DEFENSE STRATEGIES IN EARLY HUMAN EVOLUTION

MATERIALS OF AN INTERNATIONAL CONFERENCE

Jim Corbett International Research Centre

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MATERIALS
OF AN INTERNATIONAL CONFERENCE, HELD AT
GRIGOL ROBAKIDZE UNIVERSITY

TBILISI, GEORGIA, 23 – 26 JUNE, 2023

Dedicated to the memory of ADRIAAN KORTLANDT

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Book cover photos: (1) African male lion; (2) Reconstruction of Homo georgicus, first hominin out of Africa, 1.8 mya. (Both images from Wikipedia)

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Introduction: Neglected Topic of Human Evolutionary History

A valid defense strategy from predation is essential for the survival of any animal species. Consequently, articles and even books dedicated to defense strategies in animal kingdom are plentiful (e.g., Ruxton, et al., 2004; Caro & Girling, 2005). At the same time, studies on the defense strategies of early humans so far have been strangely neglected. Two articles by Dutch ethologist Adriaan Kortlandt represent rare exceptions (Kortlandt, 1965, 1980).

In June 23-26, 2023, a special interdisciplinary online conference "Defense Strategies in Early Human Evolution," was organized by the Jim Corbett International Research Centre at Grigol Robakidze University in Tbilisi, Georgia, with the participation of evolutionary biologists, paleoanthropologists, evolutionary psychologists, primatologists, neuroscientists, cognitivists, evolutionary musicologists, and conservationists, dedicated to the memory of Adriaan Kortlandt.

There are several historically significant reasons for the strange neglect of this important topic in evolutionary scholarship.

The first reason for neglecting antipredator defenses in human evolution was Charles Darwin and his theory of sexual selection. When musing over the evolution of humans, Darwin abandoned his own greatest theoretical contribution to biological science – the theory of natural selection (Darwin, 1859). Instead, he proposed that an alternative theory, sexual selection, could better explain human evolution (Darwin, 1871). In his brand-new theory, tellingly, there was no place for human natural predators. According to Darwin, humans evolved in an environment lacking dangerous predators, such as Australia, Borneo, or New Guinea (p. 173). In the 1870s when Darwin published his ideas on the evolution of humans, there was no consensus about where humans had evolved, and all the major regions of the Old World (including Africa, Europe, and South-East Asia) were considered possible to become the "cradle of humanity." Today the scholarly community strongly agrees that humans evolved in Africa, which abounds in large predator species, including fierce competition among them. Therefore, Darwin's theory of human evolution via sexual selection in a predator-free environment is unsustainable. Nevertheless, although no one remembers today the Australia-New Guinea-Borneo “cradle of humanity” hypothesis, Darwin’s model of human evolution via sexual selection remains popular among many contemporary scholars, particularly evolutionary psychologists (e.g., Cronin, 1991; Richards, 2017; Miller, 2000).

The second important reason for the neglect of early human defense strategies comes from another great scholar of human evolution, Raymond Dart. Dart initially thought that hominins were small-time hunters and scavengers (Dart, 1925), but he later changed mind and declared that early humans required no defense strategies because they were the apex predators and ruthless killers in their ecosystem (Dart, 1949). This model, known as the “killer ape hypothesis,” was later popularized by Robert Ardrey (Ardrey, 1961). This image of our human ancestors as powerful big-game hunters had a commanding grip on the human psyche and still has an influential place in scholarship. The theory is particularly popular in explaining the contemporary human passion for conflicts and warfare (e.g., Merker, 1984; Milam, 2019).

Critical reaction to the “killer ape hypothesis” came from two contrasting research paradigms. Authors of the first critical development, the theory known as “man the hunted” hypothesis, argued that early humans were a weak prey species, whose best survival option was still to climb trees. This model was based on Charles Brain’s diligent study of hominin taphological remains (Brain, 1981; cf. Hart & Sussman, 2005). As a positive development, this model acknowledged the immense pressure of predators on early humans, but on the negative side, it could not explain how such a weak primate prey species without any serious means of defense managed to live and sleep on the open savannah, much less travel outside of Africa, gradually becoming the widest distributed mammalian species on the planet.

The second development critical of the “killer ape hypothesis” argued that our ancestors were not big-game hunters, but rather scavengers. This model developed within the 1980s “new archaeology” paradigm revolution (e.g., Binford, 1985; Shipman, 1986; O’Bryan et al., 2019). When discussing the “scavenging hypothesis,” it is necessary to distinguish two very different modes of scavenging, which differ radically in terms of the defense/attack capabilities available to early humans: (1) passive scavenging, in which the carcass is accessed only after the original killer has left, and (2) confrontational (aggressive) scavenging, in which the original killer is chased from the carcass. Current consensus favors confrontational scavenging in early human evolution, but how early humans managed to chase the original hunter away remains a major question (e.g., "[M]icroscopic analyses indicate that cut marks on some bones overlay predators' teeth marks, showing that the hominins arrived afterward. How they got meat away from scary scavengers is anyone's guess" Welker, 2017, p. 149). The generally negative attitude towards scavenging in downplaying the possible scavenging evolutionary past of our ancestors remains noteworthy: people prefer to see themselves as the descendants of big game hunters, not scavengers (e.g., Ehrenreich, 1997, on people's overinflated attitude towards hunting and war).

The most recent development is the hypotheses, according to which hominins and early humans were actively using the aposematic defense strategy, and this strategy of being constantly seen, heard, smelt, and surviving predation by intimidating the predators, profoundly affected our morphology and behaviour (Jordania, 2014; Weldon, 2018).

Possibly the final reason for neglecting the defense strategies in humans' evolutionary history is the fact that it is very hard to distance ourselves from humanity's current towering position in the contemporary world, and objectively imagine the ancient past when our ancestors had to confront powerful predators in order to save their lives.

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Before the brief introduction of the chapters included in this book, a few words about the conference. It initially was planned to take place in Tbilisi, in a new building of the Grigol Robakidze University, but because of the uncertain political situation in Georgia and Europe, the conference was moved to an online format. It ran for four days, from June 23 to June 26, and each day had a single chair. Gigi Tevzadze from Georgia chaired the sessions on the first day, Klaus Zuberbühler from the UK chaired the second-day sessions, Piotr Podlipniak from Poland chaired the third-day sessions, and Manfred Waltl from Germany chaired the last-day sessions.

The conference was opened by the Rector of Grigol Robakidze University, Mamuka Tavkhelidze. The first paper was delivered by David Lordkipanidze, Georgian archaeologist and paleoanthropologist, the prime scientist who brought the Dmanisi Hominids to international scholarly attention. In his presentation, dedicated to the Dmanisi hominids, Lordkipanidze spoke about many facets of our 1.8 mya ancestors, among other ideas, discussing the possibility of using stones to chase predators and about arguably the first recorded instance of subsistent life of an elderly group member.

An American evolutionary biologist and cognitive scientist at the University of Vienna, where he is co-founder of the Department of Cognitive Biology, William Tecumseh Fitch delivered a paper on music and group defense strategies in human evolution, in which he concentrated on hypotheses about the evolution of human musicality, combining group cohesion and group advertisement hypotheses. For the contribution to this collection of materials, Tecumseh Fitch & Klaus Zuberbühler decided to co-author a shared paper "Group vocal displays, anti-predator behavior, and the evolution of musicality."

A. J. T. Johnsingh, eminent Indian conservationist from WWF India, and the Corbett Foundation, prepared a presentation on the practice of stealing carcasses by Indian tribes in the wilderness, probably continuing the long tradition of our distant ancestors. His presentation was delivered absentia, because of his health.

Canadian evolutionary musicologist, Steven Brown, Department of Psychology, Neuroscience & Behaviour of McMaster University, Hamilton, proposed a new look at the ancient tradition of beading, proposing an interpersonal origin of the phenomenon of rhythm in human evolution.

Evolutionary musicologist Piotr Podlipniak from Adam Mickiewicz University, Poland, dedicated his presentation to the role of pitch in choral singing as an intraspecific defense strategy.

An Australian/Georgian ethnomusicologist and evolutionary musicologist, Joseph Jordania from Grigol Robakidze University, delivered a paper, dedicated to warning display as a strategy of defense and offense in early human evolution.

Margaret Kartomi, an Australian ethnomusicologist from Monash University, presented interesting material discussing the defense potential of music and trance according to ethnomusicological materials from the Indonesian province of Aceh.

An evolutionary biologist from the Center for Welfare Metrics, Brazil, Wladimir Alonso prepared a presentation on the evolution of conspicuousness in early humans, discussing whether camouflage could have been unnecessary or impractical (the presentation was delivered absentia).

A joint presentation by Wladimir Alonso (Brazil) and Joseph Jordania (Australia) discussed a distinction between intrinsic and semantic aposematism and proposed hypothetical ways of their evolution.

Georgian philosopher, historian, and evolutionary ecologist Gigi Tevzadze from Ilia University, Georgia, delivered a presentation in which he spoke about hominids of the Eurasian continent and phenotypic variations from the point of view of population ecology.

A Switzerland-based evolutionary psychologist from the School of Psychology and Neuroscience, University of St. Andrews, Scotland, UK, and the Institute of Biology University of Neuchatel, Neuchatel, Switzerland, Klaus Zuberbühler discussed the possible role of the primate heritage of early human cognition in defense strategies. For the compilation of materials Klaus Zuberbühler & Tecumseh Fitch presented a co-authored paper mentioned above.

German biologist Manfred Waltl from Grigol Robakidze University delivered two interconnected presentations on the reasons for man-eating in Corbett's time and today, and the importance of moon phases on the problem of nocturnal attack by man-eating animals.

David Blake from the UK, a retired researcher and co-founder of LifeForce Charitable Trust, shared his first-hand experience of working with wild and captured big cats, and discussed why humans are not natural prey for big cats in the wild.

Jenny Wade from the California Institute of Integral Studies, San Francisco, USA, dedicated her presentation to the specific, and so far neglected altered state of consciousness, battle trance, tracing the phenomenon from ancient survival technique to its use in our time.

David Schruth from the University of Washington, Seattle, USA, spoke about a deep ancestry of primate rhythm that decreases with larger groups but increases with terrestriality. He further explored how ballistic tools, bipedal carrying, and positional diversity could have driven a both attractive and repulsive functionality in the diverse musicality of early hominins.

Priyvrat Gadhvi, based in India, from Grigol Robakidze University, discussed an interesting case study of interaction between leopards and domestic dogs, recent evolutionary behavioral changes observed, and possible inferences.

Preetum Gheerawo, based in Mauritius, from Grigol Robakidze University, discussed the long struggle for survival against lethal predators from Plio-Pleistocene hominins to anatomically modern humans.

Alejandra Wah, cognitivist from Netherlands, Assistant Professor of Arts and Cognition at the University of Groningen, discussed a possible role of the tree-to-ground sleep transition in the imagination of defense strategies by means of music, song, dance, and pantomime in early hominins. This was the only paper added to this collection without participation in the actual conference.

And finally, Elizabeth Marshall Thomas, from the USA, best-selling author and naturalist, shared her unique experience on the peaceful coexistence of the South African San people with the lions in the 1950s.

This conference, and the materials gathered in this book, hopefully, will bring scholars' attention to this so far neglected and important topic of human evolutionary history.

And finally, all four days of the sessions of the conference are available on YouTube:

Day 1 (23.06.2023): https://www.youtube.com/watch?v=qnKS1E8Jbpw
Day 2 (24.06.2023): https://youtu.be/rodUehq3fNg
Day 3 (25.06.2023): https://youtu.be/EtywlTDG2Vg
Day 4 (26.06.2023): https://youtu.be/uLe2aS95pdE

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Dmanisi Hominids: Anatomy, Paleoenvironment, and Behavior

David Lordkipanidze (Georgia)

Despite many exciting paleoanthropological discoveries, the early evolution of genus *Homo* and a number of species are still shrouded in mystery. The hypothesis that early *Homo* represents one variable species versus multiple species is still in progress (Stringer & Andrews, 1988; Wolpoff, 1999). Excavations of the site of Dmanisi, Georgia, brought new knowledge about the evolutionary history of early *Homo* (Lordkipanidze et al., 2005, 2007, 2013, 2017). Over the past decades, this site has yielded a treasure of a unique series of 1.8-million-year-old cranial and postcranial hominin fossils. Precisely, there were found: 5 skulls, 4 of them with maxillae, 4 mandibles, and 100 post-cranial remains.

Along with many well-preserved animal fossils and quantities of primitive stone artifacts, this is the richest and most complete collection of indisputable early *Homo* remains from any single site with a comparable stratigraphic context. The Dmanisi sample comprises variations related to age and sexual dimorphism.

The discoveries document the first expansions of hominins out of Africa and into Eurasia and demonstrate that this was neither due to increased brain size, nor to improved technology. Despite certain anatomical differences among the Dmanisi specimens, we do not presently see sufficient grounds to assign them to more than one hominin taxon. Thus, the Dmanisi assemblage offers a unique opportunity to study variability within an early *Homo* population.

The vertebrate fauna found at Dmanisi reflect the diversity of the natural conditions at that time. This is also confirmed by palaeobotanical data. To date, more than 10,000 bones belonging to at least 50 different animal species have been identified. Bones excavated at Dmanisi prove that saber-toothed tigers, hyenas, giraffes, rhinoceroses, elephants, ostriches, deer, and other animals lived here (Gabunia, Vekua & Lordkipanidze, 2000).

Surrounding habitats included drier areas, probably of open wooded savannah and grassland and mountainous to semiarid rocky terrain. There is evidence that Dmanisi records short intervals of increased aridity in the middle part of the succession contemporaneous with the occurrence of *Homo*.

We know very little about the behaviour of early hominids as our evidence mainly comes from stone tools. Dmanisi preserves a complex archeological record of numerous reoccupations, which are registered in both stratigraphic and spatial concentrations of artifacts and faunal remains across all areas of the site. To date almost 5000 stone tools have been found (Lordkipanidze, 2017). While flakes comprise the majority of tools recovered, some cores and choppers have also been found. The raw material for lithic artifacts comes from nearby rivers. The difference in technology is not seen only in changes in the composition of the assemblages. Before the Dmanisi finds, experts believed that humans could not have left Africa before having developed an advanced technology, such as the Acheulean, in which tools were symmetrically shaped, manufactured and standardized. The tools found at Dmanisi, however, are simple flakes and choppers according to much the same primitive Oldowan tradition that hominids in Africa were practicing nearly a million years earlier.

We also found an abundant quantity of unmodified cobble manuports at Dmanisi. This could indicate that the manuports were used by hominins for more than just flake production and meat processing. It is possible that they were also thrown to chase carnivores away from the site.

Indirect evidence comes from a hominid edentulous skull. This individual had lost teeth several years before death, which shows not only the earliest case of severe masticatory impairment in the hominin fossil record to be discovered so far, but also raises questions about subsistence strategies in early *Homo*.

The discovery of a toothless hominid in Dmanisi shows that this individual survived for a long time without consuming solid food that required heavy chewing; it is clear, that he or she may not have been able to do so without help from other individuals, suggesting that other members of the group were sharing food with the toothless individual. We are not aware of any other fossil hominin that displays such extensive tooth loss and remodelling (Lordkipanidze et al., 2005).

Therefore, it is conceivable that we have recorded one of the earliest traces of compassion in human history. We are looking at, perhaps, the first sign of truly human behavior in one of our ancestors.

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Group Vocal Displays, Anti-Predator Behaviour and the Evolution of Musicality

W. Tecumseh Fitch (Austria), **Klaus Zuberbühler** (UK)

Abstarct. The transition from a strongly arboreal lifestyle to terrestrial bipedalism in early members of the hominin lineage, particularly australopithecines, posed a serious adaptive problem: African woodlands were populated by a variety of large, dangerous predatory carnivores, but these early hominins were small-bodied, slow-moving and lacked sophisticated weaponry or anti-predator technology like fire. How did these early hominins avoid intense predation? Here, we suggest that group anti-predator tool use (throwing stones and brandishing sticks) combined with loud, coordinated group vocal displays, provided our early ancestors with a potent anti-predator behaviour. We support this hypothesis by reviewing social anti-predator behaviours in African forest monkeys, gibbons, and chimpanzees. In these primates, predator-elicited vocal displays both provide social learning opportunities to younger animals and serve as potent signals to the predators themselves. Both predators and neighbouring groups are highly sensitive to these group vocal displays. We therefore hypothesize that the production of coordinated group choruses as anti-predator defence mechanisms provided a heretofore neglected potential adaptive function for rhythmic vocal displays, a core component of human musicality.

Introduction

A major early transition in human evolution transformed largely arboreal apes to habitually terrestrial bipeds, and is well represented by the nearly one million years during which *Australopithecus afarensis* roamed the mixed woodlands and savannahs of eastern Africa, from about 3-2 MYA. These, and their immediate forebears like *Ardipithecus*, were rather small-bodied and well-adapted to bipedalism (Leakey, et al., 1995), and already used primitive but effective stone tools (their “Oldowan toolkit” consisted mainly of small sharp blades). Crucially, australopithecines were small brained, with brain sizes only slightly larger, and heavily overlapping, those of modern chimpanzees.

The fauna of east Africa from 4-2 MYA included both the large carnivores familiar from today (lions, leopards, cheetahs, hyenas, etc.), several extinct large carnivores, and a host of large dangerous snakes. With their small bodies, limited technology (there is no evidence that australopithecines controlled fire, which is found only in the genus *Homo*), and new terrestrial lifestyle, these small primates thus trod on dangerous ground. Neither fleet of foot, nor armed with horns, fangs or other biological weaponry, how did these early members of our lineage avoid being wiped out?

In this paper we argue, based on data from extant primates, that social behaviour and cognition played a crucial role in solving this early adaptive problem. In particular, early hominins must have known about predators, understood their behaviour and lifestyles, and passed this knowledge on to younger group members by providing opportunities for social learning to occur. Just as in modern apes and monkeys, predator encounters were social affairs, in which the group combined vocal displays and distinctive, predator-specific behaviours, including mobbing of the predator, to both educate naive individuals (indirect benefit via increased inclusive fitness) and repel the predator itself (direct benefit).

Second, based on analysis of primate vocal behaviour in predatory contexts, we suggest that the vocal component of these anti-predator defence behaviours provided one building block of human musicality: our capacity to mutually entrain our voices, body movements, and often non-vocal sounds (claps, foot stamps, or percussive sounds). By modifying existing primate chorus behaviour from the loud, impressive, but unsynchronized screams and hoots seen in other primates to synchronized displays, early hominins could have significantly increased the effectiveness of anti-predator vocal displays (and potentially recruited other group members to join the mob). Although this would have been impressive by itself, when combined with stone throwing or clubbing with sticks, these entrained group displays would have been a powerful deterrent to predators, and thus provided a significant adaptive advantage to members of groups competent in such displays. We thus hypothesize that predator defence played a significant but neglected role in the evolution of early beat perception and synchronization skills that are a crucial component of musicality in modern humans.

In this paper we begin with a review of anti-predator behaviour in nonhuman primates, focusing on African monkeys, chimpanzees and gibbons. This review demonstrates that vocalizations produced by groups of primates are both effective signals to modern predators (particularly those like leopards, which hunt by stealth) and provide a rich learning environment for young animals naive about predators. We then discuss modern human musicality and review existing hypotheses about its evolution, concluding that anti-predator behaviour deserves consideration as a potentially potent, if neglected, force in the evolution of group rhythmic abilities.

Part I: The problem with large predators

How did early humans—medium-sized mammals without specific antipredator adaptations—survive in habitats populated with dangerous animals? Most primates live in forest habitats that offer various microhabitats inaccessible to predators, but the open savannah offers less protection and escape options, so how did early hominins protect themselves in this environment? In particular, Australopithecus afarensis, one of the longest-living early humans, survived for nearly 1 million years (between 3.85 and 2.95 million years ago) in woodland and open savannah habitat (Kimbel & Delezene, 2009).

One hypothesis for successful cohabitation with predators in open habitat is advanced cognition. However, brain size expansion in the human lineage only started relatively recently in human evolution (Ponce de Leon, et al., 2021). Over a few million years only, hominins increased their cranial capacities from ape-sized brains (modern chimpanzees: 300-500 cc; Australopithecines: 350-600 cc) to a modern human brain (1.350 cc), a three-fold increase. Since Australopithecus afarensis had brain sizes comparable to modern chimpanzees, roughly 500cc, the suggestion is that ape-like cognition must have been sufficient as an antipredation device. If the main brain expansion (>1,000 cc) only happened very recently, less than 500,000 years ago, then our smaller-brained, savannah-living ancestors must have been sufficiently equipped to deal with their predators, but what cognition was necessary? Comparative studies of primate cognition, especially in the predation context, can reveal something how early humans dealt with predation and the cognitive capacities recruited for solving such problems.

