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Converging on Ancient Bones: A Review of the Evidence for the Close Relatedness of Humans (*Homo sapiens*) and Spotted Hyenas (*Crocuta crocuta*)

Introduction. Spotted hyenas — Africa’s second largest of carnivores — are adaptable, highly social creatures living in fission-fusion groups of between five and ninety individuals (Holekamp). Group members adhere to a strict social hierarchy in which females are dominant and cubs inherit social ranks just below those of their mothers. On maturity, males normally disperse and join nearby groups where they acquire the lowest rank (East and Hofer). In many ways hyenas are like humans to the extent that they have earned the (dubiously anthropocentric) title of “honorary primate[s]” (Despret 360). They are highly intelligent and adept at cooperative problem solving, flexible with regard to the landscapes they occupy, have a rich vocabulary of sounds with which they communicate, adhere to dominance hierarchies, and enjoy eating meat (Holekamp, Sakai and Lundrigan; Theis et al.; Drea and Carter). Ironically it is this likeness to humans that Brottman (114) argues underpins the projection onto hyenas of the worst of human attributes. To say that hyenas have a bad reputation needs little qualification. From the time of Aristotle, hyenas have been historically vilified and with a few exceptions are loathed across the African continent and beyond (Glickman; Baynes-Rock). Hyenas evoke strong reactions in humans, and as anyone who has studied hyenas knows, humans elicit strong reactions from hyenas. Nevertheless, these two species are usually studied separately.

Until recently, studies of free ranging spotted hyenas have primarily been undertaken in national parks, national reserves, and conservation areas where there has been a limited human presence. Few have been conducted in non-protected areas where hyenas and humans co-occupy the landscape (see for example Abay et al.; Yirga & Bauer). Indeed, of the twenty hyena study areas listed in Holekamp and Dloniak, all but three are national parks, national reserves, conservation areas, or game reserves. While some of these studies examine hyenas’ responses to tourism and pastoralist encroachment (see for example Boydston et al.; Kolowski & Holekamp; Kolowski et al.), those that are concerned with hyenas “natural” behaviors neglect to include humans. Scientists note that gregariousness and vigilance in hyenas evolved as adaptations to the need to defend resources against competitors, but these hypothesized competitors only include lions and other carnivora as effectors in hyena evolution (see for example Smith et al., “Social and ecological determinants” 631). Meanwhile, humans are only

discussed where hyenas are argued to be their analogues in the evolution of social intelligence (Smith et al., “Evolutionary forces” 298; Holekamp, Sakai and Lundrigan 545; but see Pangle and Holekamp 264). While the studies themselves do not abnormalize the co-occurrence of humans and hyenas, I argue that their chosen locations reflect conceptions of hyenas “natural” ecologies as being exclusive of humans. As I will show below, such conceptions disregard not only the influence of humans and hyenas on each other’s evolutionary histories, but the place of humans in so-called “natural” processes (Evernden 35). Daniel Gade’s account of historical relations between humans and spotted hyenas in the Horn of Africa challenges such conceptions. In his paper, Gade describes how the persistence of hyenas in the region is a “vestige” of an ancient relationship in which both humans and hyenas changed and adapted to the presence of the other (625). He offers a bio-cultural framework for better understanding the ongoing patterns of “predation, competition and complementarity” in the Horn. Accordingly, “nature” and “history” meld together so that the present is but a window looking into an ongoing ecological process that began millions of years ago when humans and hyenas first crossed paths on the African Savannah. Here I review the archaeological evidence for these processes which in light of Gade’s thesis demonstrate how the similarities between humans and hyenas are not coincidental. Rather these reflect a relatedness to hyenas that is integral to the human condition and vice versa.

