

Testing the “shift in the balance of power” hypothesis at Swartkrans, South Africa: Hominid cave use and subsistence behavior in the Early Pleistocene

By: Travis Rayne Pickering, [Charles P. Egeland](#), Manuel Dominguez-Rodrigo, C.K. Brain, and Amy G. Schnell

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Abstract:

C.K. Brain documented two interesting patterns in the Pleistocene faunas of Swartkrans Cave, South Africa: (1) The earliest depositional units, Members 1 and 2, preserve high numbers of hominid fossils, while the numbers drop sharply in the more recent Member 3. (2) Burned bone specimens, which seem to have been altered in fires tended by hominids, appear for the first time in Member 3. It was suggested that mastery of fire provided a “shift in the balance of power”, allowing hominids to carry out activities in the cave for the first time unmolested by predators. A lack of butchered bones in Members 1 and 2 and their presence in Member 3 provided support for the hypothesis. However, we have now identified butchered bones in all three units. Further, our findings reveal a lack of variability in butchery patterns through time at Swartkrans; in all cases hominids appear to have been proficient carcass foragers. The real “shift” at Swartkrans does not appear to be one of eventual hominid dominance over carnivores, but rather one of a predominance of leopards at Swartkrans in Member 1 times to the alternating presence of leopards and hyenas in Members 2 and 3. Consistent leopard presence in Member 1 seems to have discouraged hominid activity in the vicinity of the cave. In contrast, by the time Members 2 and 3 were forming hominids may have temporarily used the cave, taking advantage of those periods of carnivore absence.

Keywords: Swartkrans; Archaeofaunas; Taphonomy; Zooarchaeology; Hominid butchery; Carnivore ravaging

Article:

Swartkrans is one of the most paleoanthropologically important of a number of dolomitic cave sites located in the Sterkfontein Valley (Gauteng Province, South Africa). Nearly 60 years of research at Swartkrans has revealed the synchrony and sympatry of *Australopithecus robustus* and *Homo erectus* (e.g., Broom and Robinson, 1949, 1950, 1952; Clarke et al., 1970) and has yielded abundant archaeological evidence of the behavior of these hominids. Lithic artifacts and traces of a bone tool culture are known throughout the cave’s earliest Pleistocene geological sequence, Members 1–3 of the Swartkrans Formation (e.g., Brain, 1985, 1989, 1993a,b; Brain and Shipman, 1993; Brain et al., 1988; Clark, 1993; Egeland et al., 2004; Field, 1999; Pickering et al., 2004a,b, 2005a,b, in press).¹ Abundant tooth marks and measures of skeletal element frequency indicate that a majority of hominid and other primate remains from Members 1 and 2, the earliest stratigraphic units of the site, were deposited in the cave as prey of carnivores (e.g., Brain, 1970, 1981, 1993a; Carlson and Pickering, 2003; Pickering and Carlson, 2002; White, 1988). In addition, the absolute number of hominid fossils (as measured by the number of identified specimens, NISP) drops dramatically between Members 1 and 2 and the more recently deposited Member 3 assemblage (Brain, 1981, 1993a). Further, based on the estimates of minimum number of individuals (MNI), hominids comprise only 5% of the total number of mammals recovered from Member 3. This is compared to their 20% and 16% representation, respectively, in Members 1 and 2 (Brain, 1993a).

This decline in hominid numbers suggested to Brain (1981, 1993a) that a major change in hominid behavioral capabilities took place over time at the site. No longer was hominid presence at the site indicated primarily by

the remains of the unfortunate victims of carnivore predation. Rather, evidence of hominid presence takes a more prominently archaeological form in Member 3. Brain (1993a) thus argued for a “shift in the balance of power” between hominids and carnivores, with the former actually being able to utilize space in the cave, unmolested by the latter, for carrying out activities. Based on comparison of the archaeology between Members 1–3, this dramatic shift did not seem to be predicated on innovation in stone tool technology. Each of the three lithic assemblages is attributed to the Developed Oldowan or Early Acheulean and is indistinguishable technologically from the others (Clark, 1993; Field, 1999; Kuman, 2003). Instead, Brain (1993a,c; Brain and Sillen 1988) pointed to 270 burned bone specimens recovered from Member 3 to explain the shift. These are argued to have resulted from the first hominid control of fire at the site (and in the world; see also Bellomo, 1994 for claims of similarly ancient fire control at Koobi Fora, Kenya), and it was this crucial advance that led to hominid primacy over carnivores at Swartkrans.²

Concurrent with the dramatic technological progression represented by domestication of fire, Brain (1993a) documented the presence of 16 butchered bones in the Member 3 fauna. Pickering et al. (2004a,b, 2005a,b, in press), in their analysis of the Member 3 limb bone shaft subassemblage,³ increased the total number of butchered specimens (including those that are cutmarked and hammerstone per-cussed) to 163. Taken together, Brain (1993a, 263) concluded: “The presence of bones, including four burnt ones, bearing [butchery] marks...suggests that hominids were using stone tools for the removal of meat from bones while sitting round their camp-fires [*in the cave*].” Based on the combined available data, it seemed that the relationship of hominids to the cave had shifted radically by Member 3 times. No longer was Swartkrans a constantly dangerous place in which hominids entered at their own risk, many of whom fell to predation because of their unguarded boldness. The cave went from the exclusive domain of large carnivores to a place in which hominids, with the protection afforded by their control of fire, could linger in its mouth for extended periods of time and carry out activities, including carcass butchery.

Several archaeologically testable predictions derive from this hypothesis. First, it was expected that Member 3 would yield a relatively “undisturbed” lithic assemblage created by the primary flaking activities of hominids using the cave as temporary shelter. This is in contrast to the incomplete assemblages that would be predicted in Members 1 and 2, which assumedly accumulated through periodic capture of surface materials through slopewash and hillside erosion, when hominids were not occupying the cave. These predictions are not met at Swartkrans; Field (1999) found that all three members yielded incomplete assemblages based her model of a primary flaking area and those of others (e.g., Schick, 1987; Kuman et al., 2005).

Expanding on these results from lithic analysis, we evaluate here the “shift in the balance of power” hypothesis using new zooarchaeological and taphonomic data generated on the limb bone shaft samples from all three Early Pleistocene members at Swartkrans. Our results also indicate that the hypothesis, as outlined above, needs to be modified. Specifically, we investigated the following predictions that emanate from the hypothesis: (1) the anatomical patterning of hominid butchery might take a different form in Member 3 compared to Members 1 and 2; (2) traces of hominid butchery (i.e., cutmarks and hammerstone percussion damage) should be more frequent in Member 3 than in Members 1 and 2; (3) traces of carnivore feeding in the cave (i.e., tooth marks) should be less frequent in Member 3 than in Members 1 and 2. Our results show just slight differences between members with regard to these predictions. Further, in contrast to that expected by the “shift in the balance of power” hypothesis, the one noteworthy change we document in taphonomic patterns is between Member 1 versus 2 and 3, rather than between Members 1 and 2 versus 3. This change is from a near-exclusive leopard signal in Member 1 to a combination of leopard and hyena signals in Members 2 and 3. The specific scenario of local hominid ascendancy through the use of fire at Swartkrans is equivocal in light of these conclusions. The findings do not, however, diminish the wider importance of Swartkrans in preserving persuasive evidence of the earliest control of fire by hominids. The profound impact of that technological advance in human evolution is evident and we argue that Swartkrans should be drawn back into serious discussions of the topic.

Materials and methods

Systematic zooarchaeological analyses of the complete limb bone shaft samples from Swartkrans Members 1, 2 and 3 (1979–1986 excavations) were conducted (Table 1). Limb bone shaft fragments were chosen as the analytical sample because most current, actualistic models of hominid carcass use focus in large part on limb elements (e.g., Blumenschine, 1988, 1995; Blumenschine and Marean, 1993; Blumenschine and Selvaggio, 1988; Capaldo, 1995, 1997, 1998; Cleghorn and Marean, in press; Dominguez-Rodrigo, 1999a,b, 2002; Marean and Cleghorn, 2003; Marean et al., 1992, 2004; Pickering et al., 2003; Selvaggio, 1994, 1998; Selvaggio and Wilder, 2001). The reasons for this focus are articulated most explicitly in the work of Marean and Cleghorn (2003, 15), in which they demonstrate that limb bones are high survival elements, “defined by the presence of thick cortical bone portions lacking cancellous bone.” In particular, limb bone midshaft fragments will be relatively abundant in most archaeofaunas of interest; because of their high bone mineral density and low nutritional yields (i.e., they lack grease-laden trabeculae), they survive relatively well the rigors of density-mediated destruction throughout the biostratigraphic and diagenetic phases of faunal assemblage formation (reviewed in Pickering et al., 2003; Marean and Cleghorn, 2003; Marean et al., 2004). Second, this set of high survival elements are “sufficiently diverse and behaviorally sensitive to allow [zooarchaeologists] to ask interesting foraging theory questions.” (Marean and Cleghorn, 2003, 39). For instance, the upper (humerus and femur) and intermediate (radioulna and tibia) limb bones of ungulates bear significant amounts of overlying musculature and have large medullary chambers, while the lower limb bones (metapodials) are relatively meatless with small marrow cavities (Fig. 1). The variable representation of these elements in a faunal assemblage created by a biotic actor has the potential to inform about the foraging behaviors that were involved in producing it (e.g., hunting/ aggressive scavenging or early carcass access as indicated by a predominance of meat-bearing upper and intermediate elements versus passive scavenging or late carcass access as indicated by an abundance of metapodials; see discussions in Bunn, 1991, 2001; Dominguez-Rodrigo, 1997, 1999a,b, 2002; Dominguez-Rodrigo and Pickering, 2003; Pickering and Dominguez-Rodrigo, 2006).

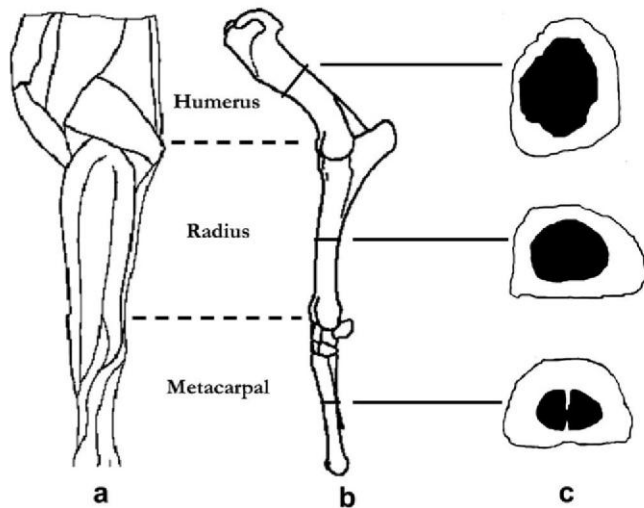


Fig. 1. Differential distribution of edible tissues across the length of an ungulate forelimb. Proximodistally, note the heavy meat cover on the humerus and radius, while the metacarpal has no overlying muscle (a and b). Cross-sectional views of the midshaft of each bone reveal the large medullary cavities of the humerus and radius versus the more restricted volume of the metacarpal's marrow chamber (c). These differences are mirrored in the ungulate hindlimb, with the femur and tibia possessing thick overlying musculature and large medullary cavities and the metatarsal lacking these features.