Anti-predator behaviour in nonhuman primates

Visibility is very limited in most forests, usually around 5-10m. Sound travel is also limited, but usually covers a wider area than visual information, and it appears that primates monitor their environment largely by listening to the soundscape. Predators differ in their hunting strategies, so all members of a primate group need to know how to respond adaptively to each predator species.

What are the minimum requirements for a cognition-based antipredator strategy? Clearly, an individual has to be able to distinguish other animal species and recognise the dangerous species. For each predator type, it needs to have a basic understanding of its hunting behaviour and general ethology, in order to deploy adequate antipredator responses. Knowing each predator's hunting technique and more general behavioural propensities is a likely advantage.

Some of this may be partially hardwired, but much will have to be learned. In vervet monkeys, it was found that infants already distinguish between aerial and terrestrial predators (Seyfarth & Cheney, 1980). The two categories appear to be quite broad with young monkeys giving aerial alarms to many flying objects, such as storks or even falling leaves. As they grow up their predator knowledge becomes increasingly sharper, mainly by learning to discard irrelevant species and stop responding to them while retaining the dangerous ones (martial eagles, crowned eagles). The same pattern has more recently been found in sooty mangabeys, with a developmental study on alarm calling. Here, as it was found during natural predator encounters, juveniles alarm called to a significantly wider range of species than adults, with evidence of refinement during the first four years of life (León et al., 2023).

In all likelihood this pruning process of predator categories is guided by social learning. By observing the behavioural responses of older group members to predators and non-predators, young monkeys can learn to discriminate which events are dangerous and which ones can be ignored. This has been demonstrated recently in two field experiments on the development of alarm calling behaviour in monkeys, a good behavioural proxy of competence in dealing with predators.

In a first study with vervet monkeys, juveniles were exposed to unfamiliar raptor models in the presence of audiences that differed in experience and reliability (Mohr et al., 2023). One result was that older monkeys barely responded to the models, with an overall negative correlation between alarm call production and caller age. A second result was that juveniles called more when with siblings than with their mothers. It appeared that juveniles monitored the behaviour of other group members to the unfamiliar raptor models, especially whether or not they showed vigilance behaviour, suggesting that juvenile vervet monkeys, confronted with unfamiliar and potentially dangerous raptors, rely on others to decide whether or not to alarm call, demonstrating that other group members play an important role in alarm call development.

In a related study with sooty mangabeys *Cercocebus atys*, individuals were exposed to leopard, eagle and snake alarm calls given by other group members or by another monkey species, sympatric Diana monkeys (Leon, et al., 2023a). Young juveniles responded in inadequate ways, showing locomotor and vocal behaviour that was often not appropriate. At the same time, this age group also showed the highest levels of social referencing, i.e., looking at adults when hearing an alarm call, compared to older individuals. This study further suggests that competence in dealing with predators is individually acquired from observing others, that is, via social learning. This appears to happen during the early juvenile stage, with comprehension preceding appropriate usage but no difference between learning their own or other species' alarm calls.

Social learning abilities, in other words, are crucial in predation avoidance. The alternative, individual trial-and-error learning (i.e., operant conditioning), is unlikely to play an important role, simply because of lack of learning opportunities and because of the potentially fatal fitness consequences when making errors. Acquired predator knowledge, finally, needs to be retained long-term, again because learning opportunities are often rare and individuals will not get 'refresher' trials; forgetting is likely to have dire consequences (León et al., 2022).

Behaviour of a typical forest predator: African leopards

Forest leopards *Panthera pardus* are major primate predator but, due to their stealthy hunting behaviour, they are very difficult to observe and a challenge to study. Predation can rarely be witnessed directly, but there is good indirect evidence about their predation habits from systematic collection and analysis of faecal samples, which allow determination of prey spectra. Two such studies have been conducted at Tai Forest of Cote d'Ivoire, spanning a 15-year period. Jenny (1996) reported several years of data consisting of about 200 droppings over an area of about 100 square kilometres. An earlier study by Hoppe-Domenic (1984) obtained a similar sample size in the same area. Taking into account that the average lifespan of a leopard is 15 years, the individuals sampled in the two studies must have been different. Assuming that the distribution of prey species has not changed much over the 15 years, a first remarkable finding is that Hoppe-Dominic's study reported a real preference for black duikers, which Jenny's study did not find, despite that overall comparable number of ungulates. Moreover, while one study indicated preference for red colobus monkeys, the other found a preference for black-and-white colobus monkeys. Strikingly, Jenny also found a strong preference for pangolins, which disappeared after the resident leopard died.

Also remarkable was that chimpanzees did really well regarding leopard predation. Despite a high density, there was only one faeces with chimpanzee remains, possibly a scavenging event, suggesting that chimpanzees are good models of early humans' ability to cope with large predators (Zuberbühler & Jenny, 2002).

Predator Alarm Calling

A playback experiment with six monkey species found that all six species responded to leopard growls with high rates of alarm calling, whereas their responses to equally dangerous chimpanzees was the exact opposite; they immediately fell silent (Zuberbühler et al., 2009). Here, Jenny's tracking data provided a plausible explanation for this striking difference in primate alarm calling behaviour (Jenny & Zuberbühler, 2005). Leopards actively seek out monkey groups but their hunting success largely depends on remaining undetected, and primates seem to be aware of this. They can be hiding in the vicinity of a group of monkeys for hours, presumably waiting for an individual to descend to feed or play. But with the exception of a few cases, the leopards will inevitably move on once the monkeys alarm call and are gone in less than ten minutes.

Primate alarm calls are more than perception advertisement signals, as they have a demonstrated function in intraspecific warning (Berthet & Zuberbühler, 2020). For example, Campbell's monkeys have two basic alarm calls which can be combined with an acoustically invariable suffix to modify levels of urgency (Ouattara et al., 2009) and which can be further concatenated into context-specific sequences (Ouattara et al., 2009). All of this is understood not only by conspecifics but also by other monkey species. Interspecies communication is of major importance in forest habitats, even between mammals and birds (Rainey et al., 2004).

This dual function of communicating to the predator and warning other group members may be the default for primate alarm calling. Of particular interest here are the gibbons, which have been shown to sing not only for social reasons but also to repel predators and inform neighbours. In particular, lar gibbons have been found to sing to clouded leopards and tigers, with the songs made up of the same notes as territorial songs, although strung together in different ways (Clarke et al.,). Playback experiments confirmed that this communicative behaviour was relevant for others and revealed something about the song-eliciting event (Andrieu et al., 2020).

In summary, primates alarm call when they see predators, and this both acts as a signal to other group members and sometimes nearby neighbours and also to the predators themselves. For stealth predators, these vocalizations are effective deterrents and lead to the predator's giving up and departing.

All of this suggests that there are deep evolutionary roots to group-level vocal behaviour as a means to deter predators, which leads to the key hypothesis we advance in this paper. Early hominins may have built on this predisposition to deter predators (as well as signal the presence of predators to other groups) by means of coordinated vocal behaviour, and this provided the context in which key components of musicality evolved in our own hominin line.

Part II: Evolutionary Approaches to Musicality

We start with a brief overview of previous hypotheses about the evolution of music in our hominin line. The fossil record of music is relatively recent. There exist modern Homo sapiens flutes that are about 40,000 years old. There is also a much-debated Divje Babe flute (whose definition as a flute is questionable) from Neanderthal times, which would extend the origins of music to our common ancestry with the Neanderthals, approximately 500,000 years ago. However, it is widely believed that human musicality has deeper roots beyond this timeline. So, if we initially assume that these basic rhythmic and singing abilities have existed for several million years, it provides a valuable perspective on the evolutionary time scale.

It is important to note that discussing the evolution of "music" per se is misleading, because "music" encompasses various styles and forms, such as jazz, baroque, specific songs, or pieces. It is thus more appropriate to focus on the evolutionary development of **musicality:** the human biological capacity to produce and perceive music. There exists much evidence to support the idea that this capacity is an inherent part of human biology, with deep evolutionary roots. One term that has been introduced to discuss research on the evolution of human musicality is "bio-musicology," which indicates the biological perspective on the topic that we will adopt here. This includes various aspects of human musicality from neural, cognitive, and perceptual bases to comparative and evolutionary questions.

A key aspect of biomusicology is that we should address all of Tinbergen's four questions, as is standard in ethology and evolutionary biology. Tinbergen (1963) emphasized the importance of posing multiple "why" questions to comprehend the biology of any given system. When examining the reasons behind a blackbird's singing, it is necessary to consider the **mechanisms** that produce the song, such as the neural mechanisms responsible for learning and controlling the song, as well as its **adaptive function** for territoriality or mate attraction. Additionally, we must examine the **ontogeny** or development of the song in individual blackbirds, including how they learn to sing, and the **phylogeny**, or evolutionary history, of song in other songbird species. Tinbergen emphasized the necessity of address all of these questions concerning a given trait or behavior, without giving priority to any one of them. We should not limit our focus solely on mechanisms or the adaptive function; rather we should take a broad view of the entire biological spectrum of questions.

Some further basic principles of the bio-musicological approach (cf. Fitch, 2015) are: 1) Rather than solely focusing on high art music, such as Mozart, Bach, or Beethoven, we should concentrate on the music produced by people from all around the world. Popular music, therefore, should be our prime focus. 2) Perhaps less obvious is that we should always include dance in our understanding of musicality. This entails recognizing that musicality encompasses not just singing and playing instruments but also our ability to move to the beat, to form large groups whose behaviors are synchronized, with some members dancing, others singing, and others playing instruments. It is this broader capacity for synchronization that we focus on here. We should also 3) adopt a comparative approach, examining other animals for evidence on how and why specific traits might have evolved in our species. Furthermore, 4) we need to adopt a divide-and-conquer strategy towards musicality, acknowledging that it encompasses multiple cognitive capacities. For instance, melody requires relative pitch perception, while rhythm necessitates the ability to synchronize to a beat, among others. Thus musicality, as a whole, is made up from multiple different sub-components that might have different functions from an adaptive point of view, and they also might have different evolutionary histories.

Adopting this multi-component viewpoint, three core components of music that we can identify without much argument are (1) song, the capacity to learn new melodies, (2) dance, the capacity to synchronize movements to a beat, and (3) drumming, a capacity to create highly rhythmic structures.

Hypotheses concerning the function of musicality

Questions about the adaptive function of music have been almost an obsession of this field of bio-musicology for the last 25 years or so, and so we give a brief overview of some of the hypotheses that are on offer and some of the ways we might test those, before coming to our main topic, which is the possible function of music in territorial defence.

Darwin famously thought it was rather obvious why language evolved because language allows us to communicate meaning, and language is very useful for many different things. But he found the evolution of music quite a puzzle because, as he said, it is "…neither the enjoyment nor the capacity of producing musical notes are faculties of the least use to man in reference to his daily habits of life, they must be ranked amongst the most mysterious with which he is endowed. They are present, though in a very rude condition, in men of all races, even the most savage." (Darwin, 1871, p 333)

I think a first hypothesis always to be given priority because essentially it is a "null hypotheses," is that basically music is not an adaptation at all; it does not have a proper adaptive function, rather it is simply a technological innovation that is best seen as a biproduct of other things (like language or auditory scene analysis). Steve Pinker (1994) is probably the most famous proponent of this idea, and he referred to music memorably as "**auditory cheesecake.**" Our attraction to cheesecake has not evolved—we simply have a taste for fat, we have a taste for sweets, which maybe had more to do getting fruits, and getting seeds, etc. —and cheesecake is a modern creation that pulls these things together. Pinker famously suggested that music is in same category as cheesecake making or consuming: In the same way it would be silly to talk about the "adaptive function of" music; it is an invention that pushes certain auditory buttons that are there for other reasons. Many people in bio-musicology do not accept this proposal, mainly because of the many specializations that we see across our entire species for music, some developed very reliably early in childhood. We know that there are dedicated neural mechanisms for relative pitch perception or our capacity to be entrained to a beat. But still, this null hypothesis always deserves to be mentioned: that musicality is not even an adaptation at all.

Moving on to hypotheses about truly adaptive functions, probably the best supported empirically, in terms of the multiple studies showing that it really works, is in **mother-infant communication**. Parents all around the world sing to their babies, and these songs are incredibly effective. For example, lullabies are common all around the world, and are used to calm babies down and to put them to sleep, and we can take lullabies from anywhere in the world, play them to babies, and show that they really have quite soporific effects. They help settle down babies more than, for example, their mother speaking and more than play songs that parents around the world also sing to their children to get them excited and happy. This is the work that was mainly spearheaded by Sandra Trehub and Laurel Trainor (1998). An interesting observation from this work is that even people who say, “I can’t sing” or “I’m not a musician,” if asked, “Have you ever sung to your child?” will very often answer “yes.” Some other would say “I don’t even sing is showers, but I still sing to babies.” We thus think this is a function of music that we have to take seriously, and that was potentially quite adaptively useful, as soon as hominin mothers began putting down their babies, we used these vocal means to soothe the babies.

Coming back to Darwin, his favoured idea for why music evolved early on in our species was that it resulted from some sort of **sexual selection** (Darwin, 1871), and was used in mate choice to charm the members of the opposite sex. Darwin had in mind rhythmic melodies, not specifically love songs, so to speak. This remains a popular hypothesis, particularly among the lay public, but actually the empirical evidence for this is not particularly strong. This is one case where we can use song in other species as a very nice test. When we look around the animal world, most of the cases when we clearly know of vocal learning and using melodies “to charm” the members of the opposite sex involve males who sing, and they do so only as adults, often only during the mating season. And human music, of course, violates all three of these regularities: both sexes are equally skilled; musicality appears early in childhood (even infancy); and it happens in a diverse set of contexts. Children, even babies, are very interested in music and in singing at the age of two or three. Clearly men and women have roughly equal musical abilities, and certainly women are just as able to learn songs and sing as are men, so these predictions, based on comparative evidence, do not provide much support for the sexual selection hypothesis.

Turning now to the idea that group music-making, especially loud rhythmic music-making by groups, typically including singing, maybe percussion, and dancing, may have evolved as a way of basically signalling group power, the strength of groups. This idea has been around for a while, and probably the most concise specification of the hypothesis came from Ed Hagen, and his colleagues, especially Greg Bryant (Hagen & Bryant, 2003). They suggested that (a) “music and dance may have evolved as a **coalition signalling** system that could, among other things, credibly communicate coalition quality” (page 21) and (b) “This capability may have evolved from coordinated territorial defence signals that are common in many social species, including chimpanzees" (page 21). They also suggested that these signals, once established, may also support multiple groups joining together into larger coalitions. This is thus a two-part hypothesis: first, music-making can be used to protect a group's territory, to scare enemies away. But that alone would lead to a question why listening to the music of other groups would be attractive. Why should outsiders approach when, on the contrary, it might be supposed to be repulsive? The suggested explanation that Hagen and Bryant offered for this was that other groups might be attracted by impressive displays to join them to create even more impressive (and thus safer) displays. As a classic example, the Haka Dance, a very impressive group display done by groups of Māori from New Zealand, is a highly synchronized display that is apparently quite successful in striking fear into the hearts of potential competitors. This is precisely the kind of display that Hagen and Bryant had in mind when they talked about "coalition signaling."

However, deterring others is not the only function of the group display. Less well known is that female Māori groups also do a Haka display which does not have the same aggressive, repellent function as the male Haka displays.

To consider some other things we do with music, we have group dancing, which can be used in partner choice; we have large groups of people dancing and having fun, including both males and females, neither seeming very plausibly to fit the idea that group music-making functions to repel others. This suggests a more general hypothesis, that music serves for **social bonding**, between the individuals who are making music. So, when people sing together, in a sense they are not only singing for outsiders, as much singing to the members of their own group. Given that most of music-making throughout human history, and throughout world cultures, is a group endeavor where everyone gets involved in some way, and there is no strict distinction between the performers and the audience, we should definitely consider the potential role of group-internal functions. For example, considerable evidence suggests that singing together makes people feel happy and bonded. More support comes from the strong evidence already mentioned, that mothers interacting musically with their infants strengthens the bond between mother and infant. Even the sexual selection hypothesis finds its place here in that that one of the things that couples might be doing when they are doing music together is basically building and cementing their own social bond.

This hypothesis suggests that music evolved in our species as a general means of accomplishing social bonding at many different levels between both sexes, between adults and infants, and also including group-internal functions. But building their coalition will also signal coalition strength to outsiders. So, this generalized hypothesis focuses on the internal functions of music rather than the external signaling functions of music. Thus, these two hypotheses, the “credible signaling” of coalition strength and “social bonding” hypotheses, are not mutually exclusive. The social bonding hypothesis is an overarching function of music that includes many other adaptive functions as sub-cases. Both hypotheses are applicable when we consider potential functions of group music-making as a territorial or anti-predator display.

Comparative data regarding group displays

First, let us take a brief look at some other animal vocal displays, particularly focusing on animal group territorial displays, of which there are many different varieties, to provide a sense of how widespread the use of coordinated vocalizations is in territorial defence in animal communication.

Much of this was relevant whether human group music-making was focused on other humans, as often assumed, or as a predator deterrent, as we suggest here. For example, mobbing in birds is a very widespread phenomenon. Multiple species have a particular mobbing call, essentially a vocalization that birds emit when they discover a large predator, too big for them to chase away by themselves. In this situation, the discoverer emits a mobbing call, attracting a larger group of birds, which all start screaming at the intruder, often leading to its flying away. Often, scores of small birds surround a large predator (typically done to hawks, eagles, and owls; Curio, 1978). This is an example of a group display very successfully used to deter much larger and more powerful predators. If we consider groups of *Homo erectus*, co-existing in Dmanisi with these large sabre-tooth cats (see Lordkipanidze in this volume), the idea that groups of hominins performed loud synchronized displays to help scare these cats away is certainly worth keeping in mind.

An even more common phenomenon in birds is joint territorial defence. About 90% of birds form monogamous pairs that jointly defend their territory and jointly raise the young, and more than half of those species, both females and males, join together to perform duets. This happens in many songbirds, but also happens, for example in crane dancing or stork displays. These birds make synchronized calls and movements, providing a potent sensory display of how well coordinated the group is. The is again a very widespread phenomenon among birds.

Duetting is very common in tropical bird species where male and female jointly defend a shared territory. In at least one species this goes beyond just two individuals: the plain-tailed wren. This songbird species lives in Ecuador, and groups of males and females together defend their territory. They produce a rather repetitive two core syllable that is repeated over and over, in which the first part is the females, the second part is the males, and often in a chorus with multiple males and females singing at the same time. This is very impressive, very tight interlocking, not just singing at the same time, the way wolves howl, but rather interlocking their calls in very musically sophisticated way, with multiple males doing the male part and multiple females doing the female part.

Turning to more general choruses (such as wolves, coyotes, or lions) we might ask about the perception of these group displays. Several nice studies used playback experiments to examine the effect of these territorial displays on potential intruders. Lion roaring is a very loud display often produced by groups. Lions are among the most social carnivores, other than canids, and they hunt together as groups and also defend their territories as a group, so they make these roaring displays synchronized. So, two, three, four, even five females roar at the same time. Karen McComb and her colleagues in Africa created artificial overlapping roar choruses, so they could compare playback of one single roar with that of a roar combined in a group. So it sounded like three females were roaring at the same time. They played these two different recordings to male lions and found that male lions were highly aware of the fact that there were multiple females roaring vs, a single female and were more repelled by multiple females roaring than males (McComb, Packer & Pusey, 1994).

Returning now to primates, a similar playback study was done for chimpanzees (getting closer to our own *Homo* lineage). Chimpanzees make a number of quite loud displays including most famously the pant-hoot display, which includes not just very loud vocalizations and a vigorous sort of dance routine, but also often terminates with a drumming display, in which the displaying chimpanzee will beat its hands and feet on a hollow tree trunk, producing a very loud and long-carrying sound. We think this is a very suggestive example of a display of our nearest living relatives about what might have been one of the beginnings of musicality of our own species.

Michael Wilson and his colleagues in Uganda synthesized playback experiments with a single male and multiple males (Wilson et al., 2001). One of the things they showed was that when groups of chimpanzees hear a pant-hoot display, they are very sensitive to their own numbers, not just evaluating the number of callers but also "how many of us are there." And if an individual hears this pant hoot display alone, it tends to flee silently. It is only groups of more than three individual males that will approach a single male pant-hooting. So, it appears that listeners both know what the numbers calling are, and have some sense what the odds are of them winning.

To summarize, coordinated displays are widespread in animals and

A. Are used for territorial defence; and
B. From the perceptual point of view, conspecific listeners at least are, in fact, sensitive to the number of callers, and they are dissuaded by larger group displays.

All of these comparative data come together to suggest that anti-predator defence is a rather plausible adaptive explanation for how and why synchronized group displays could have evolved in our species.