Evidence Digested. As far back in human evolutionary history as evidence permits us to see, the presence of hyenas in ancestral human landscapes is always implied, if not positively attested to by their bones and teeth marks. The story of this relationship begins on the African continent around 4.4 million years ago. At a place now known as Aramis, in the Middle Awash in Ethiopia, ancient antelopes and rhinoceroses grazed alongside old world monkeys who had descended from scattered trees to find food. Remains of six individual ardipithecines indicate that ancient hominins were there as well, alternating between frugivorous predictability in the trees and omnivorous opportunity at ground level in a mosaic environment of grasses, scattered trees, and stands of forest (Suwa et al.; White et al. “Macrovertebrate paleontology” 89). So too were hyenas present. In fact almost all of the remains of the ardipithecines from that place and time have been heavily “ravaged by hyenas, most likely *Crocuta dietrichi*, the precursors to modern spotted hyenas (Louchart et al. 66).

The most famous fossilized Ardipithecine, known as “Ardi,” came from Aramis and her remarkable state of preservation is due inversely to hyenas, as it is they who crunched, digested, and scattered so much of the other evidence in that locality. Ardi died in a

swale and was quickly buried before her remains were trampled by hippos. She escaped the local hyenas' jaws and powerful digestive juices to return to the surface 4.4 million years later to inform palaeoanthropologists of the nature of her species (White et al., "Macrovertebrate paleontology" 78). Prior to the discovery of Ardi, the only evidence for *Ardipithecus*' existence was a collection of undigested teeth, a basicranium fragment, and some shattered, gnawed arm-bone elements (White, Suwa and Asfaw 308). It is that destructive capacity of ancient hyenas that has made palaeoanthropology the treasure hunt that it is (Kruuk, *Hunter and Hunted* 104), making a find like Ardi, with postcranial skeleton uneaten, so rare as to make her and her discoverers famous. If not for hyenas, there would have been hundreds of such specimens bequeathed to us, bleached by the sun and buried beneath years of sediment to be unearthed later with the help of tectonic processes of the rift valley. If not for hyenas, Ardi would have been just another near-complete *Ardipithecine*.

Half a million years later and 800 kilometers southwest of Aramis, in the Turkana basin, hominins of another species lived and died on a plain beside a river channel. Those pre-humans were individuals of the species *Australopithecus anamensis* who comingled with bush-pigs, monkeys, and hippos in their food quest (Schoeninger, Reeser and Hallin 203). As with the *ardipithecines*, the remains of the individuals from the Turkana basin have been thoroughly modified; all from Kanapoi and several from Allia bay were "ravaged" by carnivores, so all that remains are some teeth and long bone ends (Coffing et al. 58; Leakey, M. G. et al., "New specimens and confirmation" 65; Ward, Leakey, M. & Walker 198). Unsurprisingly, there were hyenas there, too; members of an indeterminate species who were the most common carnivores in the fossil assemblages (Leakey, M. G. et al., "New four-million-year-old hominid species" 571).

Later still, 3.6 million years ago, at a place now known as Laetoli in Tanzania, a volcano now extinct was belching ash into the air above an ancient landscape that was not dissimilar from that of the present. The ash fell with rain and filled wide depressions in the ground surface, creating beds of light grey mud, across one of which three hominins ventured onto the plains from the woods to the south. There were three individuals, a male, a female and a juvenile — the earliest known nuclear family —, and their footprints became incontrovertible evidence of the bipedality of their species. The sodden ash crystallized and cemented quickly in the heat of the sun. Then, soon afterwards, another layer of sodden ash filled the depressions, miraculously preserving the moment in time for palaeontologists to discover millions of years later (Leakey, M. D. and Hay 318). And among the other animals whose footprints were preserved at

Laetoli were the ubiquitous hyenas. A Musukuma tracker employed to identify the species represented in the numerous animal footprints that criss-crossed the ancient cement identified eight trails made by hyenas (320). The respective hyenas walked, loped, and cantered their way across the cement; one of them leaving prints averaging 125mm x 102mm (length x breadth). That was a large hyena, as large as a modern *Crocuta*, the ancient species of which was one of the five hyaenid species recorded at Laetoli (Barry 240). It may not have been proof of competition or conflict, but it was incontrovertible proof of coexistence, early in human evolutionary history.