Table 1
Number of identified specimens (NISP) estimates for various levels of analysis used in this study

Member	Total limb bone shafts	Analytical Set I	Analytical Set II
1	3019	864	623
2	5859	544	1060
3	11,505	1466	3151

Sampling

We isolated two sub-samples for in-depth analyses from the limb bone shaft sample of each member. The first sample in each case is referred to as Analytical Set I and is comprised of every specimen ≥ 5 cm in maximum dimension plus every specimen < 5 cm in maximum dimension that also preserves prehistoric bone surface modifications. Each Analytical Set I is considered “unadjusted”, in the sense that it is not comparable to modern, actualistically derived samples of human butchered and carnivore ravaged bones (see discussion

below). It does, however, provide “maximum” information on the frequency and distribution of hominid and carnivore bone surface modifications. NISP totals for Analytical Sets I are presented in Table 1.

In addition to Analytical Sets I, we created adjusted samples, Analytical Sets II. The process used to create Analytical Sets II was conceived to make these sets, more so than the Analytical Sets I, comparable to actualistic samples that model the carcass-focused interactions of hominids and carnivores (see also, Blumenschine, 1995, 33–39). In each case, Analytical Set II was assembled by beginning with the original subassemblage of *all* limb bone specimens ≥ 2 cm in maximum dimension. It is important to stress that in contrast to Analytical Sets I, even specimens that bear bone surface damage but are <2 cm were excluded from Analytical Sets II. This is because the actualistic control samples (i.e., Blumenschine, 1988, 1995; Blumenschine and Selvaggio, 1988; Capaldo, 1995, 1997, 1998; Selvaggio, 1994, 1998) do not consider specimens <2 cm in maximum dimension. All specimens ≥ 5 cm were identified as specifically as possible. The most specific level of identification we achieved for many specimens was to skeletal element (humerus, radioulna, metacarpal, femur, tibia, metatarsal). We were able to categorize other specimens not identifiable to skeletal element to a limb segment, as an upper (humerus or femur), intermediate (radioulna or tibia) or lower (metapodials) limb fragment (Dominguez-Rodrigo, 1997, 1999a; Barba and Dominguez-Rodrigo, 2005). Specimens that remained unidentified after these steps were then simply entered into the database as limb bone shaft fragments. Due to time constraints, no specimen 2– <5 cm was identified beyond the level of limb bone shaft fragment; however, it is worth noting that a significant portion of these fragments are probably identifiable to skeletal part and will be considered in future analyses.

Next, processes of diagenetic fragmentation and cortical surface degradation not operant in the modern comparative samples had to be controlled in the production of Analytical Sets II. The Swartkrans samples were obtained from deposits comprising two important variables: a wide array of lithological components, from fine-grained particles to gravel and large rock fragments; and great depths of sedimentation (Brain, 1993b). The thickness of the deposits combined with their down-sloping morphologies resulted in significant pressure (static loading) on in situ bones, fracturing many of them after loss of their original organic content (=dry breakage). All specimens ≥ 5 cm were coded individually for breakage and surface preservation.⁴ However, because of the large sizes of the three assemblages, we were forced to adjust for these factors for specimens 2– <5 cm through a sampling procedure, rather than examining every specimen in this size range. This procedure is summarized below, using the Member 3 assemblage as a specific example:

1. Starting from the initial NISP of 8352, we sampled randomly 1009 specimens between 2 and <5 cm.
2. Within the new sample of 1009, we calculated the percentage of specimens with good cortical surface preservation (48.3%) and green (35.0%) versus dry (65.0%) breakage planes.
3. Next we applied these percentages from the sample back to the starting NISP of 8352. Starting with the projection of well-preserved specimens, this is $8352 \times 0.483 = 4034$.
4. Adjusting for dry breakage was accomplished by multiplying 4034 by the projected percentage of dry-broken specimens ($4034 \times 0.65 = 2622$).
5. In order to reach a NISP estimate adjusted for green breakage, however, we first considered that the dry-broken NISP (2622) is inflated by the fact that each originally deposited bone was broken into at least two pieces, at least doubling the dry-broken NISP. Thus, the most conservative approach divides the dry-broken NISP by two ($2622/2 = 1311$). That estimate was then added to the green-broken NISP ($4034 \times 0.35 = 1412$), resulting in a new NISP of 2723 of well-preserved and green-broken pieces.

Because all specimens ≥ 5 cm were already coded individually for surface preservation and breakage, there was no need to follow the sampling procedure outlined above for specimens in this larger size range. Instead, to complete the construction of Analytical Set II for Member 3, we simply added the “adjusted NISP” for 2– <5 cm

specimens (2723) to the 428 specimens from Member 3 that are ≥ 5 cm and display good cortical surfaces and green breaks. The resulting grand total of well-preserved, green-broken specimens is 3151, the final NISP for the Member 3 Analytical Set II.

Animal body size

In each Analytical Set, each specimen was assigned to an animal body size group, following the size class system constructed for bovids by Brain (1974, 1981). For some analyses, individual body size groups were combined into two broad categories: small (corresponding to Brain's Size Class 1 plus 2); large (the combined remains of Size Class 3 and larger).

Bone surface modifications

Identification of bone surface modifications was undertaken using criteria and methods reviewed by Blumenschine et al. (1996). Each specimen was inspected under a strong oblique light source with the aid of at least 10x magnification as recommended by several analysts (e.g., Bunn, 1981, 1991; Bunn and Kroll, 1986; Blumenschine, 1995; Blumenschine and Marean, 1993; Blumenschine and Selvaggio, 1988; Blumenschine et al., 1996). During examination of each specimen, the bone surface was continuously repositioned in relation to the light source in order to discern modifications of any appreciable depth. Although other classes of bone surface modification (e.g., "random" striae, rodent gnaw marks, burning, alteration by gastric acids) were observed and noted, we systematically recorded only stone tool cutmarks and hammerstone percussion marks and carnivore tooth marks.

Several researchers have stressed the potential of various abiotic processes to mimic hominid-imparted bone surface damage, complicating inferential associations of particular marks and hominid butchery activity (e.g., Behrensmeier et al., 1986, 1989; Fiorillo, 1989; Oliver, 1989; Shipman and Rose, 1983). Thus, all specimens asserted to preserve hominid-imparted damage were subsequently examined by each researcher, and only after a unanimous decision was a specimen accepted and recorded as preserving the appropriate surface modification. Although time-consuming, this procedure was ultimately necessary for secure determinations. A prominent presence of abiotically derived linear striae (closely resembling stone tool cutmarks) was indicated by our many hours of experience with the curated collection and corroborated by observations of the sedimentary matrix from which the assemblage derives. As mentioned above, the Swartkrans deposits are complex karstic coluvia, consisting of materials ranging from clays to large angular clasts, which certainly held the potential to create abundant polish, abrasion and cutmark mimics on the recovered fossils. Thus, a configurational approach to butchery mark identification, in which we considered anatomical placement as well as mark morphology, was absolutely necessary in this archaeofauna (see Binford, 1981; Dominguez-Rodrigo et al., 2005; Pickering et al., 2000).

In addition to simply identifying the presence of carnivore tooth marks (including crenulation, punctures, notches, scores and pits), we followed a growing body of research aimed at identifying taxon-specific patterns of bone modification (Haynes, 1983; Selvaggio, 1994; Selvaggio and Wilder, 2001; Dominguez-Rodrigo and Piqueras, 2003; Pobiner and Blumenschine, 2003; Pickering et al., 2004b). In particular, Selvaggio (1994) and Dominguez-Rodrigo and Piqueras (2003) have presented comparative data on tooth pit, which appear as diffuse, roughly circular depressions on bone cortices (Blumenschine et al., 1996; Pickering and Wallis, 1997) and are created by the incidental contact of tooth cusps during normal feeding by carnivores. While data on tooth pits dimensions are available for several extant taxa of African carnivores, we decided the data on leopard and hyena tooth pits are the only relevant ones for our present comparative analyses. We made this determination because leopards and hyenas are the only taxa (for which modern data are available) that regularly create collections of bones in shelter sites (e.g., Brain, 1981).⁵ Except probably in the case of the genus *Homotherium* (e.g., Marean and Ehrhardt, 1995), it is still an open question whether extinct sabertooth cats generated bone accumulations at "feeding sites". Future research will hopefully elucidate this issue. In the meantime, we simply state that our results are subject to revision should future data lead to convincing inferences of bone collecting by other sabertooth cats. We also note that sabertooth cat remains are extremely rare in the Swartkrans faunas. Less than a total of 10 specimens of *Megantereon cultridens* and *Dinofelis* sp. is known only from the Hanging

Remnant and Member 3, while no remains at all of Homotherium have been recovered from the site (Brain, 1981; Watson, 1993).

Table 2
Summary of prehistoric bone surface modifications in the Swartkrans limb bone shaft samples^{a,b,c,d}

Size Class	Skeletal element	Member												
		Total NISP			Cutmarked NISP			Percussion marked NISP			Tooth marked NISP			
		1	2	3	1	2	3	1	2	3	1	2	3	
1	Humerus	1	9	7	0	0	1 (14.2)	0	0	0	0	6 (66.7)	3 (42.9)	
	Radioulna	0	3	13	0	0	0	0	0	0	2 (66.7)	7 (53.9)		
	Metacarpal	1	1	14	0	0	0	0	3 (21.4)	0	0	9 (64.3)		
	Femur	2	4	15	0	0	0	0	3 (20.0)	0	2 (50.0)	4 (26.7)		
	Tibia	10	0	27	0	0	1 (3.7)	0	0	2 (7.4)	6 (60.0)	14 (51.9)		
	Metatarsal	3	2	12	0	0	1 (8.3)	0	0	0	0	5 (41.7)		
	Upper	2	8	23	0	0	1 (4.3)	0	0	0	1 (50.0)	3 (37.5)	22 (95.7)	
	Intermediate	1	2	17	0	0	0	0	0	0	1 (100.0)	2 (100.0)	15 (88.2)	
	Metapodial	1	2	19	0	0	1 (5.3)	0	0	0	0	1 (50.0)	15 (79.0)	
	Limb bone shaft	28	6	152	0	0	0	0	0	2 (1.3)	14 (50.0)	2 (33.3)	127 (83.6)	
	Total	49	37	299	0	0	5 (1.7)	0	0	9 (3.0)	22 (44.9)	18 (48.6)	217 (73.6)	
	2	Humerus	29	22	42	0	1 (4.5)	2 (4.8)	0	0	3 (7.1)	5 (17.2)	9 (40.9)	4 (9.5)
		Radioulna	47	21	32	0	0	2 (6.3)	0	2 (9.5)	3 (9.4)	7 (14.9)	6 (28.6)	5 (15.6)
Metacarpal		20	11	22	0	0	2 (9.1)	0	1 (9.1)	2 (9.1)	7 (35.0)	5 (45.5)	10 (45.5)	
Femur		47	30	54	1 (2.1)	0	5 (9.3)	0	0	3 (5.7)	3 (6.4)	15 (50.0)	13 (24.5)	
Tibia		94	63	120	2 (2.1)	2 (3.2)	6 (5.0)	2 (2.1)	1 (1.6)	4 (3.3)	13 (13.8)	21 (33.3)	21 (17.5)	
Metatarsal		25	21	44	0	1 (4.8)	2 (4.6)	0	0	1 (2.3)	7 (28.0)	9 (42.9)	8 (18.2)	
Upper		28	30	30	0	2 (6.7)	4 (13.3)	0	1 (3.3)	0	10 (35.7)	14 (46.7)	14 (46.7)	
Intermediate		34	34	47	0	2 (5.9)	1 (2.1)	0	3 (8.8)	0	8 (23.5)	15 (44.1)	15 (32.6)	
Metapodial		30	23	59	1 (3.3)	1 (4.3)	2 (3.4)	0	1 (4.3)	0	11 (36.7)	10 (43.5)	14 (23.7)	
Limb bone shaft		53	51	124	1 (1.9)	2 (3.9)	6 (4.8)	0	1 (2.0)	4 (3.2)	11 (20.8)	25 (49.0)	22 (17.7)	
Total		407	306	574	5 (1.2)	11 (3.6)	32 (5.6)	2 (0.5)	10 (3.3)	20 (3.5)	82 (20.1)	119 (38.9)	126 (22.0)	
3		Humerus	41	15	35	1 (2.4)	0	2 (5.7)	0	0	3 (8.6)	4 (9.8)	2 (13.3)	8 (22.9)
		Radioulna	19	8	20	0	0	2 (10.0)	0	0	0	3 (15.8)	1 (12.5)	6 (30.0)
	Metacarpal	12	5	15	0	1 (20.0)	1 (6.7)	0	0	1 (6.7)	2 (16.7)	1 (20.0)	4 (26.7)	
	Femur	35	11	28	0	0	3 (10.7)	0	0	2 (7.1)	1 (2.9)	1 (9.1)	10 (35.7)	
	Tibia	64	23	85	1 (1.6)	0	3 (3.5)	0	1 (1.6)	4 (4.7)	8 (12.5)	6 (26.1)	29 (34.1)	
	Metatarsal	7	2	31	0	0	3 (9.7)	0	0	1 (3.2)	0	0	9 (29.0)	
	Upper	19	14	24	1 (5.3)	0	3 (12.5)	0	0	0	4 (21.1)	4 (28.6)	7 (29.2)	
	Intermediate	29	15	14	2 (6.9)	1 (6.7)	0	1 (3.4)	0	0	4 (13.8)	3 (20.0)	6 (42.9)	
	Metapodial	36	13	55	0	0	1 (1.8)	0	0	1 (1.8)	3 (8.3)	5 (38.5)	17 (30.9)	
	Limb bone shaft	29	24	66	0	1 (4.2)	1 (1.5)	0	1 (4.2)	1 (1.5)	5 (17.2)	5 (20.8)	20 (30.3)	
	Total	291	130	373	5 (1.7)	3 (2.3)	19 (5.1)	1 (0.3)	2 (1.5)	13 (3.5)	34 (11.7)	28 (21.5)	116 (31.1)	