Synthesis: Rhythmic Chorusing as an Anti-Predator Tactic

With all of the comparative data reviewed above as background, we now propose that proto-music, and in particular our ability to entrain to a beat and synchronize both vocal and instrumental (e.g. drummed) performances, served as a tool for **group anti-predator defence** during early stages of human musicality, with possible precursors visible in our closest relatives (Eleuteri et al., 2022). It is plausible that this basic aspect of musicality dates back to *Australopithecus,* but we would tentatively suggest *Homo erectus* who moved into new environments and encountered new predators when doing so, as a potential locus for its full emergence.

The hypothesis entails that this aspect of music is a collaborative performance, involving groups of two or more individuals. Specifically, we suggest that displays by a group that synchronize will be a more effective deterrent by making the displays louder by acoustic summation. The arguments for such increased effectiveness of synchronized auditory displays have been concisely summarized by Bjorn Merker (1999, 2000), who applied this logic to attracting conspecifics, but the same arguments apply for intimidating predators. Combining these vocal signals with group anti-predator tool use (throwing stones and brandishing sticks) would have essentially “trained” predators not to attack humans, enhancing their effectiveness even further (see also Brown, Schruth, Jordania chapters at this volume).

By thus producing very impressive displays, our ancestors could have increased their success in defending themselves and other occupants of their territory (e.g., offspring) by repelling large carnivores. This, along with throwing of stones, brandishing of sticks or other tools, and a general mobbing of the predator, would have been both effective (as illustrated above, with monkey alarm calling deterring leopards) and gradually enhanced by increased coordination. Such displays could also have played a role in deterring other groups of conspecifics, either at the same time, or as a second evolutionary stage, making this continuous with Hagen and Bryant’s “coalition signalling” hypothesis.

To our knowledge, the suggestion that anti-predator displays could provide one adaptive function for these key aspect of human musicality (beat entrainment and drumming) is novel, and we offer it in the spirit of broadening our conceptual workspace when considering the evolution of human musicality. We hope to have shown in this review that this idea is both plausible, and that it solves a real if neglected problem that our ancestors faced when they gave up the safe havens of arboreal life several million years ago.

Note: This paper is based on loosely edited transcripts of the authors’ conference talks, and later public discussion at the *“Defense Strategies in Early Human Evolution”* conference in Tbilisi, 2023.

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Kill Stealing by People in the Wilderness

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The practice of stealing the kills of predators by native people still continues wherever predators and meat-eating people share a habitat. A field experiment conducted by George B. Schaller and anthropologist Gordon Lowther in Serengeti National Park in 1969 brings to light how the early hominids, who lived as communal hunter-gatherers, would have obtained a portion of their meat from the wild. Schaller and Lowther once followed a male lion (*Panthera leo melanochaita*) for three weeks straight, and they found that the lion killed nothing, but ate seven times, either by scavenging or joining other lions on their kills. This made them wonder whether our ancestors could have survived on the leftovers of predator kills alone. Interestingly all the seven lion groups that they encountered, while they were on foot, fled when they were at distances of 80-300m. Schaller rightly concluded that this was due to the lions' prior experience of being hunted by Masai tribesmen.

When they carried out this experiment during the calving and fawning season of Serengeti ungulates, they located in the space of two hours 80 pounds' worth of easily caught young animals and abandoned carcasses. The next time they went out, they scavenged only from existing kills, and realized that this activity, unlike looking for young calves and fawns, which could be seasonal, could be pursued throughout the year. During the course of a week, during which they walked for 20 hours (with the aid of a car to move between locations) they had the opportunity to gather (if needed) nearly 1,000 pounds of live and dead edible animal parts. This experiment was conducted in an area where game abundance resembled prehistoric concentrations of migratory animals. Schaller and Lowther concluded that under similar conditions a carnivorous hominid group could have survived by a combination of scavenging and killing young and sick animals. They also realized that members of a carnivorous hominid group could have easily dispossessed lions of their kills by aggressively approaching them armed with sticks and by shouting, screaming and pelting them with stones.

My experience with kill stealing by local people comes from three areas in India: the Sigur Range near Mudumalai Wildlife Sanctuary, Shivalik hills west of the River Ganges in the western part of present day Rajaji Tiger Reserve, and Bandipur Tiger Reserve in South India where I carried out my research on dholes (*Cuon alpinus*). My dhole study lasted from 1974 to 1978. During my two-year stay in Bandipur Tiger Reserve from 1976 to 1978 I witnessed the native tribal people, *Kurubas,* stealing kills of dholes, leopards (*Panthera pardus*) and tigers (*Panthera tigris*). The prey species in the landscape were barking deer (*Muntiacus muntjac*), chital (*Axis axis*), sambar (*Cervus unicolor*), wild pig (*Sus scrofa*), and gaur (*Bos gaurus*). Since dholes do not attack people, the tribal people, one or two in number, taking cover and going up wind, quietly followed the dholes (dholes stop hunting when they sense human presence), and the kill was appropriated soon after it was made.

Leopard and tiger kills, which are usually cached in the bush, were located with the help of jungle crows (large-billed crows, *Corvus macrorhynchos*). The tribal people slowly approached the kill site by tapping on the trees with their cutting knives, coughing and clapping occasionally, and, after ensuring that the predator was not around, they stole the kills. The quantity of meat stolen from the kills depended upon the size of the kill and the number of people involved in stealing. The tribal people may have occasionally killed the young fawns of barking deer, chital and sambar, but this happened very occasionally.

The other place where I saw frequent stealing of kills was in the Shivalik hills west of the River Ganges within the present-day western half of Rajaji Tiger Reserve. These Shivalik hills are known for the abundant growth of bhabar grass (*Eulaliopsis binata*). This grass was harvested by the extremely poor local people and sold for rope making. Harvesting the grass was done in the winter months, and I was a witness to this in the late 80s and 90s. These people, while cutting grass in the hills, kept a sharp lookout for a jungle crow or a Red-billed blue magpie (*Urocissa erythrorhyncha*) flying down to the valley. Both birds are excellent at spotting kills. As soon as the birds were sighted, they abandoned their grass cutting and went down to look for the kill by following the birds.

The major predator in the hills was the tiger, and the principal prey was sambar. I myself have seen people taking away five sambar kills and Yasin, one of our field assistants who was living in the field station, during a ten-year period, saw 40 kills, largely sambar, being stolen. This kind of stealing, almost throughout the winter, had a disastrous effect on the breeding of tigers, affecting pregnant tigresses and tigresses with young cubs, resulting in a decline in the number of tigers in the landscape west of the Ganges River. This happened in spite of moderately high prey density (51/sq.km; Harihar *et al* 2014).

Stealing of tiger kills by *khols* in Chotanagpur plateau was recorded by A. Mervyn Smith (1904). Fiona and Mel Sunquist (1990) recorded elephant mahouts stealing kills in Chitwan National Park.

Krofel et al. (2008) recorded human kleptoparasitism of Eurasian lynx. Due to their relatively small size and slow feeding behaviour, the European lynx is vulnerable to human kleptoparasitism. In Norway, after stealing the meat, people left the kill remains at the kill site, and in Slovenia the kills were removed to be used either as human or dog food, or as bait to attract other animals. The authors conclude that such kleptoparasitism can increase the predation rate of lynx.

Schoe et al. (2009) recorded humans stealing from the lion kills in Benoue National Park, North Cameroon. They argued that the lions have put in a good amount of effort to make a kill, and kleptoparasitim can speed the extinction of lions, which face the problem of poaching and suffer from their conflict with cattle farmers.

Kill stealing will continue to occur in remote parts of wildlife landscapes wherever there is a population of poverty-stricken and meat-hungry people.

Therefore, the evidence from the available scholarly publications suggests that kill stealing by the local tribes of Africa, India and Europe continues in our times, giving support to the suggestions of scholars that kill stealing (or in scholarly terminology, aggressive scavenging; Shipman, 1986, cf. Jordania, in this volume) was probably an important activity for our distant ancestors from pre-historic times.

[Conference participants also watched a short sequence from the BBC documentary “Human Planet” on the subject of stealing the kill from lions by the contemporary Dorobo tribes in Kenya. See the YouTube video: “Grasslands: Stealing meat from the mouths of lions | Human Planet”]

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Beading for Beating: Body Percussion and the Interpersonal Origins of Rhythm

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Abstract. Standard models of the origin of rhythmic entrainment in humans posit a mechanism that is asocial and individualist. They argue that humans evolved the sensorimotor ability to synchronize body movements to externally-generated musical beats, but without any consideration for the source of those beats. A better model emphasizes the *interpersonal* origin of rhythm, in which entrainment evolves through mutual mechanisms of social interaction, and in which people are simultaneously the sound-source and the producers of entrainment during joint movements. The mutual model is multisensory, permitting interpersonal coupling through entrainment-cues based on sound, touch, and vision. Regarding sound, an important source of this is people's use of body percussion to aid in beating, especially during locomotor activities. I present ideas about the potential involvement of marine-shell-derived beads in generating percussive sounds for beating, since the use of beads dates back at least 100,000 years in human history. In addition, beads are used extensively by indigenous cultures in modern times in objects like leggings and rattles to generate body percussion during group dancing rituals.

The interpersonal model of the origin of entrainment

The standard model of the origin of rhythmic entrainment in humans is one based on "external" entrainment, in other words the synchronization of body movement to sounds that are generated external to the people who are engaged in the process of entraining. This can be seen quite commonly in everyday life when people dance to music in a discotheque. The beat that the people dance to is generated by musicians, not by the dancers themselves. Therefore, the aim of the dancers is to synchronize their movements to the strong beats in the music's metrical hierarchy. But they themselves have no influence over the beat itself. They can only be followers to the musicians, but never leaders or even co-equals.

We can think about this as an individualist model, since it does not posit any social connection between the dancers and the musicians. An extreme example of this can be found in the “dancing cockatoo” known as Snowball. He has demonstrated a compelling ability to entrain to the strong beats in recordings of pop music (Patel, Iversen, Bregman, & Schulz, 2009; Schachner, Brady, Pepperberg, & Hauser, 2009), for example the songs of the Backstreet Boys. Not only does Snowball have the ability to move parts of his body in synchrony with strong beats in the music, but he possesses a varied choreographic repertoire that engages his body in a diversity of manners, thereby qualifying as a true form of dancing (Jao Keehn, Iversen, Schulz, & Patel, 2019). My undergraduate students find videos of Snowball highly entertaining to watch.

But there is a major problem with the Dancing Cockatoo model of the origins of rhythm. We know that the Backstreet Boys have no place in the evolutionary history of cockatoos. Therefore, we have to ask the following question: who is generating the beat in the wild? Who serves as the role of musicians in the behavioral ecology of cockatoos? To the best of our knowledge, the answer is nobody. And so, Snowball’s impressive dance skills raise more questions than they answer. From a Darwinian perspective, one wonders how an individualist mechanism of entrainment to an unspecified external beat could be evolutionarily advantageous. Perhaps it could serve as a type of aesthetic display for courtship purposes. But this idea conflicts with both intuitive and scientific notions that interpersonal entrainment in humans – whether through group dancing or group chorusing – most likely evolved for the purpose of cooperative social coordination. In other words, it is far more connected with *group* displays than individual displays.

I have argued in detail in Brown (2022) that there are better ways of thinking about the origin of rhythm in humans than the Dancing Cockatoo model of audiomotor entrainment. Such models eschew entrainment to an “external” beat in favor of entrainment to an “internal” beat, in other words to a beat that is generated *by the performers themselves*. I will use the term “mutual” when referring to this type of internal entrainment. The phenomenon of mutual entrainment solves the problem of the external model since it provides insight into where the acoustic entrainment-signal comes from. It posits that this signal comes from the performers themselves as part of their process of engagement in joint movement activities. An important source of such cues is "body percussion," which refers to sounds that are generated either by the body itself (e.g., clapping the hands) or through the attachment of sound-generating devices to the body (e.g., shaking a rattle or banging stones together). The coordinated use of such body percussion can create acoustic *beating* for a group of people.

I will explore the phenomenon of body percussion in more detail in the next section. For now, I will simply point out that the mutual model of entrainment – in which joint body movement among two or more individuals serves as both the source-source and the effector for entrainment – provides numerous conceptual advantages over the external model. From a purely sensorimotor standpoint, it provides *three* types of sources of entrainment cues: acoustic (body percussion), haptic (through body contact), and visual, either individually or in combination. Hence, it is a multisensory model, compared to the purely acoustic cuing of the external model. Next, the model places its conceptual focus on the specific evolutionary advantage attributed to entrainment for humans: cooperative action. Compared to the asocial mechanism of the Dancing Cockatoo, the mutual model is intrinsically social. Mutual entrainment is a form of joint action and partnering, one that leads to interpersonal coordination of movement during group rituals. The model is based on joint intentionality and the social motivation of humans to coordinate with one another, leading to socially rewarding emotions. Finally, the mutual model invokes another uniquely human capacity that is never mentioned in connection with the origin of entrainment in the music literature, namely gestural imitation. In many forms of group dancing, individuals perform their movements in unison such that they match one another's choreographic patterns and timing features, much the way that humans are able to chorus in unison. The mutual model incorporates gestural imitation and time matching into models of entrainment in a way that the external model never does.

Beating through body percussion

As mentioned, the mutual model offers three sensory cues for entrainment: acoustic, haptic, and visual. While all of them can be effective for entrainment, acoustic cues probably offer the best means of creating beating.

They do so through the employment of body percussion. We can think about this happening in two major manners, as shown in Figure 1: body percussion itself and body-attached percussion. Body percussion includes familiar behaviours such as clapping and stomping, but can also involve vocal percussion (e.g., grunts, shouts), as seen in the dances of Māori warriors in New Zealand (Youngerman, 1974). Perhaps more common than these mechanisms are the use of body-attached percussion, such as leggings, percussive attachments to regalia, and the shaking of hand-held percussion instruments such as rattles or the hitting together of stones.

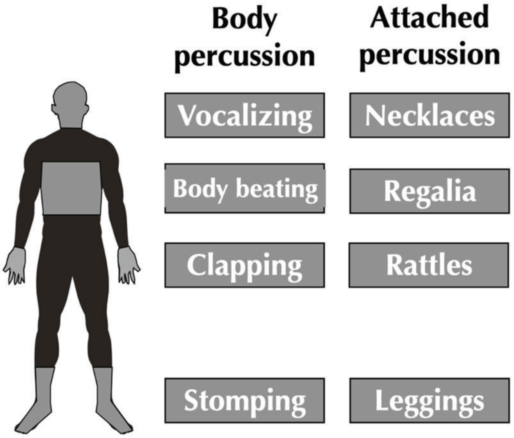

Figure 1. Two major forms of body percussion to generate beating. “Body percussion” refers to percussive sounds generated by the body itself. “Attached percussion” refers to percussive sounds generated by objects attached to the body. The two can work together. For example, stomping a foot while wearing a legging can generate body percussion from both sources.

Larsson (2014) pointed out that locomotion typically creates “audible sounds containing a number of qualitatively dissimilar acoustical events: isolated impulsive signals, sliding sounds, crushing sounds, and complex temporal patterns of overlapping impulsive signals” (p. 4). This idea need not apply to locomotion alone, but can be extended to include any kind of full-body movements that result in contact with the ground, by either standing in place (e.g. jumping, stomping) or moving about. This can be aided by shoes. William McNeill (1995) has discussed the importance of rhythmic entrainment for military drilling. A group of soldiers produces percussive sounds with the stomping sound of their boots when synchronously marching on the ground. Even non-human animals, such as chimpanzees and gorillas, use body percussion to intimidate rivals and predators, for example through chest beating in gorillas.

Body percussion is mentioned here not just as an ancient feature of an evolutionary model but as a prominent contemporary feature of dance throughout the world, from indigenous cultures to large-scale societies. Dancers attach objects to their bodies or to their regalia that allow them to make sounds as they move. This is seen in the leggings attached to the bodies of dancers in many cultures, the sequins and coins that are attached to the belts and bras of belly dancers, the shoe taps of Flamenco and tap dancers, and the hand-held rattles, shakers and frame drums of native North American dancers and well beyond. This is in addition to the sounds that dancers can generate with their bodies alone though stomping, clapping, and vocalizing.

To cite one example, traditional Aztec dancers in Mexico wear leggings (called *chachayotes*) containing seeds of the ayoyotl tree that make a loud clank with each and every step that they take. Such dance performances are accompanied by people playing large barrel drums with mallets. A dancer wearing *chachayotes* around his/her legs generates an acoustic rhythm in a manner that can be indistinguishable from the rhythm generated by the person beating a drum with a mallet. The dancer's entire body becomes a percussion instrument, and this leads to a true blurring of the distinction between dancers and musicians, as well as that between dance and music. There is a tendency to call the person who plays the drum a "musician" and the person who moves with percussion attached to their body a "dancer," but in many cases the two are producing the identical acoustic rhythms. *Dance and music are simply two different means of creating rhythmic patterns*. In the case of sonorant dances like traditional Aztec dancing, they are in fact the same manner.

What is the function of coordinated group displays that incorporate body percussion? The function is typically described in relation to the dual facets of ingroup cooperation and outgroup competition (Brown, 2000). On the one hand, activities like group dancing and chorusing can create pleasurable feelings of belonging to a group, strengthening the group itself. Synchronous activities such as these create a symbolic feeling of unity for group members (reviewed in Savage et al., 2021). However, cohesion is also a prerequisite for group defense: people have to cooperate in order to compete. Cooperative group displays not only strengthen a group internally, but amplify external lines of demarcation with other groups, enhancing competitive feelings of ethnocentrism. In addition, I have argued previously (Brown, 2007) that co-ordinated acoustic displays can produce the illusion of inflated group size, a phenomenon that is known in the animal communication literature as "the Beau Geste effect" (Harrington, 1989).

Jordania (2014) has argued that the driving force for the evolution of group-coordinative behaviors like music and dance had less to do with competing human groups as with predatory animal species via an aposematic function. He proposed that human chorusing evolved as a vocal "mobbing" mechanism against predatory species, itself a precursor to the war cry of inter-group human conflicts. The elements of Jordania's group-display system include the following features: 1) making sounds together in perfect synchrony and with strong dynamic accents; 2) singing in a low register; 3) chorusing either in octaves, in consonant harmony, or in a dissonant harmony; and 4) incorporating stomping, drumming, and the hitting together of stones, hence body percussion. The latter idea implies that the earliest stone tools might have been used not only for hunting and food processing, but also for noise-making and thus defense against predators. All of these behaviours are accompanied by a psychological transformation that Jordania refers to as the battle trance, in which soldiers "do not feel fear or pain, and where they can disregard their personal safety in the interests of their friends and the common goal" (p. 126). This state creates a psychological readiness for combat, one that is achieved through rhythmic behaviours related to music and dance.

The point of Jordania's model is that group-coordinative behaviors need not have only group-internal effects, but can have an impact external to the group through group displays, including effects on predatory animal species and competing human groups. Given the fact that the creation of stone tools is a defining feature of our species dating back to around 2.5 million years ago (Stout & Chaminade, 2012), then Jordania's proposal that the hitting together of stones was used for defensive purposes could potentially be an ancient practice. In fact, he has argued that the defensive use of stones may have predated their use as tools in the conventional sense. Larsson (2015) discusses the evolutionary significance of tool-use sounds. While his focus is on the origins of language, tool-use sounds could also be used percussively for the purpose of defense.

In such a short essay, I will not have the space to review the myriad examples of body percussion in animals, from chest beating in gorillas (Wright et al., 2021), to "tap dancing" in blue capped cordon blue birds (Ota, Gahr, & Soma, 2015), to branch shaking in many primate species, to buttress drumming in chimpanzees (Arcadi, Robert, & Boesch, 1998). The latter is a long-distance signal in which chimpanzees use their hands to bimanually beat the buttress of a tree. It is typically accompanied by vocal pant hooting by the animal. Fitch (2012) has speculated that this behaviour may be a homologue of hand drumming in humans.

Beading for beating

If one looks at the "attached percussion" column on the right side of Figure 1, one finds something common across the items. Many, if not all, of them are constructed using collections of *beads* as the percussive element to create sounds. Beads are found in necklaces, attachments to regalia, leggings, and hand-hold rattles. This leads us to the topic of marine shells, which are thought to have been used as forms of personal ornamentation and social display for more than 150,000 years in human cultures (Bednarik, 2015; Kuhn & Stiner, 2007; Sehasseh et al., 2021; Steele et al., 2019) and perhaps as much as 500,000 years (Joordens et al., 2015). Tiny shells, for example those of sea snails, were used as beads 75,000 years ago (Henshilwood, at al., 2004). Preferences for certain sizes and shapes of shells are seen in various ancient cultures, for example an affinity for rounded (basket-shaped) shells (Rogers, 2018; Stiner, 2014). Some of these shells were naturally perforated, whereas others show signs of being intentionally perforated by humans. These perforations allowed the shells to be strung together into necklaces (Bar Yosef Mayer et al., 2020). Evidence suggests that such necklaces were hung over clothing as a type of body ornamentation. In many cases, the shells were pigmented with red ochre, whose use for body ornamentation may go back as much as 200,000 years in human history. The archaeologist Ian Watts (2010) argued that the "habitual use of red ochre seems to be a hallmark of the spread of modern humans across the world". Ochre was used to pigment not only the human body, but many other types of objects that ancient humans used, including the marine shells used for beading. While we do not understand why ancient people donned necklaces, we can imagine that they served functions related to personal ornamentation, as well as ritual purposes, such as marking the social status of a person.