That was the time of the emergence of spotted hyenas (Turner 256). While designated the same genus, *Crocuta*, those ancient hyenas were not identical to those of the genus that are extant in Africa today. The bone cracking and carcass lifting adaptations of modern spotted hyenas evolved at different times in their history, and the suite of adaptations that define spotted hyenas as they are known today only evolved one million years ago (Lewis and Werdelin 93). However, early spotted hyenas were sufficiently adaptable to have been able to disperse into Asia during the late Pliocene (Rohland et al. 2435). It is difficult to determine the relationship between hominins and spotted hyenas early on in our history of coexistence, not least because it is difficult to determine the adaptive niches of each species. But assuming that spotted hyenas hunted, then a ground dwelling bipedal primate would have been likely prey, as humans are to this day in Africa (Kruuk, *Hunter and Hunted* 65). Whether the Australopithecines were in competition with the hyenas is less determinate as they left no evidence that they were exploiting carcasses (although see McPherron et al.). It was their descendants who would leave substantial evidence of a crossing over into the adaptive niches of hyenas.

Contested Bones. At around 2.4 million years ago, there emerged the first creatures in the human evolutionary line to be regarded — or at least named — as human: *Homo habilis*. If ever there were hominins whose adaptive niches had such a great degree of overlap with those of hyenas, it was *Homo habilis*. Louis and Mary Leakey first discovered these hominins' fossils in Olduvai Gorge, Tanzania, and gave them their specific name because of the material remains in association with which they had been found (Leakey, Tobias, Napier 9). The name means "handy man," and the material remains were stone tools: cobbles that had been struck with other stones to produce flakes with which the hominins cut flesh and tendons from the remains of dead ungulates, while the cobbles themselves were used to smash open long bones so that the fatty marrow could be removed. Much has been extrapolated from those few bones, cobbles, and flakes, as numerous models of adaptation and resource acquisition have

emerged and been contested. Yet all have had to include the presence and influence of hyenas.

During the 1970s and 80s, there was considerable debate in palaeoanthropological circles about the importance of scavenging as a human adaptation and what it revealed about *Homo habilis*'s ecological niches. Initially, Glynn Isaac interpreted accumulations of bones and artefacts from Olduvai Gorge and Koobi Fora, Kenya, as evidence for scavenging of body parts from kills or natural deaths and transportation of those parts to home bases where they were shared with other group members (Isaac 532). The Scavenging Hypothesis was born. In 1980, Bunn (575) examined the assemblages, finding cut marks and fractures which were consistent with Isaac's supposition that meat consumption was important at that stage of human evolution; however, he noted that the mode of acquisition remained uncertain. According to Bunn (576), there was a complex interplay of hominin carnivore activities involved in the bone accumulations, and it was not possible to rule out hunting. Using a scanning electron microscope, Potts and Shipman identified one assemblage from Olduvai (FLK Zinjanthropus) that contained bones bearing carnivore tooth marks overlain with cut marks from stone tools (Shipman, "Ancestors" 24). Shipman argued that the hominins were opportunistically scavenging bones from large carnivores, not for meat, but for tendons which were utilised for binding items ("Early hominid lifestyle: Hunting and gathering or foraging and scavenging?" 36; "Early hominid lifestyle: the Scavenging Hypothesis" 9). However, Shipman concurred with Isaac and proposed that scavenging was an adaptive complex integral to the evolution of bipedalism and tool-use ("Ancestors" 26). Lewis Binford entered into the debate, questioning whether the "tiny morsels of dried or desiccated meat" from the scavenged bones were sufficient to foster an adaptive complex (Binford 302). Yet Bunn and Kroll (439), having compared the FLK Zinjanthropus assemblage with modern hyena dens, directly contradicted Binford's findings and argued that hominins had full access to meaty carcasses from confrontational scavenging; the confrontation being primarily with hyenas.