(continued on next page)

Table 2 (continued)

Size Class	Skeletal element	Member												
		Total NISP			Cutmarked NISP			Percussion marked NISP			Tooth marked NISP			
		1	2	3	1	2	3	1	2	3	1	2	3	
4	Humerus	11	11	11	0	0	2 (18.2)	0	1 (9.1)	0	1 (9.1)	1 (9.1)	0	
	Radioulna	5	2	5	0	0	1 (20.0)	0	0	0	1 (20.0)	0	1 (20.0)	
	Metacarpal	1	0	4	0	0	0	0	0	1 (25.0)	1 (100.0)	0	0	
	Femur	3	1	12	0	0	0	0	0	0	0	0	2 (16.7)	
	Tibia	15	8	17	0	0	0	0	0	0	0	2 (25.0)	7 (41.2)	
	Metatarsal	3	0	5	0	0	0	0	0	0	0	0	1 (20.0)	
	Upper	10	5	9	0	0	0	0	0	0	0	0	0	
	Intermediate	5	4	5	0	0	0	0	0	0	0	0	0	
	Metapodial	9	4	20	0	0	1 (5.0)	0	0	2 (10.0)	0	1 (25.0)	1 (5.0)	
	Limb bone shaft	15	13	16	0	0	0	0	0	0	2 (13.3)	3 (23.1)	0	
	Total	77	48	104	0	0	4 (3.9)	0	1 (2.1)	3 (2.9)	5 (6.5)	7 (14.6)	12 (11.5)	
	1-4 combined	Upper total	228	160	290	3 (1.3)	3 (1.9)	23 (8.0)	0	2 (1.3)	13 (4.5)	29 (12.7)	57 (35.6)	87 (30.0)
		Humerus	82	57	95	1 (1.2)	1 (1.8)	7 (7.4)	0	1 (1.8)	6 (6.3)	10 (12.2)	18 (31.6)	15 (15.8)
Femur		87	46	109	1 (1.1)	0	8 (7.3)	0	0	7 (6.4)	4 (4.6)	18 (39.1)	29 (26.6)	
Indeterminate		59	57	86	1 (1.7)	2 (3.5)	8 (9.3)	0	1 (1.8)	0	15 (25.4)	21 (36.8)	43 (50.0)	
Intermediate total		323	183	402	5 (1.5)	5 (2.7)	16 (4.0)	3 (0.9)	7 (3.8)	13 (3.2)	51 (15.8)	58 (42.0)	126 (31.3)	
Radioulna		71	34	70	0	0	5 (7.1)	0	2 (5.9)	3 (4.3)	11 (15.5)	9 (26.5)	19 (27.1)	
Tibia		183	94	249	3 (1.6)	2 (2.1)	10 (4.0)	2 (1.1)	2 (2.1)	10 (4.0)	27 (14.8)	29 (30.9)	71 (28.5)	
Indeterminate		69	55	83	2 (2.9)	3 (5.5)	1 (1.2)	1 (1.4)	3 (5.5)	0	13 (18.8)	20 (36.4)	36 (43.4)	
Lower total		148	84	300	1 (0.7)	3 (3.6)	14 (4.7)	0	6 (7.1)	12 (4.0)	31 (20.9)	32 (38.1)	93 (31.0)	
Metacarpal		34	17	55	0	1 (5.9)	3 (5.5)	0	5 (29.4)	7 (12.7)	10 (29.4)	6 (35.3)	23 (41.8)	
Metatarsal		38	25	92	0	1 (4.0)	6 (6.5)	0	0	2 (2.8)	7 (18.4)	9 (36.0)	23 (25.0)	
Metapodial		76	42	153	1 (1.3)	1 (2.4)	5 (3.3)	0	1 (2.4)	3 (2.0)	14 (18.4)	17 (40.5)	47 (30.7)	
Limb bone shaft total		125	94	358	1 (0.8)	3 (3.2)	7 (2.0)	0	2 (2.1)	7 (2.0)	32 (25.6)	35 (37.2)	169 (47.2)	
Total	824	521	1350	10 (1.2)	14 (2.7)	60 (4.4)	3 (0.4)	17 (3.3)	45 (3.3)	143 (17.3)	182 (34.9)	475 (35.2)		

^a Animal size classes are based on Brain's (1981) well-known system for bovids.

^b Three separate categorizations of specimen identification are provided: (1) those specimens that could be identified to specific elements (i.e., humerus, radioulna, metacarpal, femur, tibia or metatarsal); (2) those specimens that could be identified to a limb segment, as an upper (humerus or femur), intermediate (radioulna or tibia) or lower (metapodial) specimens but no further; (3) those specimens that could be identified as limb bone shaft fragments only.

^c Members refer to Early Pleistocene units of the Swartkrans Formation; Member 1 was the earliest formed, followed by Member 2 and most recently by Member 3.

^d NISP: number of identified specimens. The raw NISP value is listed first in each cell, followed parenthetically with a percentage of the total NISP for the appropriate category.

As with butchery marks, an unanimous consensus was reached among all analysts before accepting a tooth mark as such. Each identified tooth pit was molded using Coltène© brand President Fast JET Light Body© polyvinylsiloxane. This step was taken both to avoid damaging fossils with caliper edges and to increase the clarity of pit borders for more accurate measurements (for more details see, Pickering et al., 2004b). Tooth pit length and breadth maxima (following Selvaggio, 1994; Domínguez-Rodrigo and Piqueras, 2003) were measured to the nearest 0.1 mm on these molds using high precision calipers. Each pit was measured twice and the mean used in analyses. Those pit molds too diffuse to allow a clear demarcation of pit borders were eliminated from the analysis. Tooth pit dimension data were normalized using log-transformation prior to comparative statistical analyses.

Results and discussion

Anatomical patterns of butchery marks: assessment of hominid carcass foraging capabilities

Data on the anatomical locations of stone tool cut-marks, on both the intra-skeletal and intra-bone levels, are the most convincing and direct indications of the timing of hominid access to animal carcasses (e.g., Bunn, 1982; Bunn and Kroll, 1986; Domínguez-Rodrigo, 1997, 1999a, 2002; Domínguez-Rodrigo and Pickering, 2003; Pickering and Domínguez-Rodrigo, 2006). We believe the most behaviorally informative comparisons in our sample are between upper plus intermediate elements and metapodials. The upper and intermediate limb bones of ungulates are similar in being heavily muscled and possessing capacious medullary cavities that house abundant marrow, while metapodials lack overlying meat and have constricted marrow chambers (Fig. 1). From here, we refer to the former class of bones as “meat-bearing”. We are of the opinion that the presence of butchered meat-bearing limb bone midshaft specimens in an archaeofauna indicates early access by hominids to animal carcasses. The midshaft portion of meat-bearing limb bones is a region defleshed early in the feeding sequence of a carnivore that has primary access to a carcass. For example, Domínguez-Rodrigo (1999a) observed that meat-bearing limb bones from 28 ungulate carcasses displayed a paucity of adhering flesh after ravaging by lions; midshaft sections on upper limbs in this dataset displayed a complete lack of flesh scraps, while flesh scraps on the midshaft portions of intermediate limb bones were poorly represented after lion ravaging. Assuming that the prehistoric carnivores of Swartkrans operated similarly, there would be no reason for hominids to have imparted cutmarks on meat-bearing limb bone midshafts had they been relegated to scavenging passively (i.e., late access to carcasses) from the remains of picked-over carnivore kills (see, Bunn, 2001; Domínguez-Rodrigo, 2002; Domínguez-Rodrigo and Pickering, 2003; Pickering and Domínguez-Rodrigo, 2006). In fact, there would be good reason not to put a stone tool to an exposed, meatless portion of bone since doing so would simply dull the cutting edge of that tool (e.g., Bunn, 2001). Experimental butchery data corroborate the eloquent argument, based on logic, that cutmarks are unexpected on previously defleshed limb bone midshafts. For example, analyses of Domínguez-Rodrigo’s (1997, 1999a) and Nilssen’s (2000) large, modern datasets demonstrate convincingly that cutmarks from activities other than defleshing (i.e., skinning, disarticulation) almost never occur on meat-bearing limb bone midshafts.

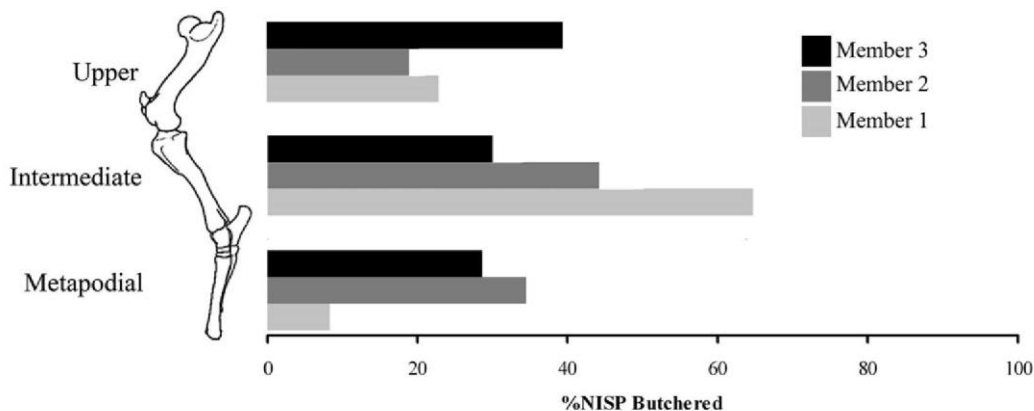


Fig. 2. Graphic representation of the proportion of butchered meat-bearing (i.e., humerus, radius, femur, tibia) versus non-meaty (i.e., metapodials) bone specimens in Swartkrans Members 1–3. Limb bone fragments that were not assignable to a more specific level of identification were excluded from analyses of meat-bearing versus non-meaty element representation. The total butchered samples in each member are comprised of high proportions of meat-bearing elements—indicating early access to carcasses by hominid foragers at Swartkrans c. 1.8–1.0 Myr ago. NISP: number of identified specimens.

