of shelters by brown hyenas. However, hominins could also have hunted or otherwise obtained the carnivore remains (cf. Val et al., 2020).

The usefulness of the CRI as an additional method can be shown when applied to Sibudu Cave, located in KwaZulu-Natal, South Africa. Here, Wadley (2010) proposed the use of snares during the MSA Howieson's Poort at Sibudu Cave. This is based on the high number of forest-dwelling taxa, notably blue duikers (*Philantomba monticola*) and bushpigs (*Potamochoerus larvatus*), the high number of small mammals

**Table 5**

Carnivore taxa present in the fossil hyena samples (EF: Elandsfontein Bone Circle, HP: Hoedjiespunt, SH: Sea Harvest, DF: Duinefontein, SK: Swartklip, PP: Pinnacle Point) per NISP/MNI.

| Taxa                                                          | DF   | EF    | HP     | PP    | SH     | SK     |
|---------------------------------------------------------------|------|-------|--------|-------|--------|--------|
| <b>HYAENIDAE</b>                                              |      |       |        |       |        |        |
| <i>Crocuta crocuta</i> (spotted hyena)                        |      | 8/1   | 1/1    |       | 2/1    |        |
| <i>Parahyaena brunnea</i> (brown hyena)                       | 1/1  | 6/2   | 4/1    | 44/3  | 52/6   | 19/3   |
| Hyaenid general (hyena)                                       | 51/2 |       | 19/3   |       | 91/6   |        |
| <b>FELIDAE</b>                                                |      |       |        |       |        |        |
| <i>Acinonyx jubatus</i> (cheetah)                             |      |       |        |       | 1/1    |        |
| <i>Panthera leo</i> (lion)                                    | 7/1  | 12/2  | 3/1    | 4/1   | 20/2   | 61/4   |
| <i>Panthera pardus</i> (leopard)                              |      |       | 22/2   | 1/1   | 59/3   | 1/1    |
| <i>Caracal caracal</i> (caracal)                              | 4/1  |       |        | 3/1   |        |        |
| <i>Caracal cf. caracal</i> (possibly caracal)                 |      | 17/2  |        |       |        |        |
| <i>Felis silvestris</i> (wildcat)                             | 1/1  | 2/1   | 14/2   | 2/1   | 44/3   | 21/1   |
| <i>Felis nigripes</i> (small spotted cat)                     |      |       | 1/1    |       |        |        |
| <i>Leptailurus serval</i> (serval)                            |      |       |        |       |        | 66/3   |
| <i>Leptailurus cf. serval</i> (possibly serval)               |      |       |        |       | 48/3   |        |
| <i>Caracal caracal/Leptailurus serval</i> (caracal\serval)    |      |       | 27/2   |       |        |        |
| <b>VIVERRIDAE</b>                                             |      |       |        |       |        |        |
| <i>Genetta tigrina</i> (Cape genet)                           |      |       | 3/1    |       |        |        |
| <i>Genetta cf. tigrina</i> (possibly Cape genet)              |      |       |        |       | 4/2    |        |
| <i>Genetta sp.</i> (genet)                                    | 3/2  |       |        |       |        |        |
| Viverridae general (mongoose)                                 |      |       | 3/1    |       |        |        |
| <b>HERPESIIDAE</b>                                            |      |       |        |       |        |        |
| <i>Suricata suricatta</i> (suricate)                          |      |       | 2/1    |       |        |        |
| <i>Herpestes ichneumon</i> (Egyptian mongoose)                | 8/2  |       | 7/1    |       | 17/3   | 6/1    |
| <i>Herpestes pulverulentus</i> (Cape grey mongoose)           |      |       |        | 3/1   | 22/2   |        |
| <i>Atilax paludinosus</i> (Water mongoose)                    |      |       | 3/1    |       |        | 4/1    |
| <i>Herpestes sp.</i> (mongoose)                               |      |       |        | 3/1   |        |        |
| <b>CANIDAE</b>                                                |      |       |        |       |        |        |
| <i>Lupulella mesomelas</i> (black-backed jackal)              | 50/4 | 142/7 | 343/11 | 190/9 | 251/13 | 377/20 |
| <i>Lupulella cf. mesomelas</i> (possibly black-backed jackal) |      |       |        | 33/5  |        |        |
| <i>Lycaon pictus</i> (wild dog)                               |      |       | 8/1    | 13/5  | 21/2   | 7/2    |
| <i>Otocyon megalotis</i> (bat-eared fox)                      |      |       |        | 1/1   |        |        |
| <i>Vulpes chama</i> (Cape fox)                                |      |       | 15/2   | 10/3  | 39/3   | 38/2   |
| Canid                                                         |      |       |        | 65/1  |        |        |
| <b>MUSTELIDAE</b>                                             |      |       |        |       |        |        |
| <i>Aonyx capensis</i> (clawless otter)                        |      |       | 9/2    |       | 10/1   | 10/3   |
| <i>Ictonyx striatus</i> (striped polecat)                     | 34/6 |       | 5/2    | 3/2   | 2/1    | 1/1    |
| <i>Mellivora capensis</i> (honey badger)                      |      | 10/2  | 5/1    | 2/1   | 20/2   | 11/2   |
| <b>OTARIIDAE</b>                                              |      |       |        |       |        |        |
| <i>Arctocephalus pusillus</i> (Cape fur seal)                 |      |       | 34/2   | 65/1  | 172/4  |        |
| <i>Lobodon carcinophaga</i> (crab-eater seal)                 |      |       |        |       | 1/1    |        |