The debate over the circumstances that had led to the formation of the bone assemblages led to a series of actualistic studies over a period of fifteen years. Several researchers attempted to replicate as closely as possible the conditions in which the bones had accumulated, and all of the studies involved hyenas. Between August 1983 and June 1984 Robert Blumenshine of Rutgers University conducted research in Serengeti National park and Ngorongoro Crater to assess which scavenging opportunities and strategies might have accounted for the abovementioned

assemblages. Blumenschine concluded that the only alternative to confrontation with, and risk of predation by, spotted hyenas was to scavenge from natural deaths in riparian woodland (Blumenschine 388). Furthermore, Blumenschine and Cavallo (76) proposed that hominins supplanted some hyena species, which led to those species' extinctions at the end of the Pliocene. Binford, Mills and Stone conducted field experiments to determine the effects of hyena activity on bone assemblages similar to those found at Olduvai and Koobi Fora. They noted that the ways in which hyenas scattered bones indicated that hominins at Olduvai were accumulating bones scavenged from hyenas (Binford, Mills and Stone 132). Gary Tunnell spent five and a half months patrolling an area around Olare Orok Stream in the Masai Mara in 1984. He found that lions killing more than they could consume provided numerous passive scavenging opportunities, but those were constrained by the presence of hyenas (Tunnell 117). The author concluded that familiarity with the local lion pride would have paid dividends for hominins; however, the presence of hyenas as competitors and predators on the hominins themselves would have been a "major problem" in habitat selection (122). Marie Selvaggio ("Carnivore tooth marks and stone tool butchery" 217) drove around the Serengeti and Ngorongoro areas, locating carnivore kills and measuring the amount of food available after the carnivores had abandoned the carcasses. She found that without confrontational scavenging, the only resource available to hominins was marrow, which could be accessed with hammer stones (227). Selvaggio's findings ("Evidence for a three-stage sequence" 200) contradict those of Binford, Mills and Stone, and suggest a three stage carnivore-hominin-carnivore feeding sequence whereby hyenas were scavenging from hominins.

In all of the above studies, there was a trend towards viewing human ancestors and hyenas as being in direct competition over the same resources. Brantingham (327, 329) saw such models as problematic, arguing that co-evolution of different species in competition over the same resources inevitably led to "character displacement," in which sympatric species' morphological or behavioral traits diverged. He compared Olduvai and Koobi Fora assemblages with modern carnivore assemblages and argued that hominin feeding strategies were not directly comparable to those of spotted hyenas, but intermediate between modern wolves and modern hyenas (343). However, Brantingham qualified that, recognizing that the bones from the Olduvai level FLKNN-2 (an accepted hyena accumulation) fell within the range of hominin food transport strategies. Indeed, hominins might have been utilizing food procurement and transport strategies that differentiated them from *modern* spotted hyenas, but the same may have been the case for the ancestral hyenas with whom they were competing. After all the physiological adaptations that are definitive of modern spotted hyenas, including post-

cranial morphologies that allow them to pursue prey over long distances, have only been present in the species for the past one million years (Lewis and Werdelin 93; Lansing et al 305). Hyenas have never been trapped in a timeless present, but have changed and adapted to the presence of some very dangerous hominins, who in turn had to adapt to the presence of hyenas.

Beyond the studies focused on the composition of the bone assemblages, further studies examined modifications to the bones themselves. Selvaggio and Wilder used casts to measure tooth marks left by carnivores on the surfaces of the fossil bones in the sample from FLK Zinjanthropus. They concluded that the bones were first modified by flesh eating felids, then by hominins, and then hyaenids who accessed any grease or tissues remaining (Selvaggio and Wilder 468). However, they did not make it clear how this feeding model was arrived at, other than that there were multiple carnivore taxa involved. Dominguez-Rodrigo and Piqueras (1387) challenged Selvaggio and Wilder's findings, arguing that tooth pits alone could only be used to differentiate large from small taxa and not individual species. They compared length and breadth ratios of different species to demonstrate that there were not sufficient differences to be able to identify species in the archaeological record. They conducted yet another actualistic study in Africa and found that little flesh remained after lions had first access to carcasses. Additionally, the study found that carcasses found in riparian woodland provided less flesh than those found in open country, directly contradicting Blumenschine's findings. Dominiguez-Rodrigo concluded that hominins must have had had first access to carcasses in a two stage sequence in which hominins preceded hyenas (43). More recently Dominiguez-Rodrigo and Barba argued (188) that pits which were originally considered to be carnivore tooth marks were in fact evidence of bioerosion and that the only evidence for carnivore action is the absence of cancellous bone, consumed by hyenas. Blumenschine et al. refuted (422) Dominiguez-Rodrigo and Barba's claims, citing flaws in methodology, sample sizes, and analysis, where the researchers had failed to recognize key differences between tooth pits and bioerosion. They reiterated that there would have been a passive scavenging niche available to a quick-witted hominin in Plio-Pleistocene east Africa, and that there needed to be an accurate way of discriminating different carnivore species by measurement of tooth marks. In all, the only consistent thread throughout the debate over the taphonomic processes which created the bone assemblages is the "likeness" of humans and hyenas converging on the same resources.