Based on the non-adjusted data (utilized in this analysis because of the small sample size), there are more butchered meat-bearing specimens than metapodials in the assemblages from all three Swartkrans members (Table 2). Butchered meat-bearing specimens comprise 91.7%, 65.4% and 71.4% of the total butchered samples (minus skeletally unidentifiable specimens) in Members 1–3, respectively (Fig. 2). The differences in percentages are not statistically significant ($\chi^2 = 2.8$, 2 df, $p < 0.5$), suggesting a similar degree of high competence in carcass acquisition abilities for Swartkrans hominids (i.e., early access to preferred, heavily muscled carcass parts) through the time span covered by Members 1–3. It thus seems unlikely that the possible control of fire during Member 3 times increased relative success in carcass foraging. Our data suggest instead that hominids were hunting and/or aggressively scavenging much earlier, at least as early as Member 1 times.

Table 3
Adjusted samples (Analytical Sets II) for the Swartkrans faunas^{a,b}

Member	Total NISP	Cutmarked NISP	Percussion marked NISP ^c	Percussion flakes ^d	Total hominid modified minus percussion flakes NISP	Total carnivore modified (tooth-marked) NISP
1	623	3 (0.5)	0	15 (2.4)	3 (0.5)	46 (7.4)
2	1060	5 (0.5)	8 (0.8)	7 (0.7)	13 (1.2)	58 (5.5)
3	3151	19 (0.6)	28 (0.9)	50 (1.6)	47 (1.5)	135 (4.3)

^a Data adjusted to make the samples comparable to modern actualistic samples. The Swartkrans bone surface modification percentages fall far short of experimental standards for both human- and carnivore-processed limb bones. For example, Blumenschine (1995) found that in his “carnivore-only” experiments on average 83.9% of limb bone specimens are tooth-marked. Blumenschine and Selvaggio (1988) report that ~30% of the total specimens in their experimental sample of hammerstone-broken limb bones bear at least one percussion mark. Finally, ethnoarchaeological and experimental studies indicate that hominid tool-assisted defleshing results in 15–30% of specimens bearing cutmarks (Bunn, 1982; Domínguez-Rodrigo, 1997, 1999a; Lupo and O’Connell, 2002). Thus, when compared to actualistic controls the adjusted damage values for Swartkrans are inconsistent with scenarios of intense hominid or carnivore involvement in the formation of each member’s fauna.

^b NISP: number of identified specimens.

^c Percussion marks refer to “pits and striae, which are sometimes but not always associated with percussion notches. Diagnostic morphology and configuration of percussion pits and striae are described and illustrated by Turner (1983) and Blumenschine and Selvaggio (1988, 1991). Pits are often closely associated with and/or have emanating from them patches of striae that result from slippage of stone against bone during impact events” (Pickering et al., 2004a, 215; adapted from Blumenschine and Selvaggio, 1988).

^d Percussion (or impact) flakes are a specific type of bone flake, and not all bone flakes are percussion flakes. Bone flakes “display the same basic technical attributes of percussion as occur on flakes...of knapped fine-grained stone: (1) flakes possess a platform at the impact point and a bulb of percussion below the platform; [and] (2) they sometimes show ‘ripple’ marks and/or hackle (stress) marks originating at or near the platform or bulb...” (Fisher, 1995, 21). Vexingly, bone flakes with some of these same attributes have also been observed in modern bone samples known to be created by carnivores (e.g., Blumenschine, 1988; Blumenschine and Selvaggio, 1988; Bunn, 1989) and in paleontological assemblages inferred to have been created largely by hyenas (e.g., Villa and Bartram, 1996). The inescapable conclusion is that static loading by the teeth and jaws of large carnivores is as capable at creating bone flakes as is the dynamic loading of hammerstone percussion. Thus, we were maximally conservative in our analyses, eliminating from statistical consideration pieces that, in our experience (e.g., Pickering and Egeland, 2006), are likely percussion flakes, but that lack the percussion marks that could independently corroborate that inference.

Frequencies of butchery and carnivore feeding damage: assessment of assemblage formation

While the anatomical pattern of butchery damage points to little difference in hominid carcass foraging capabilities across time, overall frequencies of butchery damage are very low in all members, not even close to matching frequencies in experimentally butchered control samples (see note [1] in Table 3 legend). This is the case whether viewing the unadjusted data of Analytical Sets I (Table 2) or the adjusted data of Analytical Sets II (Table 3). Carnivore damage frequencies are also very low compared to modern actualistic samples (see note [1] in Table 3 legend). This is not surprising considering the depositional nature and time depth of the Swartkrans faunas: like most other South African cave assemblages, the Swartkrans assemblages were formed, at least in part, by secondarily deposited material derived from the cave’s surface catchment. Over long periods of time it is likely that abiotic processes in addition to biotic actors not dealt with systematically in this study (e.g., rodents) contributed significantly to assemblage formation, deflating the measures of the relative contributions of hominids and carnivores. In the final evaluation of our data, however, it is still fair to conjecture that Swartkrans was always a place of only moderate focused activity by both hominids and carnivores—a decidedly different notion of the cave than the textbook perception of an intensely dynamic micro-environment.

Another interesting result is the trend of weakly increasing butchery mark and decreasing tooth mark frequencies through time at Swartkrans (Table 3). At first glance these results seem to support the “shift in the balance of power” hypothesis, with the eventual near-eviction of carnivores by hominids by Member 3 times. However, deeper inspection of the data reveals that the variation is actually more nuanced. Only one of the differences in either type of frequency across members—butchery mark frequencies between Members 1 and

3—is significant (Table 4). Similarly, differences in tooth mark frequencies approach significance only between Members 1 and 3. All this suggests that as hominid and carnivore relationships transformed over time, the change was probably more subtle than hominids simply becoming dominant over carnivores. We present carnivore tooth mark and other data in the next section that substantiate this view.

Table 5
Tooth pit dimension statistics for Swartkrans Members 1–3^a

	Small		Large	
	Length	Breadth	Length	Breadth
<i>Member 1</i>				
<i>N</i>	53	53	9	9
Mean	1.92	1.22	2.42	1.46
SD	0.79	0.53	0.64	0.58
95% CI	1.70–2.14	1.07–1.37	1.93–2.91	1.02–1.90
<i>Member 2</i>				
<i>N</i>	51	51	10	10
Mean	2.25	1.43	2.81	1.65
SD	1.10	0.73	1.22	0.66
95% CI	1.94–2.56	1.23–1.63	1.94–3.68	1.18–2.12
<i>Member 3</i>				
<i>N</i>	121	121	40	40
Mean	2.34	1.64	3.20	2.28
SD	0.99	0.76	1.33	1.09
95% CI	2.16–2.52	1.50–1.78	2.77–3.63	1.93–2.63

^a Small: bone specimens from Size Class 1 and 2 animals combined; large: bone specimens from Size Class 3 and larger animals combined. *N*: number of measured pits. See Brain (1974, 1981) for bovid Size Classes.

Table 4
 χ^2 test results

	Member 1	Member 3
<i>(a) Adjusted butchery mark frequencies in the Swartkrans faunas</i>		
Member 2	$\chi^2 = 2.2, 1 \text{ df}, p < 0.2$	$\chi^2 = 0.4, 1 \text{ df}, p < 0.5$
Member 3	$\chi^2 = 4.0, 1 \text{ df}, p < 0.05$	
<i>(b) Adjusted tooth mark frequencies in the Swartkrans faunas</i>		
Member 2	$\chi^2 = 2.5, 1 \text{ df}, p < 0.2$	$\chi^2 = 2.6, 1 \text{ df}, p < 0.2$
Member 3	$\chi^2 = 12.6, 1 \text{ df}, p < 0.001$	

Tooth mark dimensions and complementary taphonomic indicators: assessment of carnivore taxonomy and cave use through time

Table 5 summarizes tooth pit dimensions for Swartkrans Members 1–3, while Fig. 3 provides graphic comparison of these dimensions with the modern tooth pit data on leopards and hyenas. Data are broken down by inferred body sizes of the animals from which tooth pitted specimens derived (small = Size Class 1 plus 2; large = Size Class 3 and larger). Considering the data collectively, one-way ANOVA indicates that the Swartkrans tooth pit lengths ($F = 7.02, 2 \text{ df}, p = 0.001$) and breadths ($F = 12.96, 2 \text{ df}, p = 0.00$) are significantly different between members.

For all three members, the mean values for tooth pits on bones from small animals are less than those for pits typically created by hyenas but similar to those created by leopards. The same holds for tooth pits on large animal bones recovered from Member 1. Of course, hyenas can also create small, “leopard-sized” pits, but the limited ranges of variation for the small animal bone samples from Members 1–3 and the large animal bone sample from Member 1 are more in line with populations of leopard-rather than hyena-generated pits (Fig. 3). Proposing that leopards were the primary collectors of the small animals in all three members is unsurprising given that such sized prey is typical of leopards (e.g., Brain, 1981). The more tenuous link suggested here is between leopards and the collection of larger animals in Member 1. We note, however, that leopards are known to occasionally kill Size Class 3 animals (e.g., Bailey, 1993; Bertram, 1982; Grobler and Wilson, 1972; Kruuk and Turner, 1967; Pienaar, 1969; de Ruiter and Berger, 2000; Schaller, 1972; Scott, 1985). That rare capture of large prey by leopards could account for the leopard-sized tooth pits on large animal specimens in Member 1, as well as for the relatively low frequency of tooth-marked specimens (10.6%; Table 2) in the total large animal bone sample from that member. Like other cats, leopards are primarily carcass defleshers rather than bone crushers and thus create minimally tooth-marked faunal accumulations (e.g., Dominguez-Rodrigo et al., in press).

Frequencies of tooth-marked specimens within the total large animal bone samples from Members 2 (19.7%) and 3 (26.8%) are significantly higher than in Member 1 (Member 1 versus Member 2: $\chi^2 = 8.4, 1 \text{ df}, p < 0.01$; Member 1 versus Member 3: $\chi^2 = 34.7, 1 \text{ df}, p < 0.001$). These observations agree with a hypothesis that, in contrast to the large animal bone sample from Member 1, hyenas created the large animal bone subassemblages

recovered from Members 2 and 3. In addition, tooth pit dimensions on large animal bones from Members 2 and Member 3 exceed those documented for leopards by several orders of magnitude. Although there are extensive ranges of variation evinced in the large animal bone pit samples from Members 2 and 3, it is the large maximum values for pit length and breadth and their correspondingly high means that are most important in leading to an inference that hyenas created these samples (Table 5). Simply said, leopards are not capable of creating pits of the great size (>2.2 mm) prevalent in the large animal bone samples from Members 2 and 3 (Dominguez-Rodrigo and Piqueras, 2003). Any tooth pit longer or broader than 2.2 mm is very likely to have been created by a carnivore with more robust teeth and stronger jaws than possessed by a leopard. Of the species considered in this study (see above in methods section), hyenas are just such a carnivore.