including rock hyraxes and rabbits, a high taxonomic richness, and the presence of small carnivores. The use of snares have been used to infer, along with other lines of evidence, the technological and cognitive capabilities of early modern humans (e.g. Bader et al., 2022). Considering the fauna from the Howieson's Poort (Clark and Plug, 2008; Clark, 2017), the carnivore–ungulate ratio is 2.85, which is low (Badenhorst et al., 2021). The low carnivore–ungulate ratio is no doubt caused by the large quantities of blue duiker and indeterminate small Bovid remains, amounting to 1110 specimens from the total of 2408 (thus 46% of the

**Table 6**

Summary of the CRI values (Ave = Average, Min = Minimum, Max = Maximum, SD = standard deviation, CV = coefficient of variation).

| Sample                                                                            | Ave  | Min  | Max  | SD   | CV   |
|-----------------------------------------------------------------------------------|------|------|------|------|------|
| Hominin-Induced Samples (only samples with 10 or more carnivore + ungulate NTAXA) | 0.26 | 0.07 | 0.46 | 0.13 | 0.48 |
| Hominin per Site                                                                  | 0.30 | 0.13 | 0.42 | 0.12 | 0.42 |
| Fossil Hyena                                                                      | 0.45 | 0.4  | 0.52 | 0.05 | 0.11 |

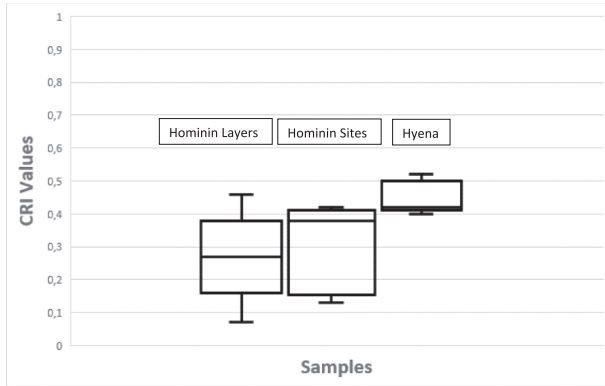


**Fig. 2.** Data for hominin samples per layer, per site, and for hyena samples. Data shown for minimum and maximum values, median, as well as first and third quartile.

**Table 7**

Unpaired Mann-Whitney *U* test of CRI values.

| Samples                                 | Z-Score  | P-Value | Result                           |
|-----------------------------------------|----------|---------|----------------------------------|
| Hominin-Induced Samples vs Fossil Hyena | -3.64516 | 0.00026 | Result significant at $p < 0.05$ |
| Hominin Overall vs Fossil Hyena         | -2.4875  | 0.01278 | Result significant at $p < 0.05$ |

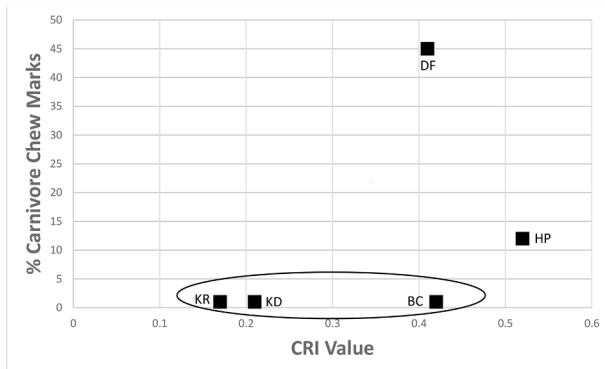


**Fig. 3.** CRI and % carnivore chew marks for a selection of samples where the data were reported. The hominin-induced samples are encircled, showing a low representation of carnivore chew marks as well as CRI values (DF Duinefontein, HP Hoedjiespunt, BC Blombos Cave, KD Klipdrift, KR Klasies River Mouth 1B).