Dispersals. Such is the influence of Olduvai Gorge over constructions of prehistory that it has even lent its name to a span of geological time, the Olduvai Subchron. This marks a period during the Matuyama magnetic reversal, 1.8-1.7 mya, in which the earth's poles were flipped for a short time — a hundred thousand years is a short time, geologically speaking — and then flipped back: a reversal within a reversal (Cox, Doell and Dalrymple 1951). However, the Olduvai Subchron is not just a geomagnetic flip-flop, standing alone in the long geological record of pole reversals. It marks an important boundary between two epochs, the Pliocene and the Pleistocene. It was during this brief time that the relatives of the Olduvai hominins began to disperse out of Africa, after which they rapidly colonized much of the Eurasian landmass (however, see Morwood and Jungers for their argument of a previous dispersal of Australopithecines). What is significant in the story of the first human diaspora is that they did not do it on their own; rather, the first human travellers out of Africa were in the company of other species, notably hyenas.

The inherent ambiguity and paucity of the evidence for the first human dispersal out of Africa is such that the reasons for the dispersal and the directions in which the hominins dispersed are the subject of much speculation. The Olduvai Subchron marks a point in western Eurasia's prehistory in which there was a faunal turnover, named the "wolf" event after a species of canid, *Canis etruscus*, which makes its first appearance in the fossil record of Europe at that time (Azzaroli 1979). So too at that time, several African species — including monkeys, hippos and zebras — were expanding their ranges northwards and eastwards through the Levant and possibly across the narrowed straits of Gibraltar into western Eurasia. Fossils have been found from seven African genera which appeared in both Europe and Asia after the Matuyama reversal, including hominins and hyaenids (Gibert et al. 1986; Arribas and Palmqvist, "The first human dispersal to Europe" 55; O'Regan et al. 1998). Arribas and Palmqvist noted (571) the close association of three of the African taxa, suggesting that there was an ecological interdependence between the three. The first were *Homo ergaster*, hominins who had thrived in the competitive conditions in east Africa and were apparently adaptable enough to be able to infiltrate the northern latitudes with their marked seasons (Stiner, "Carnivory, Coevolution, and the geographic spread" 8). The second were *Megantereon whitei*, heavily built saber-toothed felids who were powerful enough to capture prey many times their weight but too specialized to be able to consume entire carcasses (Turner and Antón, *The Big Cats* 124; Kruuk, *Hunter and Hunted* 110). That left a niche available for both the hominins and the third members of the carnivore guild, *Pachycrocuta brevirostris*. These giant hyenas, with heads as large as those of modern male lions (Turner and Antón, "The giant hyaena" 459), were supposed to have made a

living cleaning up the leftovers from the kills of the abovementioned sabre-toothed felids. Such was the extent of the expansion of the range of the “superabundant” *Pachycrocuta* (Turner, Antón and Werdelin 684), and the impact and influence that it has had on the fossil record, that Martínez-Navarro suggested (210) that the early Pleistocene faunal turnover should be re-named the “*Pachycrocuta brevirostris* event.” If only the name rolled off the tongue as easily as “wolf.”