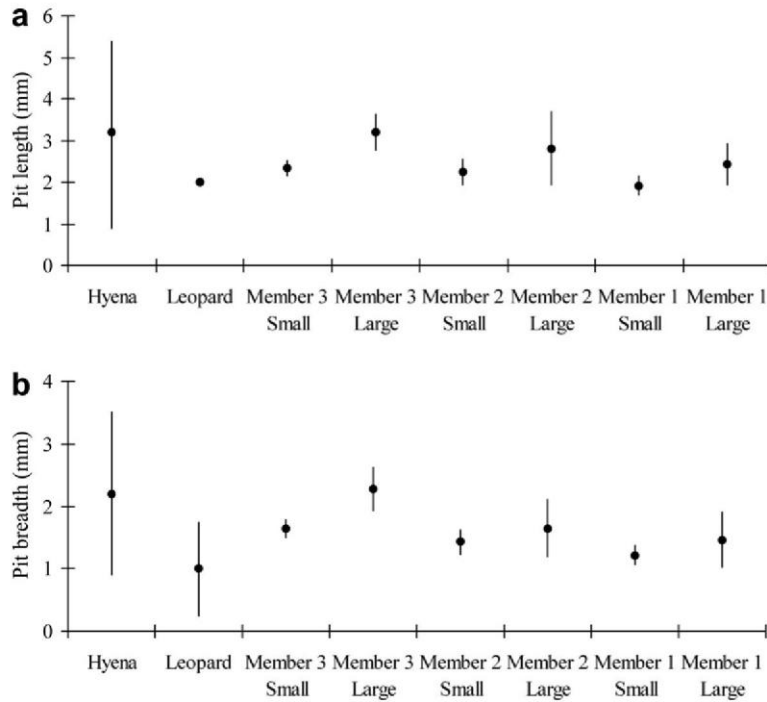


Fig. 3. Lengths (a) and breadths (b) of tooth pits created by modern leopards (Selvaggio, 1994) and hyenas (Domínguez-Rodrigo and Piqueras, 2003) on dense cortical limb bone diaphyses compared to those variables of tooth pits in the Swartkrans Members 1–3 faunas. Small: tooth pit distributions for pits on bone specimens of Size Class 1 and 2 animals; Large: tooth pit distributions on bone specimens of Size Class 3 and larger animals. Circles indicate means, range bars indicate 95% confidence intervals (see Table 5 for statistical details).

Independent data are available to test the hypothesis that leopards were primarily responsible for small carcass collection in Swartkrans Members 1–3 but for large carcasses only in Member 1, with a shift to large carcass collection by hyenas in Members 2 and 3. Local ecological conditions impact the intensity with which any carnivore(s) ravages a carcass. For example, even hyenas show reduced levels of carcass ravaging when they experience low competition and/or a glut of edible biomass (Dominguez-Rodrigo and Organista, in press). However, all conditions being equal, the standard taphonomic prediction is that a hyena-generated bone assemblage will appear more intensely ravaged than one produced by a leopard. Hyenas possess astonishingly robust teeth, driven by powerfully thick jaw muscles (e.g., Ewer, 1973; Brain, 1981). Equipped with this impressive masticatory battery, they are able to demolish prey skeletons and gain access to the nutrient-rich marrow contained within bones. Indeed, hyenas were and are among the most effective mammalian destroyers of bone to ever have existed (Sutcliffe, 1970). This characteristic means that carcass destruction by hyenas is often more complete than that of other carnivores with lesser chewing capabilities.

Applying this conventional wisdom, the Swartkrans Member 1 fauna should appear less ravaged than do the Member 2 and 3 assemblages, given the postulated predominant role of leopards in the formation of Member 1 and hyenas in Members 2 and 3. Building on the work of others (e.g., Brain, 1967, 1981; Bunn, 1983; Blumenschine and Marean, 1993; Marean et al., 1992; Capaldo, 1995), Dominguez-Rodrigo and Organista (in press) have created three indices based on MNE estimates to measure ravaging intensity in a faunal assemblage (in each case, leopard-derived assemblages should resemble a non-ravaged assemblage more closely than does a hyena-derived one):

- (1) Axial bones (ribs and vertebrae, minus sacral and caudal vertebrae): limb bones—a non-ravaged carcass will show a higher frequency of axial bones than appendicular bones because of the higher numbers of the former in a complete carcass.
- (2) Femora: tibiae—a non-ravaged carcass will have a ratio of 1. Because femora are overall less dense than are tibiae (e.g., Lam et al., 1998), ratios progressively closer to zero should indicate a greater degrees of carcass ravaging.
- (3) Proximal humeri plus distal radii: distal humeri plus proximal radii—a non-ravaged carcass will show a ratio of 1. The proximal humerus and distal radius are among the least dense limb portions of ungulate forelimbs (e.g., Lam et al., 1998), and because of this these portions are predicted to be preferentially deleted by bone-consuming carnivores. The lower the number of these least dense portions, the greater the degree of ravaging.

Table 6
“Ravaging indices” for the Swartkrans Members 1–3 faunas^a

Index	Member		
	1	2	3
Axial bones: limb bones ^b	22: 134, 0.2	218: 854, 0.3	39: 314, 0.1
Femora: tibiae ^b	18: 17, 1.1	73: 146, 0.5	25: 38, 0.7
Proximal humeri + distal radii: distal humeri + proximal radii ^c	25: 49, 0.5	15: 58, 0.3	34: 143, 0.2

^a “Ravaging indices” from Domínguez-Rodrigo and Organista (in press); see text for details.

^b Based on minimum number of element estimates from de Ruiter (2001: 247, Table 4.23; 259, Table 4.34; 268, Table 4.43).

^c Based on minimum number of element estimates from de Ruiter (personal communication, 2006).

Table 6 summarizes that two of the ratio results (femora: tibiae and proximal humeri + distal radii: distal radii + proximal humeri) we derived from published sources meet the predictions of our hypothesis of primary carcass input by leopards in Member 1, with a turn-over to hyenas in Member 2 and 3 times. Inter-assemblage results for axial bones: limb bones ratios are less distinct. In any case, assessment of these ancillary results need to be tempered by the fact that the Swartkrans assemblages derive from decidedly different depositional contexts than do the Olduvai Bed I (Tanzania) archaeofaunas for which the ravaging indices were developed. In most cases, those latter assemblages are composed of predominantly green-broken bone fragments and were often recovered from single thin depositional horizons (Domínguez-Rodrigo and Organista, in press). The contention in these cases is that carnivore ravaging was the predominant process acting to delete less dense bones and bone portions from the accumulated assemblages. As discussed above, the Swartkrans faunas, in contrast, were recovered from great depths of deposit and accordingly display a high degree of dry breakage. In these cases, additional “density mediated processes”, including sediment compaction and rock fall, were also likely major contributing forces in removing less dense bones and bone portions from the accumulated assemblages. Fortunately, this aspect of the Swartkrans faunas does not impact the interpretations of tooth mark and body size data as put forth above.

In summary, we infer the consistent presence of leopards throughout Members 1–3. Recovery of leopard remains from all three members (e.g., Watson, 1993) corroborates this inference. However, leopard food residue input seems to be largely limited to small carcasses by Member 2 and 3 times. It is unlikely that leopards and hyenas shared the cave during the formation of Members 2 and 3, suggesting serial occupation of the site by the two taxa. This conclusion can be interpreted variously, but we present below an interpretation that best matches the other lines of independent data presented in previous sections.

Synthesis and conclusions

Putting together the various pieces of evidence discussed above, we have formulated a model of hominid–carnivore dynamics through time at Swartkrans Cave, which has implications for the “shift in the balance of power” hypothesis. The six basic points of the model are as follows:

- (1) We agree with Brain (e.g., 1981, 1993a) that the majority of hominid skeletal remains recovered from Swartkrans Members 1–3 were deposited by feeding carnivores (who presumably also preyed upon those hominids).
- (2) The other type of hominid presence at Swartkrans that can be inferred from the paleoanthropological record is a behavioral one. Stone and bone tool assemblages are known from all three members (e.g., Brain and Shipman, 1993; Clark, 1993; Field, 1999), as well zooarchaeological remains, as documented in this paper. Judging from the small size of the artifactual samples and the paucity of butchered bones, that presence was, however, relatively ephemeral during the span of time each member was being deposited.
- (3) We infer at least two reasons for this relatively ephemeral presence. First, each of the three faunal assemblages is very large, the frequency of its hominid-derived components “swamped” by osseous contributions from many other types of taphonomic agents and processes (e.g., Brain, 1981; Pickering, 1999). Second, except possibly in the case of Swartkrans Member 3 (see below), it is very unlikely that hominids ever actually spent considerable time in the caves of the Sterkfontein Valley. The form of many Pleistocene caves, with steeply vertical entrances, was unlikely to have been conducive to hominid occupation (e.g., Pickering, 2002). As discussed above, taphonomic evidence also suggests that the caves were, in general, dangerous places, the haunts of large predators (e.g., Brain, 1981, 1993a).
- (4) That said, we recognize the great time depth represented by each geological member of the Swartkrans Formation. There is no consensus about sedimentation rates for infilling the South African caves (e.g., Brain, 1993b; Partridge, 1978, 1985; McFadden et al., 1979; Tobias et al., 1993; Clarke and Tobias, 1995; McKee, 1996; Tobias and Clarke, 1996), but it is possible that it took tens to hundreds of thousands of years to accumulate the average depositional thicknesses represented in each member at Swartkrans. That means that in addition to concurrent use of the cave by various taphonomic agents, it could have also been used serially during the formation of each member. This is certainly the case over much shorter, humanly observable spans of time in modern, African shelter sites (e.g., Mills, 1990).
- (5) Given the likelihood of serial use of Swartkrans, our admittedly crude (but currently best available) inference, based on tooth pit dimensions, is that leopards were the major carnivore to use the site as feeding lair during the entire depositional phase of Member 1. Modern behavioral observations (e.g., Corbett, 1954; Pienaar, 1969; Altmann and Altmann, 1970; Saayman, 1971; Isbell, 1994; Boesch, 1991; Fay et al., 1995) and inferences of the fossil record (e.g., Brain, 1981, 1993a) agree that leopards are/were successful predators of primates of early hominid body size. Together, we believe that the consistent and dangerous presence of leopards for the duration of Member 1 times was more than sufficient to deter regular hominid activity in and around the cave.
- (6) Tooth pits of hyena dimension appear in the Member 2 and 3 faunas. A salient inference that arises from these data is that the orientation of the cave’s entrance(s) may have changed from roughly vertical during Member 1 (which would have effectively limited hyena but not leopard access) to more horizontal in Members 2 and 3. Other lines of evidence, including geomorphological reconstructions of a gently sloping gully for Member 3 (e.g., Brain, 1993b), support this inference. This means that the cave would have also been more conducive to hominid use at these times. More importantly, the irregular presence of leopards during the formation of Members 2 and 3 presented hominids with periods of relatively safe access to the cave.