NISP). Coupled with the low incidence of carnivore chew marks (<1% of Howiesons Poort sample), the lack of hyena remains (although an indeterminate hyena-sized medium carnivore is present in the sample) or hyena coprolites, the role of carnivores like hyenas in accumulating the fauna from the Howiesons Poort component was considered to be low (Clark and Plug, 2008; Clark 2017).

However, while Sibudu Cave falls outside the modern-day

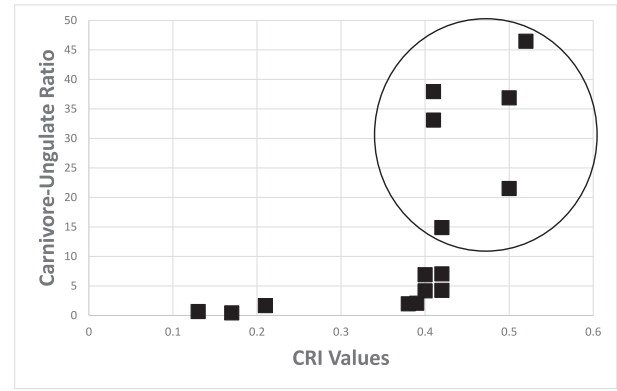


**Fig. 4.** CRI values and carnivore-ungulate ratios of samples. The hyena samples are encircled.

distribution of brown hyenas (Skinner and Chimimba, 2005), they do venture into KwaZulu-Natal province (Von Richter, 1972; Mills, 1982) as is reflected in their presence at many archaeological sites in KwaZulu-Natal (e.g. Plug and Badenhorst, 2001; Plug, 1993). The CRI value for the Howiesons Poort at Sibudu Cave is 0.4, which overlaps with hominin (higher end of the scale) and fossil brown hyena (lower end of scale) samples. While hyenas may prefer caves that have chambers suitable for securing juveniles (Clark, 2017 citing Pokines and Kerbis-Peterhans, 2007), this did ‘...not preclude hyena from having visited the site.’ (Clark, 2017:59). This introduces the possibility that brown hyenas accumulated some of the specimens during the Howiesons Poort component at Sibudu Cave that have been used to infer human activity through snares.

In another example, the Cave of Hearths is an important site in the interior of South Africa, with occupations spanning from the Early, Middle and Later Stone Ages, Iron Age and historical times (Mason, 1969, 1988). The fauna from the Early Stone Age (ESA) and MSA were studied by Cooke (1969). At the time, Cooke based his identifications on teeth and crania only, and he did not quantify the fauna. A taphonomic analysis of the ESA fauna indicate some specimens with carnivore chew marks (Ogala, 2009). In this case, the CRI values show low probabilities of brown hyena activity (Table 8).

Using another example, Herolds Bay is a coastal last interglacial deposit in the Eastern Cape containing coprolites, but also high frequencies of bones gnawed by porcupines and carnivores (Brink, 1980; Brink and Deacon, 1982). The carnivore ungulate ratio is low (14.75, Badenhorst et al., 2021), but the CRI is relatively high (0.35), confirming the role of brown hyenas in the accumulation at least some of the fauna. At another example from the Eastern Cape, Oyster Bay, where the sample contains hyena coprolites, bone specimens with carnivore chew marks and MSA lithics, the fauna was not quantified, thus it is not possible to calculate the carnivore-ungulate ratio (Carrión et al., 2000). However, the CRI value is also low (0.07), thus suggesting the fauna may have been accumulated by humans.

The CRI is a method that allows faunal analysts to distinguish and recognise samples with high probabilities of hyena or hominin activities in conjunction with other lines of evidence. Samples accumulated by brown hyenas show a higher richness of carnivore taxa (reflected in higher CRI values), whereas hominin-induced samples, typically have a lower richness of carnivore taxa (reflected in lower CRI values). Brown

**Table 8**

CRI values for the ESA and MSA components at the Cave of Hearths.

| Sample        | CRI Value | Notes                             |
|---------------|-----------|-----------------------------------|
| ESA           | 0.12      | Low probability of hyena activity |
| MSA           | 0.14      | Low probability of hyena activity |
| ESA/MSA Mixed | 0.28      | Low probability of hyena activity |

hyena samples from the Eastern and Western Cape of South Africa often contain taxa such as black-backed jackals, caracals, wildcats, mongooses, hyenas, striped polecats, hunting dogs, honey badgers, lions, leopards, and Cape foxes. Jackals are especially common in fossil brown hyena samples, reflecting the competition between these two carnivores. However, multiple lines of evidence are required to establish the agent of accumulation.

### CRedit authorship contribution statement

**Shaw Badenhorst:** Writing – review & editing, Writing – original draft, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Anelisiwe C. Siteto:** Writing – review & editing, Formal analysis, Data curation, Conceptualization.

### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

### Data availability

No data was used for the research described in the article.

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