Spotted hyenas were already present in eastern Eurasia by the time the carnivore guild arrived. In some places they must have been replaced by the larger *Pachycrocuta*, as fossils of the two species have rarely been found in the same deposits (although see Patnaik and Nanda 135). *Megantereon*, *Pachycrocuta*, and *Homo* persisted on that continent, appearing together in deposits from Spain to Georgia to China (Gibert et al. 36; Boaz et al. 231; Gabunia et al. 24) until 0.5 million years ago, which marked the replacement of Oldowan with Acheulian type stone tools and the disappearance of the saber-toothed cats and giant hyenas. Interestingly, the appearance of Acheulian tools in Africa, one million years earlier, has been held to be implicated in the demise of *Megantereon* and *Pachycrocuta* on that continent (Arribas and Palmqvist, “On the ecological connection between sabre-teeth and hominids” 581; Arribas and Palmqvist, “The first human dispersal to Europe” 73).^{*} Spotted hyenas, however, persisted in Eurasia, in the face of faunal turnovers and new technologies, so that 0.8 million years ago they crossed into Europe west of the Caucasus in what has been called the *Crocuta crocuta* event (Martinez-Navarro 213). Intense glacial cycles saw the ebbing and flowing of many of the African species in Europe, so that when ice sheets advanced to their southernmost limits the only African species that remained in Europe were humans and spotted hyenas (Lambeck, Esat and Potter 199; Stiner, “Carnivory, Coevolution, and the geographic spread” 7). It is difficult to determine the kind of habitat to which spotted hyenas were best adapted, as they preceded humans into the British Isles when ice sheets retreated leaving tundra and herds of reindeer and mammoth (Gibbons 490). Yet in Southeast Asia, their remains have been discovered in association with “wet, tropical forest fauna”; they occurred with orang-utans and Pandas in Thailand (Schepartz, Miller-Antonio and Bakken 6).

Towards the end of the middle Pleistocene, the archaic humans in Europe, the Neanderthals, were replaced by modern *Homo sapiens*. We know the European hyenas tolerated modern humans for some time after the disappearance of Neanderthals because the modern humans made art of them. One ivory sculpture from La Madeleine in France depicts a hyena, ears folded, heaving backwards as if in a tug of war over a

carcass (Kurtén 72). It indicates a degree of familiarity that the artist had with hyenas and their salience in her imagination that led her to see one in a piece of antler. Another depiction, also found in France, is the only known Palaeolithic painting of a hyena, appearing on one of the cave walls in Grotte de Chauvet (Chauvet, Deschamps and Hillaire 110). The image of a solitary hyena in a cave which features scores of lion images is poignant. While lions were still comparatively abundant in the upper Pleistocene and persisted in Europe into classical times (Quammen 25), hyenas in Eurasia were on the way out. After millions of years of persistence in the face of human presence and harsh conditions, hyenas could not adapt successfully to the modern human presence when combined with encroaching forests and competition from wolves (Stiner, “Comparative ecology and taphonomy” 782). The species disappeared from Europe and Asia just prior to ten thousand years ago, briefly dwarfing in the Middle East, as if making one last effort to persist before withdrawing completely into the continent of their genesis (Garrard 272; Rabinovich 30).

In Pleistocene Africa, there had been no sudden changes to drive the spotted hyena population over the edge of extinction; no forests encroached to limit their ranges; there was no sudden appearance of socially and technologically novel humans competing for similar resources. In Africa, hyenas and humans had emerged together, the former making alterations to the remains of the latter as they discarded the pieces for future discovery (see for example Tappen 40; Shreeve 44). Thus, as the humans gradually transformed their technologies and their food procurement strategies, the hyenas had time to adapt to the increasingly dangerous primates whose descendants spread out and displaced less human-savvy hyenas. Hence, the first real shock to those African, human-adapted hyenas came when Europeans began colonizing the continent south of the Sahara and, all too quickly, exterminated hyenas from southern Africa (Gade 613).