The trend of weakly increasing butchery mark and decreasing tooth mark frequencies through time at Swartkrans agrees with this model. Leopard predation was still a potential danger to hominids at various stages during which Members 2 and 3 were forming, but it was a less consistent one compared to its impact during Member 1 times. Our taphonomic data seem to indicate that hominids took advantage of the lessening predation pressure as early as Member 2 times, when butchery mark frequencies began to rise, tooth mark frequencies lowered and hyenas appeared as major bone modifiers. These trends were amplified during the formation of Member 3, but their initiation in Member 2 is significant because there is no evidence of burned bones in that earlier-formed unit (Brain and Sillen, 1988; Brain, 1993c). The “shift in the balance of power” hypothesis is partly predicated

on the protection from predation afforded to hominids by their control of fire. In contradistinction, our data suggest that rather than a shift in the balance of power, contrasting taphonomic patterns throughout Swartkrans Member 1–3 might instead reflect opportunistic use of the cave by hominids when leopards vacated it periodically. Further, butchery mark data from all three members are consistent in suggesting early access to choice carcass parts by hominids, implying that control of fire had little impact on these capabilities as well.

These specific inferences do not, of course, diminish the general importance of the control fire in human evolution. It was the advance that allowed early hominids to eventually render novel foods edible and to colonize new lands in high latitudes and at high altitudes previously too cold to occupy. We believe that Swartkrans still represents one of the best early contexts for investigating the emergence of this essential human technology. Three independent lines of evidence—histological, chemical and spatial (Brain and Sillen, 1988; Brain, 1993c; Sillen and Hoering, 1993)—converge to present a compelling case for hominid control of fire at Swartkrans. We do not mean to imply that the Swartkrans data are above critique, but it is frustrating that, for example, a heralded recent report on early fire fails to even comment on them (Goren-Inbar et al., 2004).

It is our hope that a newly initiated round of fieldwork at Swartkrans will produce more data to clarify the fire issue and rectify dismissal of the site from some current discussions of this vital human technology. In that case, the clear challenge remaining will be to accommodate the sympatry of *A. robustus* and *H. erectus* at Swartkrans into scenarios of fire use, as it has been for other aspects of hominid behavioral ecology in the region (reviewed in Pickering, 2006). Conventional wisdom assigns authorship of the technology (e.g., artifacts) and its functional residues (e.g., butchery damage) preserved at Swartkrans to the more “human-like” species *H. erectus*. But, unbiased consideration of the evidence can only lead to the conclusion that a choice is not yet possible. In view of our current inferential limitations, it is likely that discerning the party or parties responsible for fire will remain equally intractable. The conclusions reached in this study indicate that one or both of those parties was/were an adept procurer(s) of ungulate carcasses, gaining access to and exploiting the most nutritious components of those resources before potential competitors. It seems that the hominids in question were not, however, completely immune to the dangers presented by those potential competitors. In particular, taphonomic traces of carnivores are present in each of Members 1–3 faunas, implying that they were never completely evicted from the cave by hominids. Instead, it appears that the periodic absence of leopards during the formation of Members 2 and 3 was the rather mundane factor exploited by hominids in their gradually more frequent use of the cave.

Notes:

¹ Currently, there are five recognized geological members in the Swartkrans Formation, with Members 1–3 preserving fossil and archaeological materials that derive from the Early Stone Age (ESA) (Brain, 1993b). Member 1 is further subdivided into the Lower Bank and Hanging Remnant infills. The cave’s stratigraphy is extremely complex, having formed through a number of cycles of deposition and erosion. Swartkrans lacks volcanic material, so its members have been difficult to date absolutely; however, a recent electron spin resonance date of 1.6 Myr old for the Hanging Remnant of Member 1 (Curnoe et al., 2001) corresponds broadly with age estimates based on biostratigraphy. The most recent taxonomic analyses of the Swartkrans bovids and primates conclude that the three members cannot be differentiated chronometrically, and each is estimated to be between c. 1.8 and 1.4 or 1.0 Myr old (e.g., Brain, 1993a; Delson, 1988; Vrba, 1982). However, a combination of studies on sedimentology, stratigraphy and faunal seriation and archaeology suggest that the units are discrete and time successive, with the Member 1 Lower Bank representing the first of the four infills, followed by the Hanging Remnant, Member 2 and, most recently, Member 3 (Brain, 1993a,b; McKee et al., 1995). Our analyses exclude Hanging Remnant materials because, in contrast to the Lower Bank and Members 2 and 3 samples (Brain, 1993b), they were collected with relatively uncontrolled excavation.

² While two burned bones are also known from Member 2, “[i]t is expected that occasional lightning-induced fires would have swept through the grassland at the cave’s entrance and could have ignited logs and branches lying there, which in turn may have heated pieces of bone on the cave floor [during Member 2 times]” (Brain, 1993c, 238). In contrast, the Member 3 burned bone specimens were recovered from a 6 m deep profile, throughout a laterally restricted area, which was a gully during Member 3 times. Referring to just one of the

excavation units in Member 3, as an example, “burnt bones occur in 23 excavation spits, each 10 cm deep, indicating that the bones were heated in frequently recurring fires during the deposition period of this stratigraphic unit, which may have spanned several thousand years. The spatial distribution of the burnt bones suggests strongly that the fires occurred within the confines of the gully, which was beneath a dolomite roof and had an inclined entrance towards the southeast” (Brain, 1993c, 240). Finally, chemical and histological studies of these fossils suggest that they were heated in fires that reached temperatures equivalent to those measured in fires created and tended by modern humans (Brain and Sillen, 1988; Sillen and Hoering, 1993).

³ Limb bone shaft specimens are defined here as pieces from ungulate humeri, radioulnae, metacarpals, femora, tibiae and metatarsals that preserve less than their complete, original diaphyseal circumferences and do not possess their articular ends (modified from Pickering, 1999; see also Pickering et al., 2003).

⁴ For assessment of cortical surface preservation, each fossil specimen was assigned to a subaerial weathering stage (Behrensmeyer, 1978). In addition, our observations suggest that bone surface preservation on specimens from Swartkrans was also affected by various diagenetic processes, including water action, manganese formation and soil leaching. Thus, to account for overall surface condition, a subjective score of poor, moderate or good was assigned to each specimen (e.g., Pickering, 1999; Pickering et al., 2000). This is a qualitative assessment used to convey the relative “fidelity” of current bone surfaces for continuing to preserve prehistoric bone surface modifications. Distinguishing green- from dry-broken fracture edges is relatively simple. Green fractures occur on bone before loss of its organic fraction and are associated with smooth release surfaces and possess fracture angles (i.e., the “angle formed by the fracture surface [of a broken bone and its] cortical surface” [Villa and Mathieu, 1991, 34]) $<85^\circ$ or $>95^\circ$ (Pickering et al., 2005a). In contrast, dry fractures occur after loss of a bone’s organic content and are characterized by fracture angles closer to 90° .

⁵ Using tooth pit dimensions to identify its carnivore creator is still a relatively unrefined analytical technique; it is not yet possible to allocate a pit to a particular species or even genus. Instead, pit dimensions can discriminate between three groups of carnivores based on jaw and tooth size and strength. Larger-bodied carnivores (group 1: hyenas and lions), with more robust dentitions and greater masticatory power can generate larger tooth pits on cortical bone surfaces than can intermediate (group 2: dogs, leopards and cheetahs) and smaller (group 3: jackals) carnivores. Most of the tooth pits created by carnivores in each group (95%) can be understood within a certain size range, defined by a mean and a 95% confidence interval. In this context, it is opportune that hyenas and leopards occupy distinct groups and that lions, cheetahs and jackals can all be eliminated from consideration in the context of Swartkrans, since none are known to accumulate bones in caves. In addition, experimental work has also revealed that whereas group 1 carnivores can create the entire known size range of pits, from very small to very large, for group 2 and 3 carnivores tooth pit sizes reach maximum thresholds. More specifically, leopards have never been reported to create pits >2.2 mm on dense cortical bone—well under the mean size for hyena-created tooth pits (Dominguez-Rodrigo and Piqueras, 2003). Differentiating among carnivore groups is thus relatively reliable when using a large number of tooth pits and considering their entire size range.

References

- Altmann, S.A., Altmann, J., 1970. Baboon Ecology: African Field Research. Karger, Basel.
- Bailey, T., 1993. The African Leopard: Ecology and Behavior of a Solitary Felid. Columbia University Press, New York.
- Barba, R., Domínguez-Rodrigo, M., 2005. The taphonomic relevance of the analysis of bovid long limb bone shaft features and their application to element identification: study of bone thickness and morphology of the medullary cavity. *Journal of Taphonomy* 3, 29–42.
- Behrensmeyer, A.K., 1978. Taphonomic and ecologic information from bone weathering. *Paleobiology* 4, 150–162.
- Behrensmeyer, A.K., Gordon, K.D., Yanagi, G.T., 1986. Trampling as a cause of bone surface damage and pseudo-cutmarks. *Nature* 319, 768–771.
- Behrensmeyer, A.K., Gordon, K.D., Yanagi, G.T., 1989. Nonhuman bone modification in Miocene fossils from Pakistan. In: Bonnicksen, R., Sorg, M.H. (Eds.), *Bone Modification*. Center for the Study of the First Americans, Orono, ME, pp. 99–120.

- Bellomo, R.V., 1994. Methods of determining early hominid behavioral activities associated with the controlled use of fire at FxJj 20 main, Koobi Fora, Kenya. *Journal of Human Evolution* 27, 173–195.
- Bertram, B.C.R., 1982. Leopard ecology as studied by radio-tracking. *Symposium of the Zoological Society of London* 49, 341–352.
- Binford, L.R., 1981. *Bones: Ancient Men and Modern Myths*. Academic Press, New York.
- Blumenschine, R.J., 1988. An experimental model of the timing of hominid and carnivore influence on archaeological bone assemblages. *Journal of Archaeological Science* 15, 483–502.
- Blumenschine, R.J., 1995. Percussion marks, tooth marks and the experimental determinations of the timing of hominid and carnivore access to long bones at FLK Zinjanthropus, Olduvai Gorge, Tanzania. *Journal of Human Evolution* 29, 21–51.
- Blumenschine, R.J., Marean, C.W., 1993. A carnivore's view of archaeological bone assemblages. In: Hudson, J. (Ed.), *From Bones to Behavior: Ethnoarchaeological and Experimental Contributions to the Interpretation of Faunal Remains*. Southern Illinois University Press, Carbondale, IL, pp. 273–300.
- Blumenschine, R.J., Selvaggio, M.M., 1988. Percussion marks on bone surfaces as a new diagnostic of hominid behavior. *Nature* 333, 763–765.
- Blumenschine, R.J., Selvaggio, M.M., 1991. On the marks of marrow processing by hammerstones and hyenas: their anatomical patterning and archaeological implications. In: Clark, J.D. (Ed.), *Cultural Beginnings: Approaches to Understanding Early Hominid Life-Ways in the African Savanna*. Dr. Rudolf Habelt GMBH, Bonn, pp. 17–32.
- Blumenschine, R.J., Marean, C.W., Capaldo, S.D., 1996. Blind tests of inter-analyst correspondence and accuracy in the identification of cut marks, percussion marks, and carnivore tooth marks on bone surfaces. *Journal of Archaeological Science* 23, 493–507.
- Boesch, C., 1991. The effects of leopard predation on grouping patterns in forest chimpanzees. *Behaviour* 117, 220–241.
- Brain, C.K., 1967. Hottentot food remains and their bearing on the interpretation of fossil bone assemblages. *Scientific Papers of the Namib Desert Research Station* 32, 1–11.
- Brain, C.K., 1970. New finds at the Swartkrans australopithecine site. *Nature* 225, 1112–1119.
- Brain, C.K., 1974. Some suggested procedures in the analysis of bone accumulations from southern African quaternary sites. *Annals of the Transvaal Museum* 14, 1–8.
- Brain, C.K., 1981. *The Hunters or the Hunted? An Introduction to African Cave Taphonomy*. University of Chicago Press, Chicago.
- Brain, C.K., 1985. Interpreting early hominid death assemblages: the rise of taphonomy since 1925. In: Tobias, P.V. (Ed.), *The Past, Present and Future of Hominid Evolutionary Studies*. Alan R. Liss, New York, pp. 41–46.
- Brain, C.K., 1989. The evidence for bone modification by early hominids in southern Africa. In: Bonnicksen, R., Sorg, M.H. (Eds.), *Bone Modification*. Center for the Study of the First Americans, Orono, ME, pp. 291–297.
- Brain, C.K., 1993a. A taphonomic overview of the Swartkrans fossil assemblages. In: Brain, C.K. (Ed.), *Swartkrans: A Cave's Chronicle of Early Man*. Transvaal Museum, Pretoria, pp. 257–264.
- Brain, C.K., 1993b. Structure and stratigraphy of the Swartkrans cave in the light of the new excavations. In: Brain, C.K. (Ed.), *Swartkrans: A Cave's Chronicle of Early Man*. Transvaal Museum, Pretoria, pp. 23–33.
- Brain, C.K., 1993c. The occurrence of burnt bones at Swartkrans and their implications for the control of fire by early hominids. In: Brain, C.K. (Ed.), *Swartkrans: A Cave's Chronicle of Early Man*. Transvaal Museum, Pretoria, pp. 229–242.
- Brain, C.K., Shipman, P., 1993. The Swartkrans bone tools. In: Brain, C.K. (Ed.), *Swartkrans: A Cave's Chronicle of Early Man*. Transvaal Museum, Pretoria, pp. 195–215.
- Brain, C.K., Sillen, A., 1988. Evidence from the Swartkrans cave for the earliest use of fire. *Nature* 336, 464–466.
- Brain, C.K., Churcher, C.S., Clark, J.D., Grine, F.E., Shipman, P., Susman, R.L., Turner, A., Watson, V., 1988. New evidence of early hominids, their culture and environment from the Swartkrans cave, South Africa. *South African Journal of Science* 84, 828–835.
- Broom, R., Robinson, J.T., 1949. A new type of fossil man. *Nature* 164, 322.