While the archaeology literature mainly discusses beads in relation to personal ornamentation, I would like to speculate that beads also served a *beating* function in human cultures during group dance rituals, just as they do in modern times. As mentioned in the previous section, dancers in indigenous cultures employ all of the types of body percussion described in Figure 1. I would like to propose that, if beading with marine shells did indeed emerge 150,000 years ago or earlier in human history, such beads could have been attached to the bodies of dancers for the purpose of creating body percussion to aid in beating. I strongly believe that the first percussion instrument of human history was the human body itself. While percussive sounds can be achieved through the use of body parts alone – for example, by stomping the feet on the ground or clapping the hands together – they can also come about by attaching sound-generating objects to the body or by holding handheld rattles. It is thus quite possible, although completely unverified, that beads from marine shells could have comprised a key component of the body percussion of ancient dance rituals and helped contribute to the rhythmic pulse of group dancing. In other words, *beading could have contributed to beating*, exactly as it does in modern times in many indigenous cultures.

Conclusions

The mutual model of the origins of interpersonal entrainment provides a parsimonious evolutionary narrative since the achievement of mutual entrainment through the use of body percussion allows for sound generation and motor entrainment to co-evolve. To the extent that dance does have a connection with instrumental music, it is far more frequently connected with percussion music than with melodic music, most commonly drumming. The mutual model of entrainment argues that *dancers were the first percussionists* and probably the first percussion instruments as well. According to this view, a distinct class of percussion musicians later evolved by shifting the primordial body-percussion mechanisms – which included objects attached to the leg, held in the hand, or attached to one’s clothing, in addition to body-percussive mechanisms such as clapping and stomping – to individuals dedicated to playing percussion instruments in the absence of dancing, as was described earlier for the arrangement of traditional Aztec dancing. The mutual model argues for a social origin of rhythmic entrainment, rather than the typical individualist perspective. Social interaction becomes both the cause and effect of entrainment. The mutual model offers a multisensory and multi-effector mechanism in which body percussion serves as a mutually-generated acoustic cue for entrainment. I argued that body percussion in ancient humans may have received an important contribution from the use of marine shells to serve as beads that were attached to the body in some form. According to this scenario, beading contributed to beating in rhythmic acts of mutual entrainment through group dancing.

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The Role of Pitch in Choral Singing as an Intraspecific Defense Strategy

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Abstract. It has been proposed that music could have evolved as an aposematic display against predators (Jordania, 2011). By the same token, Hagen and Bryant (2003) have argued that music together with dance could have acted as a credible signal of coalition quality that evolved directly from territorial defense signals. Most recently, Mehr et al. (2021) have suggested that musical rhythm could have served as an extra-group deterrent, but also as an "invitation" to create cooperative alliances with other groups. They have also proposed that pitch could have been used in credible parents-infant signaling. However, as hominins' choral singing was probably composed of culture-specific pitch variants which had to be acquired by means of strenuous learning within the group, pitch could also have become an important part of acoustic signaling used as an extra-group defense strategy. From this point of view, culturally invented schemes of pitches could have served as the hallmarks of group identity by the means of indicating group size and consolidation. As such, choral singing could have deterred other groups or individual competitors. This idea can extend the scope of hominins' musical defense strategies as mentioned above. However, while Jordania's hypothesis is focused on the defense strategy against predation, and Hagen's view is concentrated mainly on musical rhythm as a source of extra-group signaling, the proposed idea adds to these defense strategies the use of pitch structure as a deterring signal against intra-species competitors.

Introduction

Explaining the evolutionary origin of human musicality, i.e. the set of abilities enabling the recognition and production of music (Fitch, 2015; Honing, 2018), undoubtedly requires pointing to the adaptive value (or values) of music. One of the functions of communication that is often present in nature is deterrence. The deterrence strategy is common in nature because it usually benefits individuals who deter. In many cases, an individual that deters, even if the deterrence is credible (e.g., as in the case of rattlesnake rattle), reduces the risk of injury or death as a result of an attack by a predator. Deterrence is also used against sexual competitors or conspecifics fighting for other resources such as food or shelter. If a deterring signal is credible, the ability to recognize it appropriately is also adaptive for a deterred individual as it avoids the same risks such as injury or death. This deterrence strategy is called aposematism. Although the category of aposematism is usually referred to visual signals, it may also refer to communication using other senses, such as olfactory (Eisner & Grant, 1981) or auditory (Hristov & Conner, 2005). Since music is a form of sound communication, an aposematic display against predators has been indicated as its possible adaptive function (Jordania, 2011). Aposematic signals can also be directed against conspecifics in case some individuals of the same species compete for certain resources. Following this logic, Hagen and Bryant (2003) have argued that music together with dance could have acted as a credible signal of coalition quality that evolved directly from territorial defense signals. More recently, this idea has been developed by pointing out how different musical features can serve different deterrent functions. Mehr et al. (2021) have suggested that musical rhythm could have served as an extra-group deterrent, but also as an "invitation" to create cooperative alliances with other groups. They have also proposed that pitch could have been used in credible parents-infant signaling. However, as hominins' choral singing was probably composed of culture-specific pitch variants such as different pitch intervals which had to be acquired by means of strenuous learning within the group, pitch could also have become an important part of acoustic signaling used as an extra-group defense strategy. After all, listening to a well aligned sounds in terms of unknown pitch patterns can be interpreted as signals of long-lasting coalition. Additionally, singing together can be also a good indicator of the number of singing individuals. From this point of view, culturally invented schemes of pitches could have served as the hallmarks of group identity by the means of indicating group size and consolidation. As such, ritualized choral singing could have deterred other groups or individual competitors. The aim of this short paper is to indicate that the use of pitch as extra-group deterrent can extend the scope of hominins' musical defense strategies as mentioned by Jordania or Hagen and his colleagues. However, while Jordania's hypothesis is focused on the defense strategy against predation, and Hagen's view is concentrated mainly on musical rhythm as a source of extra-group signaling, the proposed idea is focused on another defense strategy i.e. the use of pitch structure as a deterring signal against intra-species but extra-group competitors.

Harmonicity of sound, signaling, and aposematism

Sound as a by-product of animals' activity can be a reliable cue of animals' presence, distance, direction of movement, size etc. In contrast to cues, sound signals are the sources of information which are produced intentionally by a sender in order to elicit a response in recipients (Laidre & Johnstone, 2013). The usefulness of sounds with a harmonic structure as carriers of information results from their acoustic properties. The characteristic of each harmonic sound is that the frequencies of its partials are integer multiples of the fundamental frequency. This property of harmonic sounds allows them to be easily distinguished from other sounds present in the environment (Horowitz, 2012). As a result of this, harmonic sounds can be not only an important cue of animals' presence but have also become a frequently used element of intentional communication. In fact, the use of harmonic sounds as signals is a widespread strategy among vertebrates including mammals (Hauser, 1996). Humans also use harmonic sounds in their intentional vocalizations such as laughing, crying, speaking and singing. It has been proposed that harmonic sounds can play the role of both cues and signals in music (Huron, 2015). However, while the adaptive function of pitch in crying, laughter and speech is beyond doubt, its biological function in music is still a matter of dispute. The popular claim that pitch structure processing in music is a by-product of linguistic ability (Lerdahl & Jackendoff, 1983) does not explain the specificity of the experience of musical pitch. In contrast to speech intonation, pitch in music is perceived as a sequence of discrete units, which allows to interpret music in terms of the Humboldt system (Merker, 2002). Therefore, if this musical pitch specificity is the result of natural selection, it must have served some adaptive function. The adaptive functions of music proposed so far include sexual display (Darwin, 1871; Miller, 2000; Ravignani, 2018), strengthening social bonds (Dunbar, 2012; Harvey, 2017; Savage et al., 2021a; Storr, 1992) including mother-infant bonds (Dissanayake, 2001;

Falk, 2004), informing about group cohesion (Hagen & Bryant, 2003; Hagen & Hammerstein, 2009; Mehr et al., 2021), and deterring predators (Jordania, 2011). It is worth emphasizing that the adaptive functions indicated here are not mutually exclusive and could have contributed to a different degree in the selection of various elements of human musicality (Harrison & Seale, 2021; Savage et al., 2021b).

Musical pitch and social bonding

Although rhythm is usually indicated as the most important feature of music, which is responsible for its social consolidation power (Tarr et al., 2014), it seems that pitch may play an equally important role in consolidation by means of music (Wagner & Hoeschele, 2022). This is probably possible thanks to specific properties of pitch structure as a part of music. The use of pitch in music is based on culture-specific rules. These rules govern the organization of pitch at many levels from the musical pitch system to specific melodies. The musical pitch system is acquired in the process of enculturation in a similar way to the acquisition of the mother tongue (McMullen & Saffran, 2004), which makes it a reliable indicator of belonging to a given group. The ability to recognized a culture specific pitch system is based on our sensitivity to tuning i.e. detecting the small deviations from the fundamental frequency of harmonic sounds (F_0) that are parts of a particular musical pitch system. Recognizing that someone is singing out of tune is based on this ability. Nevertheless, people are quite tolerant of intonation when they recognize the structure of intervals that make up a particular melody. It is believed that this tolerance is related to zonal pitch hearing (Rakowski, 1999), which involves treating sounds within a certain frequency range as belonging to one musical pitch pattern (pitch class). Also the knowledge about the distribution of pitch classes in a given musical culture is acquired effortlessly by means of statistical learning (Curtis & Bharucha, 2009). This knowledge is crucial for intuitive recognition of tonal errors in native music by contemporary humans. However, hominins had not been able to learn implicitly the pitch class distribution in conspecific vocalizations before they became musical species. In the previously proposed Baldwinian scenario of music origin, our ancestors had first invented the use of vocalized pitches as the parts of a ‘consolidating ritual’ (Podlipniak, 2016). In this scenario, the learning of invented vocalizations by pre-musical hominins was strenuous and time consuming. Under these circumstances, singing a particular sequence of pitches was proof of the effort put into tedious communal learning, which could inspire mutual trust among group members and, in consequence, strengthen social bonds.

Pitch structure as a deterring signal against intra-species competitors

The harmonic sounds of consolidating ritual could have been at the same time a cue of group size and inform about potential danger to conspecifics and other species. Since cues are often transformed by natural selection into signals (Laidre & Johnstone, 2013) the vocalized pitch sequences could have become an intentional aposematic display. While the recognition of the abovementioned differences between pitch distribution in different musical cultures could have helped to check at distance the group consolidation by conspecifics, other species have probably been unable to infer much information about singer's consolidation from musical pitch sequence. However, for hominins forming competing groups listening to a well-coordinated homophonic chorusing could have induce awe and fear. This could have been possible because hominins had been endowed with the ability to recognize pitch sequences. Without the ability to implicitly learn pitch sequences, however, each well-coordinated collective singing of pitch sequences was evidence of many hours spent by a given group learning a particular melody together as part of a consolidation ritual. In this way, behavior whose primary function had been group consolidation could have become a deterring signal against intra-species competitors. It is also probable, that the same selective pressures (recognition of free riders, group consolidation, deterring conspecifics) acted as the reason for the evolution of sensitivity for tuning. The volitional control of f_0 certainly required a lot of effort from hominins, as did the creation and retention of precise patterns of musical pitch intervals in long-term memory. As spectral synchronization, especially synchronization of F_0, became the hallmark of group identity, a well synchronized (in terms of pitch) singing could have acted as a social glue for in-group members and as a deterrent for out-group individuals. The main source of these different reactions was the difference between musical knowledge of members and non-members of a particular group. Musical knowledge (cognitive patterns) acquired during long-lasting communal rituals specific to a particular group became an implicit tool for identification "friend-or-foe."

Conclusions

The proposed adaptive function of musical pitch does not have to be the sole explanation for the emergence of the ability to use and recognize discrete pitch categories. On the contrary, the complexity of human musicality and the fact that pitch perception serves many different communicative functions in humans today suggest that different aspects of these abilities may have evolved due to different functions (Podlipniak, 2022), and that the path leading to their development did not have to resemble a straight unidirectional trajectory. The fact that currently pitch in speech (speech intonation) is not used as a tool for spectral synchronization between simultaneous vocalizations, as is often the case in music, does not necessarily mean that our ancestors' ability to volitionally control F_0 was solely responsible for one adaptive function that we attribute to speech. However, more research is needed to identify what functions hominins' use of pitch may have had before the development of human musicality as we know it today.

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Warning Display as a Strategy of Defense and Offense in Early Human Evolution

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Abstract. Warning display (aposematism) is one of the well-known, but often neglected defense strategies in the animal kingdom. Unlike crypsis, which is based on the strategy "Stay invisible, silent, odorless, and flee as fast as you can if discovered by a predator," aposematism is based on the alternative defense strategy "Stay visible, be noisy, have odor, and do not flee if confronted by a predator; on the contrary, actively threaten the predator by your body size, loud sounds, odors, and fearless behavior." In this presentation I propose that human ancestors widely used the aposematic strategy of defense for several million years, and this strategy affected human morphology and behavior in the most profound way. Also, although aposematism is generally known as a defense strategy, in human evolution it was later used not only for the defense, but for attack as well, creating a case of "dual use of aposematism." I propose that the primary use of aposematism was defense, as it is used mostly in animal kingdom. Only after it became a potent tool of defense from the biggest predators of the African savannah, did our ancestors start using the aposematic Audio-Visual-Olfactory Intimidating Display (AVOID) for attack as well, in order to chase away the original predators and obtain their carcasses via aggressive scavenging.

Audio-Visual-Olfactory-Intimidating Display as a Defense Strategy in Early Humans

There is a growing understanding among behavioral ecologists that aposematic animals do not rely on a single modality (say, visual), but use all modalities – audio, visual, olfactory, and behavioral modalities – simultaneously (Ruxton, et al., 2004; Caro & Girling, 2005). This multimodal use of signals makes the display much more effective. For example, apart from its famous contrasting colours, the skunk uses an array of techniques in several modalities; namely, it produces growling sounds, displays a bipedal posture, has a distinctive body odor (apart from the infamous spray), and does not run from a predator. As a result of such a multimodal strategy, aposematic animals have very different morphology and behavior than cryptic species.

Generally, aposematic species are easier to see, hear and smell, as they are more colorful, noisy, have a stronger smell, and are more fearless than cryptic species.

These qualities affect the morphology and behavior of aposematic species. To make their bodies visible, noisy and smelly, aposematic species have colorful (or contrastingly colored) bodies, often with extra morphological additions to the body (known as "ornaments"): they can increase their body size by inflating their bodies, or by standing up in a threatening bipedal posture; they constantly generate sounds when moving around and can generate louder and more aggressive sounds (ranging from voiceless hissing to a growl) when confronted by a predator; they have a constant body odor when moving around, and can increase the intensity of the odor when confronted by a predator. Also, as an additional behavioral characteristic, they often cannot run fast, have sluggish movements, sending a message to a predator-to-be that they do not have to run for life. As a matter of fact, aposematic animals often approach predators with the display of all the available multimodal warning signals.

Aposematic multimodal signals have two strategic functions:

(1) To intimidate: or to warn the predator by the display of size, colors, ornaments, noises, fearless behavior, and

(2) To educate: or to make their visual, olfactory, audible, and behavioral signals remembered by the predator.

In order to depend on aposematic display for generations and be a successful species, aposematic animals need to have real, effective secondary defenses that will be used if the predator (particularly an "uneducated predator" or a very hungry predator) still makes an aggressive move and attacks the aposematic animal. Humans have both effective primary and secondary defense systems. We will discuss the secondary defenses after discussing the primary defenses.

So far there have been two suggestions from scholars about humans being the aposematic species.

In 1967 paleoanthropologist Louis Leakey proposed that humans are aposematic (without mentioning this term), being unpalatable for big cats.

Leakey used his personal experience to come to this conclusion, as he witnessed firsthand on more than one occasion this aversion among lions. During a series of his famous long field-researches in East Africa, lions entered the tent occupied by the scholar and his students (five lions on more than one occasion), and after sniffing human heads, left without attacking. Leakey believed that human smell somehow deterred lions. In his own words:

> "I seriously believe that one of things which protected many early primates, including early man, in the defenseless days before he had weapons or tools, and when he was living on the ground, was that he was unpalatable to the carnivores.... Whether man's natural immunity to large carnivores is smell by itself – they certainly sniff at us – or whether it is a combination of smell plus knowledge of how flesh tastes, I do not know, but I am convinced that a major defense mechanism of the earlier stages of protoman and early man was neither weapons nor canine teeth, nor claws nor physical strength, but his nature-endowed characteristic of being unpalatable, of not being good food for large carnivores." (Leakey, 1967:5)

Leakey's interesting suggestion was reviewed in 2018 by Paul Weldon from the Smithsonian Conservation Biology Institute, who proposed that humans are possibly chemically aposematic. In his words,

> "I propose that the body odor of humans and, historically, of hominins denotes chemical emitters that exhibit formidable defensive traits, including large body size, agility, vigilance, and the capabilities of deploying projectiles and other weapons and/or marshalling group defenses. This hypothesis maintains that selection acts against (1) offenders, including carnivores, that fail to avoid chemicals from hominins, and (2) hominins who fail to emit distinguishing chemicals, thereby give rise to a chemically mediated avoidance that is mutually beneficial, i.e. chemical aposematism" (Weldon, 2018:1)

I dedicated a book to this problem (Jordania, 2014; see also Jordania, 2017), arguing that humans demonstrate all the characteristics of aposematic features in every possible modality – audio, visual, and behavioral – not only in body odour, as pointed out by Leakey (1967) and Weldon (2018).

The list of the most important aposematic characteristics in humans is the central part of this presentation. I had to be brief because of the large number of these characteristics. Some of them are relatively known, but others will be discussed for the first time in the context of aposematism.

VISUAL SIGNALS

Bipedal posture. It is a relatively known suggestion. Initially Frank Livingstone (1962), then Roger Wescott (1967), and later Nina Jablonski and George Chaplin (2009) suggested that, as plenty of animal species use bipedal threat displays to look taller in order to intimidate antagonists, bipedal threat displays (probably more as a startle display) could have been the initial defensive/intimidating behavior that led hominins gradually to adopt permanent (aposematic) bipedal posture (Jordania, 2014:99-101).

Long legs. Humans have unusually long legs, one of the longest among the apes. With the obvious slow movement achieved with their long legs, it is possible to suggest that the longer legs were gradually developed in order to be taller, as a higher body profile makes humans less vulnerable to predator attacks (see Blake's presentation and practical suggestions in this volume). All the major predators (including lions and tigers) display respect and clear aversion towards the human bipedal posture and human height.

Long hair on top of a head. Nina Jablonski (2008) suggested that it was evolutionarily advantageous for hominins to retain the hair on their heads in order to protect the scalp as they walked upright under the intense African sun. An unanswered question remains: why would hominins (or early humans) need to have five-foot long hair to protect just their scalp? Many animals that live under the same burning African sun are doing just fine with a few centimeters of non-coiled hair covering their body and the skin on their head. It seems to me that long human hair conveys some kind of visual information.

Desmond Morris (2008) suggested that overgrown head hair was used as a species-specific morphological sign for hominins, visible from afar. This suggestion also has its merits, since recognizing each other is an important element for any animal species. But herein lies another difficult question: why did our ancestors, who had such unique and visually distinctive morphological features such as bipedal locomotion, need yet another visual sign? Evolution is extremely economical, and if there are no important reasons for it, then wasting energy on the growth of huge hair does not seem justified.

To better understand the evolutionary function of human head hair, we need to remember two important facts about it:

(1) If left alone, untrimmed human head hair grows about 1.5 meters long. After this, each individual hair falls out and is replaced. I am specially mentioning this because, in many scholarly reconstructions, our hominin ancestors are portrayed without this very important visual feature.

Also, (2) most likely the initial style of hominin head hair was a tightly coiled bush of hair on top and around the hominin head, very much like the contemporary untrimmed "Afro" style that all peoples of African origin (including pygmies and bushmen) grow naturally.