Hyena is Human-like. The theory of biologist Jakob von Uexküll (*Theoretical Biology; “The theory of meaning”*) provides a framework for integrating the evolutionary histories of humans and hyenas and reconceptualizing the two species as intrinsically connected. According to the theory, an organism and its environment constitute a unified whole. An organism exists within a meaningful Umwelt, a surround world, replete with signs from which the organism takes cues and responds (“An introduction to Umwelt” 107; *A Foray into the Worlds of Animals and Humans* 53). While this is the core of von Uexküll’s theory, it is not his account of sign-processes that I draw on in my analysis here. Instead, it the way in which von Uexküll conceives of Umwelts as interconnected. Even though von Uexküll rejected Darwinist views of evolution based

on mechanistic causation (Kull 6), his theory still encompasses ways in which evolved adaptations foster the convergence of organisms' *Umwelts*.

Von Uexküll outlines two ways in which organisms' adaptations might reflect those of other organisms in their *Umwelts*. One he calls interadjustment, where the organism is adapted to the form or behavior of another organism or material object. An example would be a western spinebill and an adenanthos flower; the curvature of the bird's bill is a perfect fit for the curved tube of the flower, allowing the spinebill access to nectar in return for delivering pollen to other flowers (Newland and Wooler 635). The second kind of engagement occurs under what von Uexküll calls the organism's "counter-framework" (*Theoretical Biology* 171). In this case, the base of the adenanthos flower is vulnerable to another kind of bird, the silvereve, who uses her beak to puncture the flower and extract nectar without taking on board any pollen. While these two kinds of engagement are distinct, they are in fact two sides of the same coin; they both reflect a "likeness" between organisms. Von Uexküll provides an example of this using a spider and a fly. A spider's web is an example of interadjustment. The web is in effect a representation of the size, shape, and habits of a fly ("The theory of meaning" 66). It needs to be thus in order for the web to be effective in catching flies. But in relation to the spider's web, the size, shape, and habits of the fly constitute the fly's counter-framework. And when combined, these represent a likeness between the two types. As the spider's web is fly-like in order that she catches flies, the spider, by nature of her construction of a fly-like web — her interadjustment — must also be fly-like. Meanwhile the fly, by nature of his vulnerability to spiders' webs — his counter-framework — is spider-like. In this way, the *Umwelts* of spider and fly converge not just through proximity during spider's capture of fly in the here and now, but through their likeness to each other which they inherit from evolutionary processes.

The implications of this in terms of the hyena-human relationships are profound. Von Uexküll's theory compels us to conceive of hyenas as more than bodies in landscapes (Buchanan 36). Every hyena is an accumulation, not only of the relations through which she has been engaged during her lifespan, she is also a convergence of threads of relations reaching back into evolutionary time, across the landscape, and forward into the future (Ingold, *Lines* 100). Every hyena is a congeries of other species on whom her ancestors preyed and by whom they were preyed upon, with whom her ancestors have come into conflict, or coexisted towards mutual benefit. As such, we find that in reserves and national parks where the majority of hyena studies are undertaken, something important is missing: humans and human competition. This is

unproblematic if the object of a study is to determine what it is hyenas are doing in the present time in a place where humans are absent. However, many studies are aimed at understanding spotted hyenas “in themselves,” and this is a problem. These studies subscribe to an axiom by which the elimination of human “noise” from the hyenas’ environments supposedly brings us closer to accessing an ultimate hyena reality (Lopez 80). This in turn is a corollary of the western scientific perspective which holds that wild animals — real wild animals — are those untainted by human contact (Ingold, *The Perception of the Environment* 67). But as I have demonstrated, human contact is probably one of the most significant factors in the evolutionary processes from which modern spotted hyenas have emerged. Certainly lions and various species of ungulates have also impacted on hyenas’ evolutionary and contemporary histories; the former constitute a major cause of hyena mortality and the latter eliminate the poorest hunters. But this in no way detracts from the importance of humans as quick-witted prey, confrontational competitors at carcasses, and deadly enemies in hyenas’ Umwelts. Even if there was a singular ultimate hyena reality — which I argue there is not — then it would have to include hyenas’ human-likeness.