- Broom, R., Robinson, J.T., 1950. Man contemporaneous with the Swartkrans ape-man. *American Journal of Physical Anthropology* 8, 151–156.
- Broom, R., Robinson, J.T., 1952. Swartkrans Ape-Man *Paranthropus crassidens*. Transvaal Museum, Pretoria.
- Bunn, H.T., 1981. Archaeological evidence for meat-eating by Plio–Pleistocene hominids from Koobi Fora and Olduvai Gorge. *Nature* 291, 574–577.
- Bunn, H.T., 1982. Meat-Eating and Human Evolution: Studies on the Diet and Subsistence Patterns of Plio–Pleistocene Hominids in East Africa, Ph.D. Dissertation. University of California, Berkeley.
- Bunn, H.T., 1983. Comparative analysis of modern bone assemblages from a San hunter-gatherer camp in the Kalahari Desert, Botswana, and from a spotted hyena den near Nairobi, Kenya. In: Clutton-Brock, J., Grigson, C. (Eds.), *Animals and Archaeology*, vol. 1, Hunters and their Prey British Archaeological Reports International Series 16, Oxford, pp. 143–148.
- Bunn, H.T., 1989. Diagnosing Plio–Pleistocene hominid activity with bone fracture evidence. In: Bonnicksen, R., Sorg, M.H. (Eds.), *Bone Modification*. Center for the Study of the First Americans, Orono, ME, pp. 299–315.
- Bunn, H.T., 1991. A taphonomic perspective on the archaeology of human origins. *Annual Review of Anthropology* 20, 433–467.
- Bunn, H.T., 2001. Hunting, power scavenging, and butchering by Hadza foragers and by Plio–Pleistocene Homo. In: Stanford, C.B., Bunn, H.T. (Eds.), *Meat-Eating and Human Evolution*. Oxford University Press, New York, pp. 199–218.
- Bunn, H.T., Kroll, E.M., 1986. Systematic butchery by Plio/Pleistocene hominids at Olduvai Gorge, Tanzania. *Current Anthropology* 27, 431–452.
- Capaldo, S.D., 1995. Inferring Hominid and Carnivore Behavior from Dual-Patterned Archaeological Assemblages, Ph.D. Dissertation. Rutgers University, New Brunswick.
- Capaldo, S.D., 1997. Experimental determinations of carcass processing by Plio–Pleistocene hominids and carnivores at FLK 22 (*Zinjanthropus*), Olduvai Gorge, Tanzania. *Journal of Human Evolution* 33, 555–597.
- Capaldo, S.D., 1998. Methods, marks and models for inferring hominid and carnivore behavior. *Journal of Human Evolution* 35, 323–326.
- Carlson, K.J., Pickering, T.R., 2003. Intrinsic qualities of primate bones as predictors of skeletal element representation in modern and fossil carnivore feeding assemblages. *Journal of Human Evolution* 44, 431–450.
- Clark, J.D., 1993. Stone artifact assemblages from Members 1–3, Swartkrans cave. In: Brain, C.K. (Ed.), *Swartkrans: A Cave's Chronicle of Early Man*. Transvaal Museum, Pretoria, pp. 167–194.
- Clarke, R.J., Tobias, P.V., 1995. Sterkfontein Member 2 foot bones of the oldest South African hominid. *Science* 269, 521–524.
- Clarke, R.J., Howell, F.C., Brain, C.K., 1970. More evidence of an advanced hominid at Swartkrans. *Nature* 225, 1217–1220.
- Cleghorn, N., Marean, C.W., in press. The destruction of skeletal elements by carnivores: the growth of a general model for skeletal element destruction and survival in zooarchaeological assemblages. In: Pickering, T.R., Schick, K., Toth, N. (Eds.), *Breathing Life into Fossils: Taphonomic Studies in Honor of C.K. (Bob) Brain*. Stone Age Institute Press, Bloomington, IN.
- Corbett, J., 1954. *The Man-Eating Leopard of Rudraprayag*. Oxford University Press, London.
- Curnoe, D., Grün, R., Taylor, L., Thackeray, F., 2001. Direct ESR dating of a Pliocene hominin from Swartkrans. *Journal of Human Evolution* 40, 379–391.
- Delson, E., 1988. Chronology of South African australopithecine site units. In: Grine, F.E. (Ed.), *Evolutionary History of the "Robust" Australopithecines*. Aldine de Gruyter, New York, pp. 317–324.
- de Ruiter, D.J., 2001. A Methodological Analysis of the Relative Abundance of Hominids and Other Macromammals from the Site of Swartkrans, South Africa, Ph.D. Dissertation. University of the Witwatersand.
- de Ruiter, D.J., Berger, L.R., 2000. Leopards as taphonomic agents in dolomitic caves—implications for bone accumulations in the hominid-bearing deposits of South Africa. *Journal of Archaeological Science* 27, 665–684.
- Domínguez-Rodrigo, M., 1997. Meat-eating by early hominids at the FLK 22 *Zinjanthropus* site, Olduvai Gorge (Tanzania): an experimental approach using cut-mark data. *Journal of Human Evolution* 33, 669–690.
- Domínguez-Rodrigo, M., 1999a. Meat-eating and carcass procurement at the FLK Zinj 22 site, Olduvai Gorge (Tanzania): a new experimental approach to the old hunting-versus-scavenging debate. In: Ullrich, H. (Ed.),

- Lifestyles and Survival Strategies in Pliocene and Pleistocene Hominids. Schwelm, Edition Archaea, pp. 89–111.
- Domínguez-Rodrigo, M., 1999b. Flesh availability and bone modifications in carcasses consumed by lions: palaeoecological relevance in hominid foraging patterns. *Palaeogeography, Palaeoclimatology, Palaeoecology* 149, 373–388.
- Domínguez-Rodrigo, M., 2002. Hunting and scavenging in early hominids: the state of the debate. *Journal of World Prehistory* 16, 1–56.
- Domínguez-Rodrigo, M., Organista, E., in press. Natural background bone assemblages and their ravaging stages at Bed I Olduvai. In: Domínguez-Rodrigo, M., Egeland, C.P., Barba, R. (Eds.), *Deconstructing Olduvai: A Taphonomic Study of the Bed I Sites*. Springer, New York.
- Domínguez-Rodrigo, M., Pickering, T.R., 2003. Early hominid hunting and scavenging: a zooarchaeological review. *Evolutionary Anthropology* 12, 275–282.
- Domínguez-Rodrigo, M., Piqueras, A., 2003. The use of tooth pits to identify carnivore taxa in tooth-marked archaeofaunas and their relevance to reconstruct hominid carcass processing behaviours. *Journal of Archaeological Science* 30, 1385–1391.
- Domínguez-Rodrigo, M., Pickering, T.R., Semaw, S., Rogers, M.J., 2005. Cutmarked bones from Pliocene archaeological sites at Gona, Afar, Ethiopia: implications for the function of the world's oldest stone tools. *Journal of Human Evolution* 48, 109–121.
- Domínguez-Rodrigo, M., Egeland, C.P., Pickering, T.R., in press. Equifinality in carnivore tooth marks and the extended concept of archaeological palimpsests: implications for models of passive scavenging by hominids. In: Pickering, T.R., Schick, K., Toth, N. (Eds.), *Breathing Life into Fossils: Taphonomic Studies in Honor of C.K. (Bob) Brain*. Stone Age Institute Press, Bloomington, IN.
- Egeland, C.P., Pickering, T.R., Domínguez-Rodrigo, M., Brain, C.K., 2004. Disentangling early stone age palimpsests: determining the functional independence of hominid- and carnivore-derived portions of archaeofaunas. *Journal of Human Evolution* 47, 343–357.
- Ewer, R.F., 1973. *The Carnivores*. Cornell University Press, Ithaca.
- Fay, J.M., Carroll, R., Kerbis-Peterhans, J.C., Harris, D., 1995. Leopard attack on and consumption of gorillas in the Central African Republic. *Journal of Human Evolution* 29, 93–99.
- Field, A.S., 1999. *An Analytic and Comparative Study of the Earlier Stone Age Archaeology of the Sterkfontein Valley*, M.Sc. Dissertation. University of the Witwatersrand, Johannesburg.
- Fiorillo, A.R., 1989. An experimental study of trampling: Implications for the fossil record. In: Bonnicksen, R., Sorg, M.H. (Eds.), *Bone Modification*. Center for the Study of the First Americans, Orono, ME, pp. 61–71.
- Fisher, J.W., 1995. Bone surface modifications in zooarchaeology. *Journal of Archaeological Method and Theory* 2, 7–68.
- Goren-Inbar, N., Alperson, N., Kislev, M.E., Simchoni, O., Melamed, Y., Ben-Nun, A., Werker, E., 2004. Evidence of hominin control of fire at Geshar Benot Ya'aqov, Israel. *Science* 304, 725–727.
- Grobler, J.H., Wilson, V.J., 1972. Food of the leopard, *Panthera pardus* (Linn.) in the Rhodes Matopos National Park, as determined by faecal analysis. *Arnoldia Rhodesia* 5, 1–9.
- Haynes, G., 1983. Frequencies of spiral and green bone fractures on ungulate limb bones in modern surface assemblages. *American Antiquity* 48, 102–114.
- Isbell, L.A., 1994. Predation on primates: ecological patterns and evolutionary consequences. *Evolutionary Anthropology* 3, 61–71.
- Kruuk, H., Turner, M., 1967. Comparative notes on predation by lion, leopard, cheetah, and wild dog in the Serengeti area, East Africa. *Mammalia* 31, 1–27.
- Kuman, K., 2003. Site formation in the early South African stone age sites and its influence on the archaeological record. *South African Journal of Science* 99, 251–254.
- Kuman, K., Field, A.S., McNabb, A.J., 2005. La préhistoire ancienne de l'Afrique méridionale: contribution des sites à hominidés d'Afrique du sud. In: Sahnouni, M. (Ed.), *Le Paléolithique en Afrique: L'histoire la plus Longue*. Éditions Artcom, Errance, pp. 53–82.
- Lam, Y.M., Chen, X., Marean, C.W., Frey, C.J., 1998. Bone density and long bone representation in archaeological faunas: comparing results from CT and photon densitometry. *Journal of Archaeological Science* 25, 559–570.