My suggestion is that the unusually long hominin hair on top of the head had the same purpose as long legs and bipedal posture, and this purpose was simply to look taller. Of course, because of its coiled design, five-foot long hair did not add a full five foot to one's body height, but it must have been worth about a 20 cm (8 inches) increase in body height. An untrimmed Afro hairstyle is several times as big as the diameter of a human head. Therefore, a huge ball of hair must have been a significant addition to hominin body height. A survey of the tall military helmets of Napoleonic hussars, or the colorful headdresses of the warrior men of different indigenous tribes, reflects the perennial drive to look taller among human warriors. Later humans substituted high military helmets for the Afro-style bushy hair to fulfill the same function: to look taller and visually more impressive to potential opponents.

One more detail – when we measure human height, as a rule we do not include the hair on top of the head. I suggest the length of hair must be considered in the most serious way, as extra hair volume would have added significantly to their relatively short body length, most probably saving the lives of many of our ancestors, and, by extension, us, their descendants. For example, if the body height of male Homo habilis was about 158 cm, considering the length of their most likely tightly coiled and untrimmed hair would have extended it to about 178 cm tall.

Of course, we must agree with Nina Jablonski that the skin on top of the human head needed protection, and that head hair provided this protection. We may also agree with Desmond Morris that a huge ball of hair would be an effective species-specific visual sign. But I still suggest that the primary evolutionary function of extraordinarily long and bushy human head hair was connected to the strategically important drive to look taller, in order to intimidate potential rivals and predators.

Body painting. Another possible potent visual signal might come from the use of more colors. We humans naturally change the color of our face and upper body when we are offended or angry (blushing), and usually we turn red – the most aposematic color. Apart from this legacy of our biological evolution, we have a legacy from our early cultural evolution as we began to employ more drastic colors via body painting.

The beginnings of body painting go much deeper than any rock painting, and most likely, originated with the oldest use of various pigments. Body painting, like music and dance, is a universal trait of human culture. No human culture is known to be totally free of body painting. For many tribes body painting is an important part of identity. Body painting in many traditional societies also signifies the status of a person or the moment of life they are experiencing; it also constitutes a very important part of initiation ceremonies in many parts of the world. Body painting was an important ritual for men going into a hunting session or to war. Women were also tattooed. Body painting is still widespread. Some participants at our conference may have tattoos on their body. Apart from permanent body painting, there are many more temporary body paintings in use. Using a lipstick or an eyeliner pencil is so widespread that hardly anyone would consider them to be in the same category as body painting.

Hundreds of thousands of years before the estimated appearance of the first cave paintings, our ancestors were using coloring materials – such materials have been found at several archaeological sites, although scholars have never found cave paintings of such an ancient age. The most likely explanation is that the first paintings were in fact done on human bodies.

“Stone nodules containing mineral manganese dioxide, which has been scraped with stone tools, have been found at several Neanderthal sites… As the Neanderthals have left no traces of pigment on cave walls or artefacts, the most likely explanation is body painting” (Mithen, 2005:230).

Well, even if we agree that the earliest use of painting materials was to paint bodies, why were bodies painted in the first place?

We have already discussed how the striving to become more visually impressive became paramount to our early ancestors for safety reasons.

In other words, any physiological or behavioral changes that led hominins to acquire a more impressive look (like bipedalism, long legs and long hair, blushing, or body painting) was giving certain hominin groups better chances of survival by intimidating predators and competitors more effectively. This approach places *natural selection, not sexual selection via female choice*, as the main driving force behind the tradition of body painting (Jordania, 2009a).

According to a 2012 article in the *Proceedings of the National Academy of Sciences of the United States of America*, the most popular and most enduring coloring substance – red ochre – has been in use "minimally" for 200-250 kya (Roebroeks, et al., 2012; cf. Bednarik, 1997). The users in this case were European Neanderthals, locked behind the ice sheets of Ice Age Europe. The use of painting substances among Neanderthals was doubted by scholars for decades, but growing evidence suggests that painting was widely used in isolated Europe much earlier than the appearance of anatomically modern Cro-Magnons. Here is an excerpt from the conclusion of the article:

> "Identification of the Maastricht-Belvédère finds as hematite pushes the use of red ochre by (early) Neanderthals back in time significantly, to minimally 200–250 kya (i.e., to the same time range as the early ochre use in the African record)." (Roebroeks et al., 2012)

There are indications that even *Homo heidelbergensis,* a much earlier, taller, and muscular ancestor of the *Homo neanderthalensis* who lived in Europe 600-300 thousand years ago, also used red ochre for about 400 kya. This evidence, although not universally accepted, comes from the Terra Amata site (Roebroeks et al., 2012).

Let us now ask a methodologically very important question: is it possible that our ancestors used other substances before their use of red ochre? I am talking about temporary substances that our ancestors could use to paint themselves before they found and started using durable substances like red ochre (red) and manganese dioxide (black). The idea that coloring faces and bodies started long before the use of durable materials is not only plausible, but virtually unavoidable. What materials are we talking about? We are talking about readily available coloring substances, like some colorful berries, clay, even earth, and above all, the use of blood. Blood most likely was the earliest coloring substance that human ancestors used, putting the timelines of the origins of human arts much earlier.

So, human visual aposematic signals included bipedal locomotion, long legs, long tightly coiled hair on top of the head, colors that were given from earlier evolutionary processes (blushing), and by later cultural evolution – use of the body painting. There were other powerful elements of visual display, connected to dance and visual synchrony (the New Zealand Māori "Haka" is a famous example of such a group intimidating display. Gibson, 2011).

Let us discuss now audio signals available to our ancestors for more impressive aposematic display.

AUDIO SIGNALS

Singing. Singing is a behavior that is overwhelmingly distributed in arboreal and aerial ecosystems (among the tree-living and flying species). Humans are among the very rare terrestrial species that sing (Jordania, 2020). Apart from humans, we could argue that some carnivores (like wolves and coyotes) can also sing, and sing in choruses (Harrington, 1989; Hagen & Hammerstein, 2009; Hagen & Bryant, 2003), but this is a sphere that we will not be going into during this presentation.

Human ancestors came down from the trees, and we know that tree-living birds and primates (even a lesser ape – gibbons) are among the most famous singers. So, it would be logical to propose that our arboreal common (humans and apes) ancestor was a singer. But why do terrestrial apes not sing? We know that many singing and noisy arboreal species (like birds and monkeys) stop singing whenever they visit the ground – mostly as a cryptic defense strategy from potential ground predators (Jordania, 2020). Most likely, ancestors of chimpanzees, gorillas and bonobos stopped singing because of maintaining the cryptic cover. On the other hand, in a strategically different move, human ancestors continued singing, therefore changing their survival strategy from cryptic into aposematic. I propose that not stopping singing was the first element of the new aposematic strategy of defense in hominin lineage, followed by the other elements of aposematic display.

As the common human-ape ancestor was probably not only a singer, but even sang in choruses, it would be logical to allow the suggestion that the human tradition of choral singing started while they were still in an arboreal ecosystem. The next development of arboreal singing (and groups singing) was greatly expanded with a new addition, that of a group unity, synchronicity (e.g., Bispham, 2006; Patel, 2008; Large, & Gray, 2015. See also Fitch & Zuberbuhler in this volume). Singing in dissonant intervals (the most robust sound) must have contributed to the creation of a more effective "Beau Geste" defense (Harrington, 1989; Hagen & Hammerstein, 2009; Hagen & Bryant, 2003; Jordania, 2014). Adding dance moves (initially as a threat display movements), also in perfect synchrony, contributed an emotional power to the initial group singing, as the precise synchrony of a great number of individuals created the image of a single monstrously big creature impossible to confront.

The popularity of the idea that human choral singing was used initially to defend territory is growing (Hagen & Bryant, 2003; Geissmann, 2000; Rice, 2014:108; Jordania 2014, Nettl, 2022). With the introduction of rhythmically united, synchronous singing together with dancing, the effectiveness of the audio system skyrocketed. There are no animal species that do not run from the loud wall of sound created by a large group of humans. The actual effectiveness of singing against the big cats (even the man-eating ones), had been first noted by Corbett (1944: Chowgarh tigers). Interestingly, pygmies also sing when going through the jungle to scare away leopards (Turnbull, 1961:58).

Apart from the strong external effect on predators and competitors, rhythmic synchrony brought another powerful element, probably an even more powerful *internal* effect on the group of singing humans. Synchronous singing and synchronous physical exercises (dancing, even simply walking together in time, e.g., McNeill, 1995) introduced a new phenomenon – battle trance, an altered state of consciousness, a phenomenon that still needs serious research (Jordania, 2011; Wade 2016; see also the presentation by Wade in this volume).

In this bid to achieve a more effective chorus, the human male voice additionally descended by an octave (the biggest distance between male and female ranges among primates). I fully agree with the suggestion by Desmond Morris that a low male voice would have been very useful to "intimidate human rivals, to drive prey or to scare off predators" (Morris:92).

As we can see, audio aposematic signals included singing, choral singing in dissonances, rhythmically united and augmented with foot stomping, hand-clapping, and a lower male voice range (Fitch, 2006; Jordania, 2014). Audio signals were augmented by a visual display of threatening body movements. Probably most importantly, this synchrony was the key factor to put the participants of such primordial choruses into the euphoric state of the battle trance, in which participants lose the sense of fear (aphobia) and the sense of pain (analgesia), obtain a common collective identity, and are religiously dedicated to their common goals.

OLFACTORY SIGNALS AND OTHER NIGTTIME DEFENSES

The evolutionary function of olfactory signals was somewhat different from the function of visual and audio signals. If visual and audio signals work during the actual confrontation with predators and competitors by intimidating them with threatening images and impressive sounds, olfactory signals mostly served as a reminder of the fighting abilities of hominins and early humans in the state of battle trance. “Remember me?!” was the powerful message, particularly needed when humans were asleep on the ground, without the defense of their visual and auditory modalities (let us recall the tense experiences of Louis Leakey from his close encounters with lions at night in Serengeti, when their own smell became their only defender).

The nighttime defenses need our special attention, as only after achieving relative safety on the ground at night, our ancestors became able to move away from the trees and start their intercontinental travels.

First, we need to remember that humans are one of the smelliest species on the earth (Viegas, 2011). This smell is achieved by overactive sweat glands. The prevailing suggestion for the immense number of sweat glands holds that humans used their overactive sweat glands to stay cool under the African sun (Jablonski, 2008). But sweat does not have to be smelly to cool the body, and human sweat is extremely smelly even for a species with such a bad sense of smell as ourselves. If we remember that, apart from recent historical times, our ancestors did not shower literally for millions of years, the strength of our body odor becomes more impressive.

In this connection I want to suggest that the well-known patches of hair in our armpits and groin were developed primarily for their hyper-effective smell-producing ability. Alternative suggestions for underarm hair (e.g., Hofer et al., 2018) as a sexual attraction tool or as a friction-reducing tool do not seem very convincing, as most humans diligently try to get rid of body odor, particularly when meeting the opposite sex, and humans who shave their armpits (including sportsmen) never report any complications from injuries.

As night-time defense is a very important (and yet forgotten) sphere, allow me to mention two more strategies apart from the body odor, for this important and mostly neglected domain.

Evening concerts. Adriaan Kortlandt made a brilliant (and mostly neglected) suggestion that one of the ways to secure nocturnal sleep was to organize loud evening "concerts" in order to scare away potential predators. Kortlandt cites the behavior of groups of chimpanzees, who sometimes organize loud "concerts" before they sleep, and cites also the behavior of African tribes living in the forests, who organize the same kind of loud evening displays (Kortlandt, 1973). It is difficult to measure how long such concerts would have gone on for: a perfect example is that when pygmies do not feel safe, they continue such concerts throughout the entire night (Turnbull, 1961:58). And not to forget: longer dancing session means more natural body odor to remind predators, the possible night visitors, about the identity of a large-bodied, loud, and missile-throwing species. Incidentally, we might also remember, that most concerts in human societies are still organized in the evenings; this might be a legacy of our evolutionary strategy for nighttime security: we might feel more secure after socializing with a group at a loud common display of unity.

Apart from noisy evening concerts, at least one more strategy was employed to secure nocturnal sleep for early hominins: Eyespots.

Eyespots (we can also call them "false eyes") are clearly visible marks on the body of an animal that resemble the shape of an eye. It is a popular aposematic visual signal. These spots resemble an eye in order to deceive predators and antagonists. They are extremely effective against predation and attacks from behind, because most potential predators seek a certain moment for their attack, when their prey is not looking at them. If lions and tigers see that their prey has noticed them approaching, they generally lose interest in that prey and try to find another potential meal.

Contemporary humans learned the benefits of eyespots and began to use them when dealing with potential attacks from a wide array of dangers, from the attacks of a tiger to the attacks of swooping birds. Here are two points from the list of safety precautions you can often find in Australian parks against swooping birds:

- “Draw a pair of eyes and attach to the back of your hat or bike helmet”
- “Wear sunglasses on the back of your head”

These points are about the use of artificial eyespots on the back of the head. Although these are safety suggestions for bird attacks, the same safety mechanisms work effectively against much more dangerous opponents, man-eating tigers. These safety mechanisms, which have lasted millions of years, are also the reason why cheap plastic masks worn on the back of the head became quite effective in deterring the man-eating tigers of the Sundarbans national park from attacking humans.

According to consensus, humans do not have any natural eyespots, and neither do apes. As a matter of fact, eyespots are characteristic of much more primitive animal species, such as butterflies and many other insects, some reptiles, and some birds. However, we must remember that eyespots are also present on one of the most evolutionarily advanced animal species – big cats. Many big cats, as we already mentioned, have eyespots on the back of their ears, and most important for us, the big cats, our most common natural predators, are very sensitive in noticing eyespots on others. Humans, on the other hand, are very bad in noticing eyespots, and some struggle to see the eyespots on big cats even when they are told about this.

Big cats have eyespots on the back of their heads; these are their defense tools from an attack from behind. These eyespots are also clearly seen from the frontal side when cats have their ears flat on their heads (Leyhausen, 1960). There is a possibility that, with this flattening of the ears on their head, cats show their eyespots to any antagonists in front of them. If you view the face of a big cat with flattened ears, you will notice that their false eyes (black eyespots on the back of their ears) are clearly displayed, and are bigger and spaced much wider that their real eyes. This display of bigger and wider set eyes may trick an antagonist into believing that the animal in front of them is bigger than it really is.

We have touched on how big cats all have eyespots and how they can use them for defense from attack both from behind and from the frontal area. However, not a single scholar has written that humans may have eyespots, until I proposed in my 2011 book that we do have eyespots, but we fail to notice them for two reasons:

(1) Humans are generally bad at noticing eyespots; and, more characteristically,

(2) Because we only have them when we are… sleeping.

If you have a family member with well-defined eyebrows, ask him (or her) to close their eyes, and look at their "sleeping" face. You may notice that the eyebrows, arched upwards, and the eyelashes, arched downwards, form a quite visible oval – eyespots on the "sleeping" human face. Or, alternatively, you can look at photos of sleeping human faces.

It is true that it is not easy for humans to notice the resemblance of human eyebrows and eyelashes to the eye. Because we are not by nature a predator species, we are generally bad at noticing eyespots. But we need to remember that eyespots on our face were not designed by the forces of natural selection for humans to notice. They were designed to be noticed by big African predators, particularly from the cat family, and cats are particularly good at recognizing eyespots.

I suggest that when our hominin ancestors started sleeping on the open savannah, those individuals with longer and more arched eyebrows were less attacked by prowling big cats, since it seemed to predators that our ancestors were still, in sleep, looking at them. Generation after generation, individuals with longer and more arched eyebrows and long beautiful eyelashes survived. Of course, after human stopped sleeping on the open savannah, the pressure to have nicely arched eyebrows and long eyelashes disappeared, but we still admire faces with clearly defined and arched eyebrows and long eyelashes.

According to the generally accepted view, the main function of the human eyebrow is to prevent moisture, mostly salty sweat and rain, from flowing into the eye. Desmond Morris (2008), discussing the possible function of the eyebrow in human evolution, criticized this suggestion as non-effective, and suggested that the primary function of the eyebrows was to signal changing moods (see also Godinho, 2018). There is no doubt that eyebrows are excellent communicators of moods, but I suggest that their primary function in human evolution was as an anti-predatory defense at night. At night eyebrows were simply saving lives from the attacks of predators, which served as a big evolutionary pressure to develop and maintain them. At the same time, it is also possible that eyebrows might have had more than one evolutionary function.

Therefore, olfactory signals, designed for securing the nocturnal sleep of our ancestors, gradually enabled them to move far from trees and start long journeys. Human body odor is powerful, and the patches of hair in the armpits and groin were the means to create more powerful body odor. The appearance of eyebrows (and eyelashes) provided another defense mechanism, eyespots on a sleeping face. Therefore, with the evening loud "concert" with communal singing and dancing before sleep, strong body odor that was spread with the wind (and remember, hungry prowling predators usually move upwind), and the presence of eyespots were all creating a multilayered effective defense strategy at night.

BEHAVIORAL SIGNALS

An aposematic strategy of defense requires that audio, visual and olfactory signals are obligatorily reinforced by behavioral signals (we are still talking about the primary defenses). There are a few characteristics that aposematic species are set to follow. The most important characteristic is that aposematic animals should not run away when confronted by a predator. Instead of running away, aposematic animals stand their ground and try to intimidate the potential predator with the display of audio, visual, olfactory, and behavioral signs.

Do Not Run! Aposematic Freezing, "Do not run!!!" This is a first universal message to everyone who suddenly finds himself (or herself) in dangerous proximity to a predator. Popular belief, that it would take a lot of courage not to run away when you see a predator, is not correct. Usually, people in life-threatening situations get frozen and do not move, even if they want to. Although some still may try to run away in a state of panic, but the more natural (and often life-saving) response, also instinctive, is a *freezing response*. Fortunately, our instincts formed during millions of years of interaction with lethal predators give our body wise advice, the strict order not to move. So, the freezing instinct that overtakes most humans when they find themselves near a lion or a tiger (or an armed criminal), is in fact a life-saving behavior. At least, in most similar cases this advice has been good for our survival.

Quite amazingly, the life-saving potential of the freezing response is still unacknowledged by the scientific community and lay public. At the same time, other versions of the freezing response are acknowledged:

> "Some animals stand perfectly still so that predators will not see them. Many animals freeze or play dead when touched in the hope that the predator will lose interest." (Wikipedia, Fight-or-flight response)
>
> "Freezing behavior or the freeze response is a reaction to specific stimuli, most commonly observed in prey animals. When a prey animal has been caught and completely overcome by the predator, it may respond by 'freezing up' or in other words by staying completely still." (Wikipedia, Freezing Behavior)

As we can see, two different types of freezing are mentioned: one can be called "cryptic freeing," aimed at remaining unnoticed by a predator, and the other can be called catatonic freezing (or "passive freezing").

Humans also often react to imminent catastrophic danger by freezing, which is sometimes is seen as a serious disorder:

> "Of the various action disorders, cognitive paralysis leading to 'freezing' behavior or catatonia in the face of danger is the most serious, as it prevents any survival response during the impact phase of the incident … Common speech describes such behavior in terms such as 'struck dumb,' 'petrified,' and 'frozen stiff.'" (Leach, 2016)

But what Corbett mentions in the final scene of the story "Robin" is a very different type of freezing, neither cryptic nor catatonic (passive) freezing. This is a third version of freezing that I would call "aggressive freezing," with a very different message to the predator.

If passive freezing sends the message to the predator "I am yours, I am not running away, and I am not fighting back, so there is no need for violence," "aggressive freezing" sends a very different message: "I am not running away because I am not afraid of you. I am warning you that if you come closer, I will fight you, and you will regret your decision to attack."

I would suggest using the term “aposematic freezing” for this kind of aggressive freezing. Such freezing is an important part of the defense strategies of aposematic animals (skunks, hedgehogs, porcupines, venomous snakes), who famously do not run away at the approach of predators.

Secondary defenses in early human evolution, and changing defense into an attack

Time to discuss human secondary, “real” defenses. Many secondary defenses used by aposematic animals, such as venom, stings, spikes, horns, and canine teeth, are not applicable to human ancestors. Apart from these obvious means, aposematic secondary defenses could be using sharp teeth, a big body, oversized antlers, or simply the overaggressive character of the species (like badgers or Norwegian lemmings that are not shy to attack even approaching humans).

To find out what did human ancestors used as the secondary defense, we might remember Paul Weldon’s description of human secondary defenses: “…large body size, agility, vigilance and the capabilities of deploying projectiles and other weapons and/or marshalling group defenses” (Weldon, 2018; Cf Schruth, in this volume). I fully agree with Weldon’s suggestion that the effective use of projectiles must have been the key factor of early human secondary defense.

The importance of the human ability to throw stones and other projectiles with a great force is widely known (e.g., Isaac, 1987), and it is rightfully acknowledged as the key evolutionary factor that formed the human body, particularly the male upper body (e.g., Longman et al., 2020). The only correction that I would like to make to this idea is to shift the initial aim of throwing from *hunting to defense* from predators.