By the same token, this likeness of humans to hyenas undermines human exceptionalism. The humanist ethos grounded in Judeo/Christian doctrine and cultivated in the enlightenment project trips up on the bones over which our human and hyena ancestors competed. And this is not just because our ancestors have proven to be diffident, opportunistic scavengers, rather than dominant hunters holding dominion over the other creatures of the savannah. It is because it shows that the very essence of humanity is something more than human. While humanism recognizes genetic relatedness and a shared biological framework, this is superficial likeness (Rose 59-60). What it fails to recognise is the “likeness” of humans to hyenas and other animals in an entangled, Uexküllian sense. It is not just that humans and hyenas both evolved from a small shrew-like species all those millions of years ago following separate phylogenetic paths from a unifying origin; it is that they evolved together and among other species within ecological communities of interadjustments and counter-frameworks. As the profound fear hyenas exhibit when faced with humans anticipates the lethality of the latter, so too our costly, lipid dependent brains and capacity to form boisterous mobs anticipate competition with hyenas over marrow-rich bones. While hyenas’ nocturnal boldness towards humans anticipates our limited visual acuity at night (Kruuk, *The Spotted Hyena* 144; Baynes-Rock 119), the predilection of human children to climb trees anticipates the hard, ground-adapted paws of hyenas which keep them from scaling heights. As such, we must conceptualize humans as a congeries of species — notably hyenas — who emerged together over evolutionary time within

ecologies of competition, conflict, and coexistence. The human characteristics which are held to separate humans from animals are in fact markers of our close relatedness within adaptive ecologies (Deanne-Drummond 177). Indeed, without the threat from, and competition with, hyenas, whatever species might have evolved from those early bipedal primates would certainly not have been human. Our brainy, antagonistic, sociability evolved in the presence of hyenas, with whom our ancestors competed and coexisted and who simultaneously evolved to accommodate our dangerous forebears. This in turn is why it is misguided to remove humans from the worlds of hyenas (and other animals) in order to understand them. The humanness of humans is not background noise preventing access to those animals' true beings. Rather, it is an integral part of those animals in the same way as those animals are an integral part of what it is to be (more than) human.

Conclusion. I began here with an account of how spotted hyenas are studied in areas exclusive of human bodies and argued that this reflected a conception of “real” hyenas as those untainted by human contact. The conceptions which underpin this approach to hyena studies conflict with a substantial body of evidence which demonstrates a long, shared evolutionary history. When the earliest bipedal hominins were establishing a niche at ground level, ancient hyenas were present, preying upon the small primates and disarticulating their dead bodies. From there, human ancestors gradually encroached on the adaptive niches of hyenas. *Homo habilis* adopted carnivory, utilizing carcass-based resources and becoming, as David Quammen said, “more human by acting like hyenas” (Quammen 328). So closely comparable were the meat-eating primates and the long-necked carnivores that they dispersed together and co-occupied much of the Eurasian landmass beyond the continent of their emergence. Ice sheets advanced and retreated and faunal compositions changed, but there was always a constant: humans and hyenas, and this was unaltered until the end of the Pleistocene. Meanwhile, in Africa the hyenas persisted in the face of human competition and persecution and only recently have their ranges contracted dramatically because of this. In light of this evidence, I argue that the notion of “real” hyenas as those untainted by human contact is erroneous, precisely because of the indelible marks inscribed on each species by the other through millennia of competition, conflict, and co-existence. These marks, I suggest gather meaning in light of the theory of Jakob von Uexküll, which allows us to see organisms as adaptive, congeries of other species. Hyenas are the way they are due in large part to adaptation to a human presence, so any understanding of hyena behavior should recognize their human-likeness; it should account for the ways in which humans figure in the make-up of hyenas. So too humans are adapted to hyena

presences. As such, a human body is more than an individual organ representing a single species; it is a confluence of evolutionary histories, and other species expressed in an organism which is never exclusively or merely human.

Note

* These authors also argued for a carnivore-hominin-carnivore feeding sequence, basing their argument on none other than the bone assemblage at FLK Zinjanthropus.

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