- Lupo, K.D., O'Connell, J.F., 2002. Cut and tooth mark distributions on large animal bones: ethnoarchaeological data from the Hadza and their implications for current ideas about early human carnivory. *Journal of Archaeological Science* 29, 85–109.
- McFadden, P.L., Brock, A., Partridge, T.C., 1979. Palaeomagnetism and the age of the Makapansgat hominid site. *Earth and Planetary Science Letters* 44, 373–382.
- McKee, J.K., 1996. Faunal evidence and Sterkfontein Member 2 foot bones of an early hominid. *Science* 271, 1301–1302.
- McKee, J.K., Thackeray, J.F., Berger, L.R., 1995. Faunal assemblage seriation of southern African Pliocene and Pleistocene fossil deposits. *American Journal of Physical Anthropology* 96, 235–250.
- Marean, C.W., Cleghorn, N., 2003. Large mammal skeletal element transport: applying foraging theory in a complex taphonomic system. *Journal of Taphonomy* 1, 15–42.
- Marean, C.W., Ehrhardt, C.L., 1995. Paleoanthropological and paleoecological implications of the taphonomy of a sabertooth's den. *Journal of Human Evolution* 29, 515–547.
- Marean, C.W., Dominguez-Rodrigo, M., Pickering, T.R., 2004. Skeletal element equifinality in zooarchaeology begins with method: the evolution and status of the “shaft critique”. *Journal of Taphonomy* 2, 69–98.
- Marean, C.W., Spencer, L.M., Blumenschine, R.J., Capaldo, S.D., 1992. Captive hyena bone choice and destruction, the schlepp effect and Olduvai archaeofaunas. *Journal of Archaeological Science* 19, 101–121.
- Mills, M.G.L., 1990. *Kalahari Hyaenas: Comparative Behavioural Ecology of Two Species*. Unwin Hyman, London.
- Nilssen, P.J., 2000. *An Actualistic Butchery Study in South Africa and its Implications for Reconstructing Hominid Strategies of Carcass Acquisition and Butchery in the Upper Pleistocene and Plio–Pleistocene*, Ph.D. Thesis. University of Cape Town.
- Oliver, J.S., 1989. Analogues and site context: bone damages from Shield Trap Cave (24CB91), Carbon County, Montana, USA. In: Bonnichsen, R., Sorg, M.H. (Eds.), *Bone Modification*. Center for Study of the First Americans, Orono, ME, pp. 73–98.
- Partridge, T.C., 1978. Re-appraisal of lithostratigraphy of Sterkfontein hominid site. *Nature* 275, 282–287.
- Partridge, T.C., 1985. Spring flows and tufa accretion at Taung. In: Tobias, P.V. (Ed.), *Hominid Evolution: Past, Present and Future*. Alan R. Liss, New York, pp. 171–187.
- Pickering, T.R., 1999. *Taphonomic Interpretations of the Sterkfontein Early Hominid Site (Gauteng, South Africa) Reconsidered in Light of Recent Evidence*, Ph.D. Dissertation. University of Wisconsin, Madison.
- Pickering, T.R., 2002. Reconsideration of criteria for differentiating faunal assemblages accumulated by hyenas and hominids. *International Journal of Osteoarchaeology* 12, 127–141.
- Pickering, T.R., 2006. Subsistence behaviour of South African Pleistocene hominids. *South African Journal of Science* 102, 205–210.
- Pickering, T.R., Carlson, K.J., 2002. Bone mineral densities: implications for the taphonomy of primate skeletons in South African cave sites. *Journal of Archaeological Science* 29, 883–896.
- Pickering, T.R., Domínguez-Rodrigo, M., 2006. The acquisition and use of large mammal carcasses by Oldowan hominins in eastern and southern Africa: a selected review and assessment. In: Toth, N., Schick, K. (Eds.), *The Oldowan: Case Studies into the Earliest Stone Age*. Stone Age Institute Press, Bloomington, IN, pp. 113–128.
- Pickering, T.R., Egeland, C.P., 2006. Experimental patterns of hammer-stone percussion damage on bones: implications for inferences of carcass processing by humans. *Journal of Archaeological Science* 33, 459–469.
- Pickering, T.R., Wallis, J., 1997. Bone modifications resulting from captive chimpanzee mastication: implications for the interpretation of Pliocene archaeological faunas. *Journal of Archaeological Science* 24, 1115–1127.
- Pickering, T.R., Marean, C.W., Domínguez-Rodrigo, M., 2003. Importance of limb bone shaft fragments in zooarchaeology: a response to “On in situ attrition and vertebrate body part profiles” (2002), by M.C. Stiner. *Journal of Archaeological Science* 30, 1469–1482.
- Pickering, T.R., Domínguez-Rodrigo, M., Egeland, C.P., Brain, C.K., 2004a. New data and ideas on the foraging behaviour of Early Stone Age hominids at Swartkrans Cave, South Africa. *South African Journal of Science* 100, 215–219.

- Pickering, T.R., Domínguez-Rodrigo, M., Egeland, C.P., Brain, C.K., 2004b. Beyond leopards: tooth marks and the contribution of multiple carnivore taxa to the accumulation of the Swartkrans Member 3 fossil assemblage. *Journal of Human Evolution* 46, 595–604.
- Pickering, T.R., Domínguez-Rodrigo, M., Egeland, C.P., Brain, C.K., 2005a. The contribution of limb bone fracture patterns to reconstructing early hominid behavior at Swartkrans Cave (South Africa): archaeological application of a new analytical method. *International Journal of Osteoarchaeology* 15, 247–260.
- Pickering, T.R., Domínguez-Rodrigo, M., Egeland, C.P., Brain, C.K., 2005b. The earliest evidence of hominid butchery in southern Africa: new zooarchaeological and taphonomic data on the use of large animal carcasses at Swartkrans Members 1–3. Paper presented at the Annual Meeting of the Paleoanthropology Society, held in Milwaukee, Wisconsin, April 4–6, 2005.
- Pickering, T.R., Domínguez-Rodrigo, M., Egeland, C.P., Brain, C.K., in press. Carcass foraging by early hominids at Swartkrans cave (South Africa): a new investigation of the zooarchaeology and taphonomy of Member 3. In: Pickering, T.R., Schick, K., Toth, N. (Eds.), *Breathing Life into Fossils: Taphonomic Studies in Honor of C.K. (Bob) Brain*. Stone Age Institute Press, Bloomington, IN.
- Pickering, T.R., White, T.D., Toth, N., 2000. Cutmarks on a Plio–Pleistocene hominid from Sterkfontein, South Africa. *American Journal of Physical Anthropology* 111, 579–584.
- Pienaar, U., 1969. Predator-prey relations amongst the larger mammals of Kruger National Park. *Koedoe* 12, 108–176.
- Pobiner, B., Blumenschine, R.J., 2003. A taphonomic perspective on Oldowan hominid encroachment on the carnivoran paleoguild. *Journal of Taphonomy* 1, 115–141.
- Saayman, G.S., 1971. Baboons' responses to predators. *African Wild Life* 25, 46–49.
- Schaller, G.B., 1972. *The Serengeti Lion: A Study of Predator-Prey Relations*. University of Chicago Press, Chicago.
- Schick, K.D., 1987. *Stone Age Sites in the Making: Experiments on the Formation and Transformation of Archaeological Occurrences*. British Archaeological Reports International Series 319, Oxford.
- Scott, J., 1985. *The Leopard's Tale*. Elm Tree Books, London.
- Selvaggio, M.M., 1994. Carnivore tooth marks and stone tool butchery marks on scavenged bones: archaeological implications. *Journal of Human Evolution* 27, 215–228.
- Selvaggio, M.M., 1998. Concerning the three stage model of carcass processing at the FLK Zinjanthropus: a reply to Capaldo. *Journal of Human Evolution* 35, 319–321.
- Selvaggio, M.M., Wilder, J., 2001. Identifying the involvement of multiple carnivore taxa with archaeological bone assemblages. *Journal of Archaeological Science* 28, 465–470.
- Shipman, P., Rose, J., 1983. Early hominid hunting, butchering and carcass-processing behaviors: approaches to the fossil record. *Journal of Anthropological Archaeology* 2, 57–98.
- Sillen, A., Hoering, T., 1993. Chemical characterization of burnt bones from Swartkrans. In: Brain, C.K. (Ed.), *Swartkrans: A Cave's Chronicle of Early Man*. Transvaal Museum, Pretoria, pp. 243–249.
- Sutcliffe, A.J., 1970. Spotted hyaena: crusher, gnawer, digester and collector of bones. *Nature* 227, 1110–1113.
- Tobias, P.V., Clarke, R.J., 1996. Reply to McKee, Faunal evidence and Sterkfontein Member 2 foot bones of an early hominid. *Science* 271, 1301–1302.
- Tobias, P.V., Vogel, J.C., Oshadleus, H.D., Partridge, T.C., McKee, J.K., 1993. New isotopic and sedimentological measurements on the Thabaseek deposits and their bearing on the dating of the Taung hominid. *Quaternary Research* 40, 360–367.
- Turner, C.G., 1983. Taphonomic reconstruction of human violence and cannibalism based on mass burials in the American Southwest. In: LeMoine, G.M., MacEachern, A.S. (Eds.), *Carnivores, Human Scavengers and Predators: A Question of Bone Technology*. University of Calgary Archaeological Association, Calgary, pp. 219–240.
- Villa, P., Bartram, L.E., 1996. Flaked bone from a hyena den. *Paleo* 8, 143–159.
- Villa, P., Mathieu, E., 1991. Breakage patterns of human long bones. *Journal of Human Evolution* 21, 27–48.
- Vrba, E.S., 1982. Biostratigraphy and chronology based particularly on Bovidae of southern African hominid-associated assemblages: Makapansgat, Sterkfontein, Taung, Kromdraai, Swartkrans; also Elandsfontein (Saldanha), Broken Hill (now Kabwe) and Cave of Hearths. In: de Lumley, M.A. (Ed.), *L'Homo erectus et la*

Place de l'Homme Tautavel parmi les Hominides Fossiles. 1er Congres International de Paleontologie Humaine, Nice, pp. 707–752.

Watson, V., 1993. Composition of the Swartkrans bone accumulations, in terms of skeletal parts and animals represented. In: Brain, C.K. (Ed.), Swartkrans: A Cave's Chronicle of Early Man. Transvaal Museum, Pretoria, pp. 35–73.

White, T.D., 1988. The comparative biology of "robust" Australopithecus: clues from context. In: Grine, F.E. (Ed.), Evolutionary History of the "Robust" Australopithecines. Aldine de Gruyter, New York, pp. 449– 483.