If we make a careful comparison between the hunting throwing and defense throwing strategies, we will see that defense throwing was much more effective than hunting throwing for our ancestors. There are many reasons for that:

- The distance is much closer in defense throwing. When an attacking animal (for example, a lion) is approaching you, it is your choice when to throw the rock. The later the throw, the closer the target, the deadlier the mechanical result. On the other hand, when you throw for hunting, the target (for example, an antelope) tries to stay clear of you, and getting closer to the prey is not easy;

- It is much easier to aim accurately and hit a target in defense throwing, simply because the target is running towards you. In hunting throwing, the hunter is approaching the prey, most likely, from the back, in order to remain unseen. Also, upon the commencement of hunting throwing, the target might start running away from the hunter. These two factors make hitting the target in hunting throwing much more challenging;
- Defense throwing is also more effective because it has a better chance of striking vulnerable parts of the body. When a target is running towards you, the most likely place a thrown rock will hit is the head. In hunting throwing, when the prey is generally running away from you, the most likely place to strike is the hind quarters;
- The size and the weight of the thrown missiles can be drastically different in defense and hunting throwing. Much larger rocks can be used in defense throwing, as the distance required to make an effective and realistic shot is much smaller. So, unlike more distant hunting throwing, where the best sized rock ideally should be less than 0.3 kilo, much larger rocks can be thrown in defense throwing;
- In defense throwing, when an attacking animal is coming close to the point of contact, a thrower can lift and throw a much bigger single stone using both hands, which greatly increases the size and the weight of the missile used. A close-range overhead throw of a much bigger rock would increase the damaging force of the hit dramatically;
- In defense throwing, when a target is running towards you, the speed of the running animal augments that of the thrown rock, in the same way the collision of two oncoming cars is more forceful than a back-front collision. Similarly in hunting throwing where the target is usually running away, the impact of the thrown rock is less;
- We can add a psychological factor as well. You would use the full strength of your body, and possibly even the hidden reserves of your “supernatural strength” in the moment when an attacking lion is running towards you. Hardly the same desperate supernatural force will come to your aid when trying to hit an antelope for dinner.

The conclusion is clear: defense throwing is much more effective than throwing for hunting. Therefore, I suggest to shift our attention from hunting throwing to defense throwing. Humans were most likely small-time hunters, but at the same time, they were the kings of scavengers, or apex scavengers. On one hand, it was extremely difficult for early humans to kill a decent sized pray for the whole group; at the same time, in the context of defense throwing, which would occur when early humans tried to chase away the prime hunters via aggressive scavenging, our human ancestors could obtain a more regular protein-rich diet.

As we can see, the throwing ability that initially started as a defense strategy against big predators in Africa, was turned into an attacking strategy against the same predators (primarily the lions), but this time in chasing the predators from their kills. This was the major shift in the life strategy of early humans, so far totally neglected in scholarly literature. Most likely, although early humans at first avoided lions, their natural predators, later, after finetuning their audio-visual-olfactory intimidating display (AVOID), they started attacking and chasing lions off after the kill was made. So, instead of avoiding lions, early humans started searching (and following) lions, as humans became active “vulture-searchers” in order to know about the scavenging opportunities on the open savannah. This must have been the final step away from the patches of trees to open terrain.

Cannibalism as a predator defense strategy. An important addition to the behavioral characteristics of early humans is the widespread tradition of cannibalism (White, 2001). In 2011 I suggested that cannibalism was a major element of early human defense strategy.

Jim Corbett (1944: Author’s note) was arguably the first who noticed, that when human corpses were left unburied after major epidemics, cases of predator attacks on humans increased drastically. Even the slave route across East Africa (with a high mortality involved) was connected to the appearance the infamous Tsavo man-eaters at the end of the 19th century (Waltl, 2016).

William Arens (1979) entirely rejected this shameful legacy from human history, as a gross lie and exaggeration, created by European colonizers, but this position became untenable in the light of increasing contemporary knowledge. To start with, cannibalism had a very wide distribution throughout human history around the world as a ritual practice (White 2001).

Symbolically, arguably the first anatomically fully human bones from about 200,000 years ago displayed signs of cannibalism. In Britain cannibalism was practiced until about 2000 years ago.

Another fascinating fact of deep-seated human cannibalistic aspirations is that we often overlook the ubiquitous use of words describing cannibalistic behavior as the highest expression of love and affection. When we express our excitement on seeing a cute kitten, puppy, or baby, we often declare we want to eat them. And as much as I have enquired of people from various cultures, I have found that such expressions, linking cannibalistic behavior with utmost love and affection, are virtually universal to potentially all cultures and languages.

This fact goes well with another fact. In some cultures where cannibalism was practiced, the act of consuming someone's flesh was considered an expression of great respect and love for the deceased. Cannibalizing worshipped figures (both human and animal deities) for religious reasons is another widespread fact. Even the mystery of Christian Eucharist (Holy Communion), in which members of a congregation symbolically consume the flesh and blood of Jesus Christ, is a reminder of the wide practice of cannibalism in human prehistory.

I suggest the reasons for cannibalistic behavior emerged from our long past evolutionary history, and that our contemporary aversion is the gross misunderstanding of the real reasons behind cannibalistic behavior. Corbett believed that when predators (like leopards) have easy access to the corpses of deceased humans, they quickly get used to the new food, and when access to the free food supply is cut off, they start attacking live humans. Corbett discussed two cases of the most prolific man-eating leopards in India in the first half of the twentieth century, the so-called Panar and Rudraprayag man-eating leopards, both of which he killed. They had eaten 400 and 125 humans, respectively, and were killed in 1910 and 1926. And both had made their appearances after deadly epidemics. The Panar leopard followed a severe cholera epidemic in the first years of the twentieth century, and the appearance of the more famous Rudraprayag leopard in 1918 followed the disastrous "Spanish Flu." To understand the reason I am talking about, let us remember that although there are many cultural options to deal with human remains, cannibalism was the earliest available and virtually only option for our ancestors. Simply speaking, for millions of years our ancestors had only two options: to eat bodies, or not to eat them. In the short term, if you do not eat the body, predators will eat it – goods, such as food, never go to waste in nature. You might think this does not matter since the person was already dead, but it does matter in the long run, because, as Corbett proposed (and was confirmed by later studies of tigers and lions), if predators can easily obtain and eat human/hominin corpses, there is a good chance that they will become habitual man-eaters (Waltl, 2016, see also in this volume).

It is crucial to remember that I am not suggesting that hominins were killing and eating fellow hominins, as suggested in Dart's "killer ape" hypothesis. Instead, I am proposing that hominin groups were co-operatively fighting predators, and when any of them was killed by a predator, the hominins collectively attacked hungry predators to reclaim the dead body. And then the reclaimed body was cannibalized in a ritualistic manner. To fight deadly predators for the body of a fallen group member, and then to ritually eat the body as an act of love and respect, has totally different evolutionary and moral overtones. Our distant ancestors are getting undeservedly bad publicity for their habit of cannibalism (Jordania, 2022). They loved their fallen friends, were ready to give their own lives to defend them, and to reclaim their bodies in the event they were killed by predators, unaware that with seemingly futile dedication they were saving their own lives and those of their descendants.

One more important detail must be mentioned. At least some cultures have another reason for cannibalism. This reason was the opposite: hatred and the desire to fully annihilate an enemy. In many traditional societies where cannibalism was practiced, both reasons were valid. People ate their slain enemy with a different feeling than eating their own, much-loved tribe member. This is the natural difference between endocannibalism and exocannibalism. At the same time, from the view of cannibalism as a defense strategy from predators via "predator education," both reasons are valid, as it is important not to leave any bodies available to predators, whether those of friends or enemies. So, all the possible reasons – love for kin, or hatred for the enemy, or a desire to acquire their strength by eating them – were beneficial to eliminate the available human bodies to predators.

According to the Encyclopaedia Britannica, "There is no one satisfactory and all-inclusive explanation for cannibalism. Different peoples have practiced it for different reasons, and a group may practice cannibalism in one context and view it with horror in another" (Encyclopaedia Britannica, Cannibalism). I suggest, that although practices of cannibalism were in use for various reasons in different regions throughout human history, this practice came from a single powerful evolutionary reason and was favored by the forces of natural selection. The reason was eliminating the presence of hominin and human dead bodies in the environment, so that predators did not have ready access to corpses – a very potent reason for the practice of ancient cannibalism.

CONCLUSIONS

The evolution of human defense strategies started as soon as human-chimpanzee common ancestor descended from the trees, initially, by adhering to an aposematic defense strategy, first by not stopping singing, then adding rhythmic synchrony, dissonances, body percussion, gradually leading to an altered state of mind (battle trance), and gradually developing a full set of aposematic signals in every modality:

Audio signals: Apart from singing in synchrony, using dissonant harmonies, clapping hands and hitting stones, stomping, and yelling in low range voice;

Visual signals: Erect bipedal "threat display" became the permanent mode of locomotion; also, long legs and long tightly coiled head hair were developed; colors (natural color changes related to anger, and cultural use of color substances, first temporary, then durable) for body-painting, plus threatening coordinated body movements (precursor of dance, primordial Haka).

Olfactory signals: Great number of sweat glands, resulting in the strength of body odor, with patches of hair in the underarms and groin to make the odor more effective, helped to educate predators, and particularly, ensure nocturnal sleep security in the open.

Behavioral signals: Going into battle trance, developing the freezing instinct in critical moments, slow and awkward movements, and ritual cannibalism to deny predators easy access to the human corpses were all designed as a part of effective predator education. After early humans developed effective defense strategies, they started gradually using their increased defense potential for aggressive scavenging sessions as well, becoming an apex scavenger of the African Savannah (O'Bryan, et al., 2019; Shipman, 1986; See also Johnsingh in this volume).

Humans started following lion prides, registering their kills via vulture watching, and attacking feasting lions at their recent kills. The stratigraphy and timelines of human and lion distribution over the world suggests that early humans were following lions (Jordania, 2014). When did this happen? Most likely, Homo habilis was already well equipped with the aposematic signals and crude projectiles. For example, see this: "…microscopic analyses indicate that cut marks on some bones overlay predators' teeth marks, showing that the hominins arrived afterward. How they got meat away from scary scavengers is anyone's guess" (Welker, 2017:149). I believe we can answer this question by proposing that this became possible by using a potent aposematic strategy, turned from defense into an attack.

The idea of Louis Leakey (1967), revolutionary for its time, faces a controversial fact that humans as food do not have any unpalatable components for any predators. Paul Weldon's idea (2018) seems to be closer to reality, although it also does not consider that aposematism is virtually never advertised through only one or two modalities (in Weldon's case – smell and aggressive behavior), but a combination of every available modality, including visual and audio. And as we could see, human ancestors had a rich variety of visual and audio aposematic signals. In fact, humans, as a species, display all the elements of an aposematic species.

And finally, even today, humans retain many features of aposematic animals, from individual behavior to the behavior of various human groups, and even nation states, where aposematic tactics play a major, sometimes a leading, role. The aposematic nature of humans is a powerful legacy of our evolutionary history, and its serious study might become one of the leading topics of evolutionary biology and evolutionary psychology.

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The Defense Potential of Music and Trance According to Ethnomusicological Materials from the Indonesian Province of Aceh

Margaret Kartomi (Australia)

As Bruno Nettl and Joseph Jordania have shown, music in various societies around the world has the potential to help humans defend themselves, whether in everyday life or during a state of war.

This is especially the case in societies with a history of war who still honour their ancestors, such as in some villages that still practice a form of Sufi Islam in the province of Aceh, in Indonesia's extreme northwest.

This article describes Aceh's centuries-old form of worship and self-defence called daboih (A.) or dabus (Ar., literally 'awl'), performed by scores of men aiming to reach a state of ecstatic union with Allah and invulnerability (ilmu kebal) under the protection of a religious leader known as a kalifah, kalipah, or rifa'iyyah.

Like his ancestors, the khalifah in the performance described below (in December 1982) possesses three kinds of esoteric knowledge as well as deep religious conviction:

(1) the knowledge of invulnerability (ilmu kebal),
(2) knowledge of the power of drum music (ilmu rapa'i A.),
(3) and knowledge of war (ilmu perang).

Daboih has long been performed on military occasions as a psychological weapon before going into battle, but also as a competitive game in times of peace.

Daboih originated in one of the fraternities of Islam known as Rifa'iyya, a Sufi order founded by the mystic Rifa'i who died in 1153 CE. The fraternity originated in Arabia and was once strong on the Deccan in India, as well as in parts of Aceh, though few participants in Aceh today know of the Rifa'iyya connection.

The religious idea behind daboih and other similar Sufi rituals is that ultimate truth can effectively be attained by losing one's identity through group exercises while performing or listening to appropriate frame drum and vocal music, and reaching a trance-like state of 'religious concentration' or altered consciousness, including a state of invulnerability (Kartomi 1992: 247-260; See also Wade, in this volume).

The performance I shall describe below began out of doors under a village banyan tree, with the participants (A. top daboih) saluting the kalifah with a low bow (sembah).

The kalifah was in charge of the whole assembly of performers and large audience. He wore a Muslim cap (peci) and carried an awl called a daboih, i.e. a 15 cm. long metal spike with a wooden handle.

After making sure all necessary preparations were complete, he gave the performers permission to start. Apart from controlling the drumming, the kalifah's role was to make sure the performers did not harm themselves as they entered a state of 'religious concentration,' by which time they were considered to have built up the quality of invulnerability known as ilmu kebal.

The squatting musicians played their large- or medium-sized frame drums (A. rapa'i) in unison for 20 minutes or so, and began to sway from side to side, smiling with religious joy.

They carried awls (daboih), krisses or rencong (A. Acehnese daggers) to be used for possible self-molestation if they became so inspired, as they aimed to reach a state of 'religious concentration.'

Some sang texts in chorus (A. selaweuet, I dike, Ar dhikir) based on repetitions of the '99 most beautiful names of Allah', which is a typically Sufi devotional practice. With joyful, smiling faces the men sang about Nabi David (the prophet David) whom they believe attained the highest degree of invulnerability.

A few stabbed their chests with their rencong or awls (A. daboih, Ar. dabus), and pierced the flesh on both sides of their legs and thighs and performed other self-mutilating feats without feeling any pain or after-effects, and mostly without blood-letting, due to their altered state of consciousness and feeling of invulnerability.

The men were divided into two 'sides' (Side A, Side B) of around a hundred frame-drummers each, from different villages. As they were performing in peace time, they played a competitive game.

They started by playing an initial repetitive rhythm together, after which each side tried to disrupt the concentration of the other side by playing a counter-rhythm that was out of phase with the originally established rhythm.

Eventually Side A managed to confuse Side B, though they tried several times to recover. However, in their confusion eventually they had to stop playing, as the crowd clapped Side A uproariously, and they lost the contest (although they hoped to win revenge in the next contest).

The kalifah's knowledge of invulnerability and ilmu rapa'i not only allowed him to protect the participants while in an altered state of consciousness but also to use his ilmu perang (i.e. knowledge of war), for traditionally it was the kalifah who made the final decision about whether village fighters would go to war or not.

They believe that the kalifahs inherited their skills from David who defeated Goliath with his knowledge of invulnerability, as well as the skills of Ibrahim (Abraham), the prophet who was expert in the use of fire.

The ritual use of fire among Sufi fraternities is restricted to Rifa'iyya devotions (Hughes 1885: 705), as in daboih. However, on this occasion, no fire was lit in which to heat up the awls for self-molestation, as in some other performances, especially during wars.

Daboih is still performed to this day in Aceh, but not in a war setting, as the province is currently at peace. However, its war-oriented form was performed successfully at times during the Aceh War against colonial Dutch troops in 1873-1945 and by fighters in the separatist Free Aceh Movement (Gerakan Aceh Merdeka) guerrilla force against the Indonesian Army (Tentara Nasional Indonesia/TNI) stationed in Aceh in 1976-2005 (Kartomi 2010: 452-483).

Their performances provide evidence that the ancestral practice of mass frame-drum playing and choral singing of religious texts in some Sufi Muslim societies can lead to the perception of invulnerability in everyday life or in times of war, when it may encourage village fighters to go into battle if they are convinced that the enemy is threatening their very existence, and lead to the knowledge that they can sometimes win and survive, especially if their leader is a master of military surprises.

Another example of ancestral music serving as a form of self-defence in Sumatra is the vocal repertoire sung by tiger shamans to protect themselves while praising and enticing a marauding tiger to enter a cage set for it in the forest (recorded in Solok, West Sumatra in 1972).

Despite the disapproval of some orthodox Muslim leaders, shamans still sing those ‘songs to attract a tiger by’ (dendang marindu harimau), though they originated in Animist times before the conversion to Islam. The shamans perform the songs with great respect for the tiger in freely ornamented chant-like melody set to beautiful poetry and accompanied by an elaborately ornamented bamboo flute part in a prolonged series of tiger-capturing rituals performed in a trance-like state (Kartomi 2012: 27-41).

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The Evolution of Conspicuousness in Early Humans: Could Camouflage Have Been Unnecessary or Impractical?

Wladimir Alonso (Brazil)

The ethnomusicologist and evolutionary musicologist Joseph Jordania proposed the intriguing hypothesis that primordial human evolution was shaped by the incorporation of a set of conspicuous features (like dancing and polyphonic singing to prepare for and trigger a coordinated attack) that turned fearful tree-living monkeys into assertive, erect, and noisy kill stealers from lions (2011).

In the biological world it is not contentious that bright colors and other conspicuous features in other sensorial dimensions (e.g. acoustic, olfactory, tactile, electrical) can provide several advantages, such as sexual, warning, species recognition or territorial display. But those advantages of conspicuousness are, in most species, canceled out by the generally much more pressing costs related with higher detectability to predators and/or prey. In earlier works, I proposed that there are basically two circumstances when the selective pressures for camouflage in predators and prey are relaxed: (1) The “Carefree World” (Alonso, 2016) occurs when camouflage is not essential, for instance found among non-predator species that possess effective defenses against predators (such as the strong macaws’ beaks and the flight abilities of hummingbirds); (2) The “Hyper-Visible World” (Alonso, 2016, 2015) second-case scenario is found in diurnal mobile fish of coral reef communities, which swim in clear waters against highly contrasting and unpredictable background, and therefore are not able to reduce their signal to environment background noise.

Which of those two circumstances could better explain that our early ancestors could survive and thrive despite being quite conspicuous (in many sensorial dimensions) in their new savanna environment? We need to consider that those small hominids not only were at a physical disadvantage relative to their predators, but also at a technological stage that could not produce highly effective weapons against them. Therefore, they could certainly have made good use of olfactory, visual, and acoustic camouflage. To some extent they probably achieved some degree of it using behavioral strategies (e.g., hiding downwind, using cryptic pigments, avoiding making noises when they were off guard against predators). But it seems clear that, to those hominids, camouflage possibilities against predators were very limited, and remained so until the present (if we are safe from lions, wolves or bears, in general, that should not be credited to our ability of concealing our presence in our habitats). And early hominids also did not possess any obvious weapon to neutralize putative predators (as the beak of macaws or the speed of hummingbirds do). Therefore, “Carefree World” does not seem to have been the reality of our early ancestors when facing the dangers of predation.

This leaves us, therefore, with the scenario in which most of the time early hominids could not hide. No matter how much concealing pigment they’d use, how sophisticated their decisions of movement based on wind direction, or how silent they tried to remain, they were easily detectable by predators and potential prey. They were, therefore, in an “Hyper-visible” world. This reality imposed a selection pressure in two directions: first, in the development of sophisticated social coordination (as discussed in the origins of music by Jordania, 2011; cf. Fitch & Zuberbühler, in this volume) to mount collective defensive, hunting, and martial strategies; and second, the negation of the possibility of camouflage in many situations liberated humans to evolve culturally and biologically to newer and broader features of consciousness (some of which might have even been weaponized, as suggested by Jordania).

Nevertheless, and given the behavioral sophistication of humans, we cannot place them in a single point landscape of sensorial versus ecological constraints on colouration that animals can develop to answer the predatory-prey pressure, but in an area mostly within the Hyper-Visible world and, also touching the camouflage region, whenever circumstances allowed it.

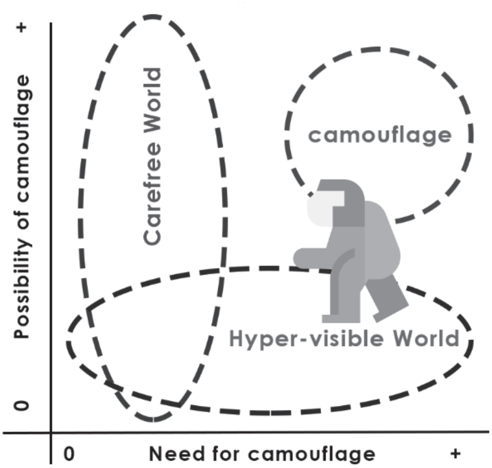

Figure 1. Possible place of early humans in the landscape of constraints on colouration that animals can develop to answer the predatory-prey pressure. The “Need for camouflage” axis refers to the selective pressures that drive camouflage. Modified from figure 1 from. (Alonso, 2016) by adding the icon (credit: Freepik) of an early hominid the relevant area of the diagram.

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Intrinsic and Semantic Aposematism: Two Concepts that Mirror Two Evolutionary Paths

Wladimir J. Alonso (Brazil), **Joseph Jordania** (Georgia/Australia)

The evolution of aposematism presents an evolutionary conundrum not solved until this day (Rojas, Valkonen, and Nokelainen 2015): high visibility by virtue of bright colours and patterns (as well making sounds and/or emitting smells) implied that potential prey were, first of all, easily detectable to predators. Predators could eventually learn that those signals meant danger – but usually only after causing major damage to the aposematic individual. All hypotheses that had been proposed to explain the evolution of aposematism had to assume at least one non-parsimonious step at some moment of their narrative. There are several problems in the solutions provided until now (Coyne, 2010). They had to assume, for instance, that two critical unrelated adaptations happened simultaneously or that benefits of the aposematic colour were not optimized by the possessor of the feature itself, but by kin who shared the gene for the aposematic display (which is immediately prone to cheating strategies; [Alonso, 1998] like having the aposematic colour without the defensive feature that legitimises it).

Here we propose that the evolution of aposematism could have developed without the need of extremely fortuitous and complicated events. In fact, its emergence multiple times in very different clades should warn us against convoluted evolutionary explanations. Our proposal rests on the premise that we should not assume more than one adaptive change at a time, which, as we will see, is of special importance in semantic aposematism. The adaptive aspect is also of the utmost importance to provide parsimony and plausibility in an evolutionary sense. For this we should expect a positive (or at least neutral) benefit to the “signal generator” (the aposematic, or aposematic-to-be), and simultaneously a positive (or neutral) benefit to the “signal receiver” (the potential aggressor).

Evolutionary route of "(semantic) aposematism"

Semantic aposematism covers what has traditionally been known to behavioural ecologists under the term "aposematism," in which the signal (for instance, black and yellow stripes in wasps) is not the weapon itself (which is, in the case of wasps, the sting and venom). The bright colours of butterflies, frogs, wasps and coral snakes are not the danger itself – the colours do not hurt anybody. Those colours, in essence, are pure information that aims to convey a semantic meaning ("stay away") for the target audience. In semantic aposematism, the weapon that gives legitimacy to the signal is a completely anatomical and functional structure of the signal itself.

The proposed evolutionary route (based on a fictitious example) could be as follows:

1. A species "S" develops resistance to eating a plant that is usually unpalatable or poisonous to many organisms (including predators of "S") by accumulating and isolating the toxin in internal compartments.
    1. Impact on species "S": access to new food resources to the insect.
    2. Impact on predators: it starts to be a bad experience preying on "S"
2. Selection of predators to identify and avoid members of species "S".
    1. Impact on species "S": just by having some distinctive features "S" starts to be a "signal generator" of information about danger, and it starts to be less attacked by predators.
    2. Impact on predators: By becoming "signal receivers" of information about danger, predators enhance their diet quality by preventing ingestion of toxin carriers.
3. Selection of "S" of several features that enhance identification by predators
    1. Impact on species "S": even lower attempts of predation
    2. Impact on predators: it becomes constantly easier to avoid attacking a poisonous species.

The result is that "S" becomes an aposematic species in which its danger to predators is expressed in features that are not themselves dangerous, but have a meaning (hence the term semantic in "semantic aposematism") to the interested audience.

Evolutionary route of the "intrinsic aposematism"

The canines of carnivores, the horns of bovids, the spines of sea urchin and the big size of elephants, whales or gorillas are both the weapons and the signals that convey quite convincingly the meaning "stay away" (cf. Schruth in this volume). These are not traditionally considered examples of aposematism, something one of us has already argued against on several occasions (e.g., Jordania, 2023, 2011). Here we will denote this sort of aposematism as "intrinsic aposematism" and also, provide an evolutionary scenario for its evolution – which is, actually, much simpler than for the semantic aposematism, as we will see.

1. Some animal species "I'' males develop antlers to fight for access to females by hardening and protruding some part of their upper skull.
    1. Impact on species "I": higher number of mates due to displacement of adversaries and, as a by-product, also a higher survival rate when faced with the attack of predators.
    2. Impact on predators: it starts to be a bad experience preying on "I", as those same antlers can hurt predators
2. Selection of predators to identify and avoid members of species "I".
    1. Impact on species "I": just by having those antlers "I" starts to be a "signal generator" of information about danger to predators, and it starts to be less attacked by them.
    2. Impact on predators: By becoming "signal receivers" of information about danger that those antlers present, predators lower the danger of attacking an animal with mighty defences.

The result is that "I" becomes an aposematic species in which its danger to predators is expressed in features that are themselves dangerous (hence the term semantic in "intrinsic aposematism") to the interested audience. If those antlers are not enough to deter predation, they can reinforce signals with other aposematic channels. But we also have to take into account that, once predators are very clear that they should not attack a species, for that species all the evolutionary pressure for camouflage is suspended:

they would be in what one of us termed a “carefree world” (Alonso, 2016). And then evolution is free to become more conspicuous, and use skin colour patterns, odours, sounds for other purposes (e.g., species recognition, sexual selection).

Another possible factor for forming an aposematism is dietary conservatism, or neophobia among the predators. In the initial experiments of checking Wallace’s idea of “warning colouration,” held by John Weir (Slotten, 2004:263), chickens proved this by rejecting perfectly valid, but brightly coloured food. Some recent studies also confirm the validity of neophobia as the potential reason for starting the phenomenon of aposematism among various prey species (Marples et al., 2005).

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Introduction of Hominids to the Eurasian Continent and Phenotypic Variations from the Point of View of Population Ecology

Gigi Tevzadze (Georgia)

This is the first attempt to describe the settlement of hominids on the Eurasian continent and the origin of phenotypic differences by means of two concepts of population ecology: living area expansion and convergence.

I want to touch on two issues in my text. It may seem that they are not directly related to predators and prey, but, I assure you, they are.

1. The first issue is the so-called hominid migrations. According to current understanding, hominids migrated from Africa to the Eurasian continent and beyond, then later emerged hominids migrated, and so on. Today, when we talk about how the first hominids spread, we intuitively imagine the "great migrations," when groups of hominids move from one place to another.

However, the population ecology of animals does not know such events. If animal migration exists, it is mostly a seasonal migration (Kennedy, 1985) and not the so-called "resettlement."

Therefore, apart from our vague notions, there is no evidence that our ancestors migrated toward Eurasia. The fact that we find the remains of the first hominids scattered is in no way evidence of the "Great Migration," but rather the result of the destruction of artifacts due to historical and environmental conditions.

So, what are we dealing with? I think that simple population ecology is in order here: what happens when you find similar animals thousands of kilometers apart from the same source?

The reason is the distribution of animals of this species: that is, when their lives are not threatened and they successfully cope with natural enemies, they reproduce more than their habitat can support. Therefore, they expand their living area and occupy more and more territory.

I think it was also the case with the hominids: since they had no strong enemies because of their skills (even big cat predators), they multiplied and because of this multiplication they migrated to the Eurasian continent. This process continued for hundreds of thousands of years; then a new subspecies of hominids arose in Africa, crossed with the existing one, became dominant, and then it began to spread as well. Moreover, today there is already a solid theory that most subspecies of hominids existed together on the earth and interbred (Choi, 2022). As a result, through sexual selection, we got one more or less solid phenotype at a time, but this does not mean that they did not carry the genes of other hominids.

2. The second issue is the phenotype traits of modern Homo sapiens: why do we have different phenotype traits when we know that the vast majority of our genes are sub-Saharan African? I mean, why are we not all black when it is highly likely that all of our out-of-Africa Homo sapiens ancestors were black? Also, when we know that when they arrived on the Eurasian continent, they were immeasurably outnumbering the hosts?

Therefore, we have this kind of picture: a lot of Homo sapiens spread over the Eurasian continent and Oceania and interbred with the hominids they were hosting. But, even though their number was incomparably greater than the found hominids, their descendants developed the phenotype features of the host hominids and almost no phenotype features of the arrived Homo sapiens remained, even though today, for example, the percentage of Neanderthal genes found in Caucasians does not exceed 2-4 percent or a little more (Wei-Haas, 2020).

So, what are we dealing with?

In population biology, there is a process called *convergence*: it is a process when a less successful species or subspecies develops the phenotypic traits of a more successful species or subspecies, but remains genetically unchanged. Are we dealing with a similar process in the relationship between Homo sapiens and other hominids, particularly, their hosts on the Eurasian continent and Oceania?

Today, there are some Caucasians in whose genes we do not find any traces of the Neanderthal genome (Wei-Haas 2020), and at the same time, there are some sub-Saharan Africans who have Neanderthal gene traits (Price, 2020).

What do these facts tell us and how can we develop a hypothesis about them?

I. Hosts were more successful than newcomer Homo sapiens, so convergence occurred: Homo sapiens began socially (sexually) selecting hosts' phenotypic traits; this explains the fact that, although today's Eurasians have few hosts' genes, according to phenotype they do not resemble their initial and dominant genetic ancestors – Homo sapiens from Africa.

The presence of Neanderthal genes in present-day Africans can be explained by failed convergence: the ancestors of these people received Neanderthal genes, but failed to change phenotype; therefore, they were forced to go back, where their phenotype traits did not mean being socially unsuccessful. And finally, about hunting and relationship with animals: I think it is clear that one, if not the only, criterion for the success of hosts, from the point of view of newcomers on the Eurasian continent, was the relationship with animals; obviously, Homo sapiens must have been surprised by the tamed wolves and the rules of hunting, as well as by alcohol. I think these three signs are enough for all Homo sapiens to be desirous to carry the phenotype traits of hosts, both as groups and as individuals.

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Reasons for Man-Eating in Corbett’s Time and Today: “Wounds and old age”? A Comprehensive View on Causes of Man-Eating

Manfred Waltl (Germany)

1. Corbett’s “classical” man-eater

4. Head of the Champawat maneater: 'the upper and lower canine teeth on the right side of her mouth were broken . . . the cause of her becoming a maneater' (Corbett)

“A man-eating tiger is a tiger that has been compelled, through stress of circumstances beyond its control, to adopt a diet alien to it. The stress of circumstances is, in nine out of ten cases, wounds, and in the tenth case old age…. Human beings are not the natural prey…” (Corbett, Man-Eaters of Kumaon, Author’s note)

– This was the “classical” view in Corbett’s time: “wounds and old age.”

– Though Corbett shared this opinion, his view was already wider, as he acknowledged, what we today would call habituation (Mukteswar) or scavenging (Rudraprayag, Panar).

– More than half a century of research brings new perspectives. And the “world of the tiger” has changed too. It is no more the intact habitat with plenty of game, where only the disabled creatures were facing hunger and desperation. Habitat destruction can bring any tiger to similar situations.

2. Why man is not the natural prey

– Since the second half of the nineteenth century, man-eating is a comparatively rare phenomenon. This is an astonishing fact, as for a big cat, a lone and unarmed human being is an easy kill. The basic question is not, why individual animals become man-eaters, but why do all of them not regularly feed on humans (Kerbis-Peterhans, 2002; Mills, 2004; cf. Blake in this volume).

– There is obviously some kind of inhibition that prevents human beings from being attacked. But the question is: Was this always the case in human history, and what are the reasons for this inhibition?

– Tigers do learn, and through growing hunting pressure in the nineteenth century avoiding people became more and more important for their survival. But there always seemed to be a certain amount of basic inhibition as a result of the unorthodox and sometimes intimidating behavior of human beings. As a cooperating group, men were able to confront predators. So, from a certain and perhaps rather early point in human evolution (Homo erectus?), it looks like we were no more "normal prey" but serious competitors (McDougal, 1987; Jordania, 2011, 2014)

3. Traditional causes of man-eating in a wider context: The keyword "Hunger"

– Carrington Turner, a forest officer in Kumaon somewhat after Corbett's time, was the first to recognize that the term "hunger" is the summarization of all traditional roots of becoming a man-eater: Wounds, old age and scarcity of prey in unfavorable terrain (Turner, 1959). That the latter was not just due to the terrain but also to human encroachment and habitat loss was later added by Charles McDougal for the buffer zones of Chitwan NP (McDougal et al. 2004) and by Nyhus and Tilson for Sumatra (2010).

– A tigress with cubs has an additional problem in feeding her offspring. This was already mentioned by General R. G. Burton (1931) and Richard Perry (1964) and might explain why most of Corbett's man-eaters were females.

– In Africa hunger by prey scarcity caused by rinderpest or game-free zones to prevent rinderpest has been responsible for many outbreaks of man-eating in African lions, for example in Njombe and Tsavo (Peterhans & Gnoske, 2001).

4. Causes of man-eating beyond extraordinary hunger

Carrington Turner's idea was an important first attempt in systematizing causes of man-eating, but the following years also showed that the topic "hunger" alone was not able to explain all cases of man-eating, and there more factors have to be taken into account:

4.1 Man-eating traditions

– Although Corbett states that the cubs of a man-eater do not become man-eaters themselves, the situation can be different when elder cubs join in the hunting or when adults hunt and feed together.

– The duration of some conflicts suggests the idea of some kind of heredity or tradition (Sundarbans).

– For predators like lions that live in prides and have much more social interaction and cooperative education, the influence of tradition should be stronger than in the more solitary living tiger or leopard.

4.2 Scavenging on human corpses – man-eating as a result of ecological crises

– If there are human corpses, for example provided by epidemic forms of diseases, then predators can acquire a taste for human flesh by scavenging on them. This was the case, according to Corbett, with the Panar and the Rudraprayag leopard. The same can be said of human corpses as a result of floods and cyclones in the Sundarbans (Neumann-Denzau, 2006) or victims of war in Burma (Perry, 1964).

– Scavenging on dead human bodies provided by slave trade, epidemics and burial practices that gave easy access to these bodies could have contributed to the man-eating habits of the Tsavo lions (Peterhans & Gnoske, 2001).

– To avoid this, it might have been a "strategy of predator control" by our early ancestors to reclaim dead bodies or even practice cannibalism, so predators have no access to them (Jordania, 2011, 2014).

4.3 Habituation to human presence

– The "Sugercane Tiger" (Shukla, 1995): With the devastation of the forests and grasslands of the Terai, tigers adapted quickly and managed to survive in the extensive sugarcane crop bordering forests and villages. The growing familiarity with man caused indifference to human activities and the dilution of fear that might have triggered the outbreak of man-eating in the Kheri district near Dudhwa NP from 1976 to 1987.

-An important factor that encourages the habituation of big predators to human presence is reduced or non-existing hunting pressure in and around nature reserves that sooner or later makes wild animals learn that there is nothing more to fear from man. A less known but presumably extremely destructive man-eating by lions in Kruger NP, South Africa, of Mozambique refugees has been recorded by Robert R. Frump (2006).

4.4 Cases of mistaken identity – Never resemble a prey species

– Never resemble a four-legged prey species! (cutting grass, crouching, squatting, "call of nature"…). There was an experiment by Kailash Sankhala in the Delhi Zoo where he found that tigers start stalking as soon as they find a man in a bent position, but lose interest when he stands up" (1993; cf Blake in this volume).

– Never behave like a fleeing animal (running, cycling)! Predators like tigers or mountain lions sometimes chase cyclists (Byrne, 2002) or follow joggers (Deurbrouck & Miller, 2001). So, the impulse of "freezing" in front of a big cat can be interpreted as an evolutionary defense strategy to overcome the urge to flee (Frump, 2006) or as "aposematic behavior," a self-confident appearance showing the human not to be afraid (Jordania, 2011, 2014).

– Never behave like a sick or wounded animal! Abnormal behavior can give such signals to predators, including deranged and intoxicated human beings looking like easy prey (Peterhans & Gnoske, 2001; cf. Marshall Thomas in this volume).

4.5 The theory of unusual high aggression with the Sundarban tigers

– Despite the high frequency of human-tiger conflicts, man-eating patterns here do not seem to follow traditional causes, such as wounds, old age and prey scarcity. Besides scavenging on human corpses and man-eating traditions, an unusually high level of aggression was suggested among these tigers caused by the high salinity of the water, affecting liver and kidneys (McDougal, 1987, referring to H. Hendrichs). Although there is no proof for this salinity theory, it is still discussed as a possibility (Neumann-Denzau & Denzau, 2010).

– More convincing and less speculative for the probably enhanced aggressiveness of the Sundarban tigers seems to me to be the tidal environment in which they are forced to live. Lacking the appropriate trees should affect the marking of territories, making it less effective and short lived. It is not hard to imagine that such reduced intra-specific communication can result in a greater number of unintended encounters and more aggressive forms of confrontations.

4.6 The "accidental changeover" – a statistical approach

– A correlation clearly shown in the Sundarbans is between the number of attacks and the number of people entering specific areas. Man killing and the frequency of man-tiger contacts are directly correlated (Neumann-Denzau & Denzau 2010).

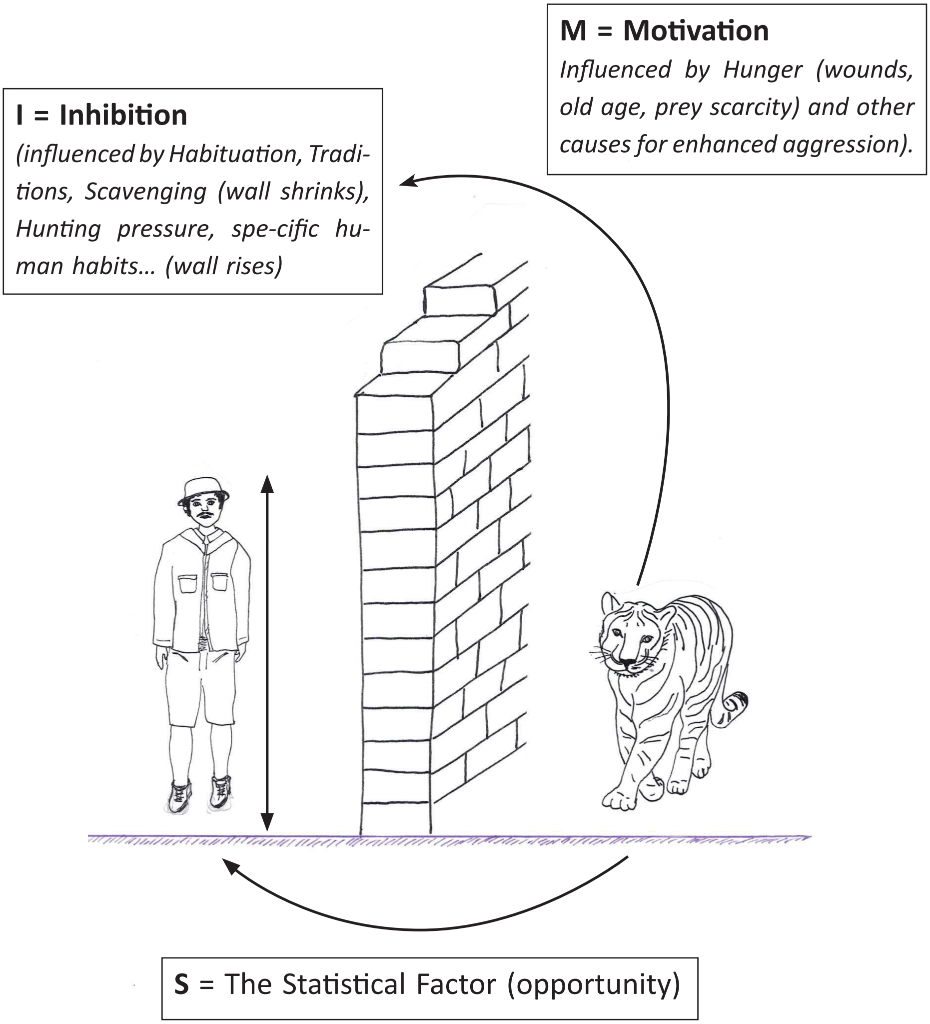
– There is no reason why such a correlation should be restricted to the Sundarbans. With the example of the Mukteshwar tigress, Corbett called the changeover from animal to human flesh in most cases accidental. And it is evident, that the probability of such accidental meetings depends – under identical conditions elsewhere – on the numbers of tigers and the number of people entering tiger habitat. The more human intrusion, the more accidental human-predator interactions and the more chances for a fatal accident that might be followed by a deliberate man-eating.

5. Man-eating as a "multi-causal phenomenon" within the bounds of inhibition and motivation – a comprehensive and systematical view

Was Corbett wrong when he wrote about wounds and old age as the main causes for tigers turning to man-eating? He was not, at least given the conditions of his time. That said, there is, of course, a wider understanding of the phenomenon today. We can look at the "stress of circumstances" in a more detailed way than Corbett could in his time. Man-eating in contemporary perspective is a multi-causal phenomenon, a view shared by many experts, such as Charles McDougal or Kerbis-Peterhans and Thomas P. Gnoske. They rightly concluded that not a single cause will guarantee, that a lion (or tiger) will turn into a man-eater, but a variety of causes will increase the likelihood.

But as far as I can see, no one has ever brought these causes into a systematic and comprehensive context that will allow assessment of probabilities and balance individual causes against others.

This is what I will try to do now with the following graphical overview:



Explanation of the graphic:

The causes for man-eating are divided in **two major categories** that reflect antagonistic forces affecting the behavior of a specific animal. The first category concerns the **MOTIVATION to attack**, the aggressiveness of a predator. In this category the major point is "hunger," be it a result of wounds, old age or prey scarcity. Other causes, too, might influence this amount of aggressiveness, such as perhaps enhanced intraspecific conflicts, as mentioned in the tidal area of the Sundarbans.

The second category is the **INHIBITION to attack**. There are factors that strengthen this inhibition, such as hunting pressure and specific human habits. Other factors, like habituation, scavenging on human corpses or learned traditions, lead to a decline of inhibition. And what could be seen as a third category but might be better described as beyond these categories is the **STATISTICAL EFFECT**, the opportunity that arises when the objects of a possible conflict do meet each other.

Looking at the graphic, you will see a **predator** (**tiger)**, a **human being** as a possible victim and a "**wall**" between them. The vector on the side of the predator indicates its **Motivation (Vector M)**. The height of the wall symbolizes the **Inhibition to attack (Vector I).** There are factors, that will increase the height of the wall, and others that reduce it. Facing a high wall, a predator will need extraordinary motivation and aggression to jump over, if he is able to do so at all. The human being on the other side will, in this case, be quite safe. But if, for some reason, the wall shrinks, medium or even low motivation would be sufficient. And there is the **Statistical factor (Vector S)** that reflects the chance of a meeting at a given time at a given place. With these three factors in mind, you can assess the likeliness of an attack and this is the quintessence of man-eating as a multi causal phenomenon.

Here is the explanation why, in many cases, even old, disabled and very hungry tigers will not become man-eaters (inhibition too high), while sometimes quite normal individuals can turn to this habit (if conditions favor low inhibition). When focusing on motivation, the amount of hunger and aggressiveness decides whether a given inhibition can be overcome. Within these bounds of motivation and inhibition, different conditions favor different decisions. Two contrasting examples will illustrate this:

a) High inhibition requiring extraordinary high motivation. This is the ***"classical man-eater"*** in Corbett's time. High inhibition caused by the high hunting pressure of the time could only be overcome by very high motivation. This usually was induced by extraordinary hunger, mostly caused by wounds or old age that prevented effective hunting. Unfavorable terrain sometimes added to such difficulties. But even then, only in rare cases was the motivation high enough to overcome the high inhibition. Sometimes accidental habituation lowered the inhibition (Mukteswar). But tigers that did not suffer from extreme pressure were – because of the strong inhibition – usually are quite harmless to humans.

b) Low to medium inhibition requiring only low to medium motivation. This seems to be the case with the ***Sundarban tigers***, in which the motivation might be called "medium." No extraordinary "hunger," but perhaps factors like increased intraspecific conflicts. But a medium motivation meets a reduced inhibition because of man-eating traditions and a practice of scavenging on human corpses, so the level of aggressiveness could be sufficient to overcome the lowered "wall." In some cases, even a low motivation not exceeding the normal level can be sufficient with an accordingly small inhibition. The ***"Sugarcane tigers***" may not have had any higher motivation and aggression at all. They can be quite normal animals under this respect. But because of the effects of habituation, inhibition is very low here, and man-eating might occur for some small reason or even just if opportunity arises.

6. Individual questions in the perspective of inhibition and motivation

6.1. Why do tigers usually attack in daylight and leopards at nighttime?

Corbett called it a general rule that *"tigers are responsible for all kills that take place in daylight and leopards … for all kills that take place in the dark."* But why is this the case? Leopards are much more accustomed than tigers to live in close vicinity to human settlements. Because of constant habituation to human activity, their inhibition to enter human dwellings at night is quite low, and a man-eating leopard is able to follow his human prey to the place where it spends the night, into the villages, sometimes even entering shacks and huts. But the leopard, as the smaller and more vulnerable predator, depends on an unexpected attack that makes it difficult for the victim to defend himself. When the enemy is a tiger, it is almost impossible for a lone and unarmed person to fight back, and there is no significant risk for the aggressor, be it night or day. For the smaller leopard, there is a considerable risk of getting hurt in an open attack, even if the victim is armed only with a stick or knife. So, the "inhibition" to attack during daylight for the leopard is higher. His "rational choice" is the night.

For the much stronger tiger the difference in inhibition between night and day is less relevant. But as an animal normally not living as close to human settlements (let aside special phenomena like the "sugarcane tiger") and therefore with less habituation to human activity, his inhibition to enter villages and houses must be considerably higher. So, the "rational choice" for the tiger is the daytime, when humans go out to cultivate their land, guard the livestock, or walk on forest paths to neighboring villages. This does not mean that the night will be safe when a man-eating tiger is around. If opportunity arises, a hungry tiger probably will not miss it. But he has learned that this opportunity will arise mainly during the daylight hours. So, it is also the "Statistical factor" used by the tiger in his favor by seeking human prey during daytime, having learned that this is the time he has the best chances to meet them

6.2 Why are man-eating tigers more often females and man-eating leopards more often males?

It has already been said that female tigers become man-eaters more often because of the additional difficulty a tigress has in feeding her offspring. Growing hunger in a female with cubs increases the **motivation** to attack (high Vector M). Concerning **inhibition** (Vector I), differences in male and female tigers seem to be negligible, since an unarmed human being is no match for either sex. So, with similar inhibition, it is the motivation that rules and makes the difference.

For the smaller leopard it is another story. Here the "**inhibition** to attack" a fully grown person for the even smaller female is higher than for the male, leading it mainly to weaker victims, like children. With the leopard, inhibition rules (high Vector I), in most cases overcompensating the effect of an increased motivation even in the female with cubs.

6.3 Why do seasonal changes exist in the frequency of man-eating?

For the Njombe prides, man-eating happened mainly during the wet season and stopped or was low during the dry season. The same was true of the Rufiji man-eaters in which the majority of cases occurred between November and January (short rains) and April and May (main rainy season). No deaths were reported in July and September, and only few in August and October (Baldus, 2004).

Regarding inhibition and motivation, the following explanation can be given: In the **rainy season** when the grass is high, the predator can come close to the places where man lives. This encourages habituation and enables unexpected attacks. So, "inhibition" decreases. In the **dry season**, there is less cover, less habituation and less opportunity for an unseen attack. Inhibition increases, and man-eating stops or declines. And there is also a different "motivation". In the **dry season** it is easier for the predator to hunt its natural prey, as the animals have to visit waterholes where carnivores lie in wait (low hunger – low motivation). In the **rainy season** the prey species are dispersed and well hidden. So at least under African conditions the rainy season is the more difficult time for predators (growing hunger – high motivation) resulting in increased man-eating activity.

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The Lion and the Moon

Manfred Waltl (Germany)

The full moon affects the mood and the sleep of many people. Often these effects are described as negative feelings of unrest and bad sleep. Based on studies by Craig Packer on lion attacks in south Tanzania this can be understood as the remains of an adaptive strategy of predator control in early human evolution. As the danger of lion attacks is significantly higher in the days following the full moon, it would be a survival advantage to take the full moon as a warning sign of upcoming danger. In an appendix we compare Packer's results with the observations of Jim Corbett in North India.

1. Human attitudes towards the full moon

Almost everyone has heard about people who are affected by the moon. Maybe even yourself. When the moon is full, these people complain about restless nights, have problems falling asleep, dream vividly or even suffer from sleepwalking.

Looking for an explanation, the first idea might be the connection between the level of brightness and the so-called sleep hormone melatonin. Darkness stimulates its production and therefore the tendency to fall asleep. If light falls on the retina, melatonin production is inhibited. Melatonin also has psychological effects. If the concentration is too high, it can cause negative mood, including depression. An unusually low concentration might boost unrest and feelings of stress.

But it seems that the effect of the full moon cannot be reduced to mere brightness. Humans from different cultures have long believed in a special and strong influence of the moon and even have aligned their everyday life and behavior with lunar cycles. Even in contemporary cultures people use lunar calendars to tell them when to plant, to harvest and which times are favorable to start diets or cut hair. You may smile about such strange convictions, but nonetheless you can ask whether there may be real effects by the moon on people and their emotions, effects that might have been be inherited and in times of early human evolution were important for survival.

There are many stories about the moon and its alleged effects. Though not undisputed, some studies seem to confirm this. They report a delay in falling asleep and shortened phases of deep sleep. In a study by the Institute for Demoskopie Allensbach, for example, 39 percent (50% female, 27% male) of the participants asserted that the moon had an influence on their sleep. Interestingly just one percent described this effect as a positive one. All the others were convinced that the full moon especially disturbed their sleep and that they felt more restless during this time (Allensbacher Berichte, 2005). If there indeed is such an influence, what could be the reason for it? Has it evolved in our emotional system for any sort of survival advantage? A new and interesting approach to this phenomenon comes from an unexpected angle. It was raised for discussion by lion expert Craig Packer on the basis of the observations of lion behavior in Tanzania.

2. Darkness and brightness as influences of lion behavior

Craig Packer wrote:

> For it is darkness … that gives the lions their courage around people. It is darkness that allows their superior senses to overcome whatever technological advances we might possess …. During the day, they remain hidden in the bushes, when pedestrians pass by, and lions will run like crazy if there is no cover… But there is nothing secretive about a lion's behavior on a moonless night. There is no skulking, no need to hide. The lion owns the darkness. Darkness gives them strength. (2015, p. 195)

In Packer's words they behave almost like a "different species" when encountering humans in the dark (Packer 2015:195).

To ensure their survival, early hominids had to adapt to lion behavior maybe in a similar way as the Kalahari Khoisan, who still live the traditional hunter-gatherer lifestyle of our ancestors (Marshal Thomas in this volume). These Bushmen hunt at night too, but, according to Packer,

> Only when the moon is above the horizon and bright enough for human eyes to detect shapes and movements. Without the light of the moon, say the Khoisan, the night belongs to the lions. So, they

> divide the night with the lions according to the phase of the moon. (2015, p. 195).

And in case of a lunar eclipse, they say: "That is just a hungry lion, placing her paw in front the full moon, stealing a little extra darkness."

Lions do not hunt and feed very successfully on bright moonlit nights. Often their presence is exposed before they are close enough for a successful attack. Alexandra Swanson from Packer's team measured belly sizes of lions in the Serengeti and the Ngorongoro area, which were significantly larger on the days close to the new moon and were thinnest at full moon. Belly size—and therefore the food intake—fluctuated with the phase of the moon (Packer et al., 2011:2). One could even make a joke that with the lion, a lunar calendar would be right in stating that the new moon would be perfect for starting a diet. But of course, this is not in the interest of the lion. Each day of growing brightness brings growing hunger, which reaches its maximum on the day of the full moon. One could assume lions might be the most dangerous on the night of the full moon. But is this true? How does it compare with the real number of attacks? To answer this question, Dennis Ikanda and Hadas Kushnir, two students of Craig Packer, have provided a very detailed documentation of such cases, following an outbreak of man-eating in Southern Tanzania.

3. The number of lion attacks in dependence of the lunar cycle

Since the 1980s, the Rufiji district in South Tanzania near the Selous NP has been notorious for lions that regard humans as part of their natural prey. This gained international attention because of a young male lion the local people called "Osama" after the well-known terrorist. It is said that this lion had killed and devoured 43 people. But it might have been also the work of other individuals, as the problems did not come to an end after destroying this animal in August 2004 (Baldus, 2009). Man-eating continued, and in the following years there were around 100 attacks each year. Similar problems were reported from the Lindi district, and so Dennis Ikanda and Hadas Kushnir visited the affected areas to document the circumstances of each case. Their documentation included age and sex of the victims and the exact date and time of day when the attacks had occurred. With these dates, Packer could compare them to the lunar cycle and look for a statistical trend. The following figure shows the correlation (Packer et al., 2011).

The figure shows the number of humans attacked by lions in the Rufiji and Lindi districts across the lunar cycle in one year. The vertical line shows the day of the lunar circle, the horizontal line, the time of the day between sunset and sunrise. The brightness of each cell is proportional to the percentage of moon's illumination. The number in the cell shows the annual victims with the italic numbers referring to attacks with the moon above the horizon and the bold numbers to the moon below the horizon.

Packer summarized his findings:

The vast majority of lion attacks occurred between sunset and 10 pm, and while the last few nights before the full moon would be the safest, the first few nights after the full moon were three-and-a-half times as dangerous. After enduring the bright evenings prior to the full moon, the lions were hungry, and they mostly attacked people on the return of evening darkness. (2015, 196f)

The night of the full moon is not the most dangerous time. To understand why, we have to look at the daily routine in rural Africa, which begins with the sunrise and terminates at about 10:00 o'clock in the evening. After that most people retreat to the relative safety of their huts. So, the crucial brightness that reflects the danger from lions is not the average brightness of the night, but the brightness in the time from sunset to 10.00 o' clock in the evening. And this strongly depends on the time when the moon rises. In the nights *before* the full moon this is before sunset. So, there is no absolute darkness in the first hours of the night. But *after* the full moon, the moon rises after sunset. Here the sunset is immediately followed by a time of absolute darkness, taking place at a time when humans are still active outside cooking, eating and talking. So, this is the situation: By the growing brightness before the full moon the lions became hungry, but in most cases were still discouraged from attacking by the light from the early rising moon. But from the first day after the full moon the situation tilts, and with the oncoming darkness the danger of an attack rises dramatically.

4. The warning of the full moon – a survival advantage in human evolution

What significance do these findings provide for human attitudes towards the full moon, as mentioned in the beginning? Especially as the time of the full moon itself does not bear any above-average danger? But even if the time of the full moon is not dangerous itself, it is for Packer “a portent of the darkness to come,” an unmistakable warning “that the risk of lion predation will increase dramatically in the coming days” (Packer et al., 2011, p. 2).

Our early ancestors always lived in close proximity to large, nocturnal carnivores and thus were exposed to the risks of predation that cycled with the phases of the moon. The most dangerous time was the darkest hours in the early evening in the days after the full moon. These were the days when lions were the hungriest after the preceding bright nights. And these were also the nights with the darkest hours immediately after sunset, when humans were still active and therefore exposed to predation. It would have been a big advantage for human survival to take the warning sign of the full moon seriously, to connect it with the following danger and to take action against it. This includes feelings of general cautiousness, alertness, light sleep and nervousness.

You can say of course that in the middle of Europe and other regions without big and dangerous predators, such adaptions have long since become irrelevant and far from being adaptive. The invention of artificial light also might have greatly reduced sensitivity to the lunar cycle. This is definitely true, but it would nonetheless be surprising, if, after hundred of thousands or even millions of years when our human ancestors shared the nights with lions, we would not deep in our emotional system “somehow sense the monthly dividing line between our time and lion time” (Packer 2015, p. 197). That people still react to the full moon with unrest, light sleep and a somewhat vague feeling of danger, might have its evolutionary roots here. For many of our early ancestors such feelings definitely saved their lives from real and deadly danger.

<u>Appendix:</u> How do Jim Corbett’s observations compare with Craig Packer’s study

(With Stuart Gelzer)

It is an interesting question, if Packer’s conclusions about lion behavior towards humans depending on the lunar cycle can be generalized and might also apply to other places and predators. There may not exist other studies as focused on this topic as Craig Packer’s, but it is nonetheless interesting to compare them with the observations of others. Jim Corbett comes to mind here. He dealt with many man-eating leopards and tigers in India, and though he did not collect such data systematically, he was a keen observer and might have left important details in his books. I am in debt to Stuart Gelzer of the Jim Corbett International Research Group for collecting such information dispersed in Corbett's books and letters. It is not the place here to refer to the findings in detail. There is a full article about this topic. Here is just the summary:

An essential requirement for generalizing Packer's study is that the lunar cycle must be the same all around the world. And indeed, it is. By definition – because it is the relative position of moon and sun to earth that causes the apparent phase of the moon – on the night of the full moon, the moon rises in the east about the same time as the sun sets in the west, everywhere. And the full moon sets in the west about the same time as the sun rises in the east, everywhere. And throughout its cycle the moon rises about an hour later each night, everywhere. So, the night after full moon there will be about an hour of dark (really dusk) between sunset and moonrise; the next night there will be two hours of dark, etc., everywhere. Therefore, in terms of the lunar cycle, Packer's study can safely be generalized to other places in the world.

But an important difference lies in the terrain and the vegetation, which in the Himalayan foothills make the "real" times of sun/moon-rises and -sets quite unpredictable. The astrophysical lunar circle can only show an "ideal" horizon comparable to the smooth sphere of an ocean. The flat East African savannah is very close to this, and so Packer could neglect the influence of terrain. But in the hilly terrain where Corbett hunted his man-eaters, it cannot be neglected. It makes a huge difference if a village is up on a mountain or at the bottom of a valley, and this makes exact comparisons almost impossible. The best you might find will be clues roughly pointing in the same direction. The generally denser vegetation in India may have a similar effect. It reduces the amount of moonlight that reaches the ground and therefore maybe also the influence of the lunar cycle in general. The effect of growing hunger during bright nights should be reduced, too, as predators may still find here enough cover for a successful attack.

The observations of Jim Corbett seem to support such expectations. The brightness of the night reduces the danger of an attack in a similar way as in Tanzania. The story of the Rudraprayag leopard shows this very clearly. It may be no wonder, as the activity of leopards is generally closely related to the night. But even man-eating tigers that usually take their human prey during the daylight hours (when they are much more easily available) do prefer dark over bright nights when coming in contact with humans. We can indirectly conclude this from Jim Corbett's behavior when, for example in Tala Des, he set out for the tigress on a bright moonlight night "without any feeling of inferiority." Otherwise in his nightwatch in Pali when unexpected darkness fell from dark clouds, he fully lost his confidence and was completely aware of the inferiority of his senses to those of the tigress. It follows the same logic by which the African bushman shares the night with the lion, as Packer told us. Bushmen hunt at night only when the moon is above the horizon and it is bright enough for human eyes to detect shapes and movement.

Darkness itself is an important factor in North India, too, but there is no evidence that for humans the amount of danger would be different before or after the full moon. There are no signs that the full moon works as a warning sign here. And the best explanation seems to be the different terrain and the denser vegetation of the Himalayan foothills.

So, we can conclude—admittedly on the basis of very few data—that the full moon is not generally relevant as a "warning sign" all over the world. It might just be an African refinement to the more general "fear of the dark rule," adapted to the special conditions of the open savannah. But as such conditions were the conditions under which Homo sapiens evolved in East Africa, Packer might nonetheless be right about the relevance of the full moon as a warning sign for predator control during our early evolution, and he might also be right about the evolutionary roots of the attitude some of us still have under the full moon.

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Humans are not Natural Prey for Big Cats in the Wild

David Blake (UK)

Humans as prey for predators is generally acknowledged to be very rare. Suggestions have been that this is because humans fought/fight back against predation, mostly as groups (Kortlandt, 1967, 1980; Jordania, 2014). Yet, individual animals such as wild boar and buffalo fight back and do so vigorously, and sometimes effectively, while even the strongest of humans individually are extremely weak in comparison to the enormous strength of predators, and devoid of defence tools (effective teeth, physical strength, speed, etc.) to offer any significant resistance.

We can definitely draw no conclusions from the fictions of Hollywood showing men resisting and sometimes prevailing over adult lions and tigers! Films merely show big cats (usually large cubs) playing with humans, with sound effects and dynamic editing trying to create the illusion of a real attack. So, even though individual humans fighting back physically is unlikely to prove effective, humans can resist in various other ways with organized strategies, e.g., in groups, throwing stones and sticks (Darwin, 1871), using thorn bushes and perimeters (Kortlandt, 1967, 1980) other types of fences and walls, pits dug, fires lit, etc.

Hunts with effective weapons (e.g. as in the Masai male’s “coming of age“ hunts with spears) is a relatively late development. However, having noted these strategies, we must not lose the most important point that humans rarely need protection. It is a fact that healthy big cats try to stay away from humans on foot in the wild but, in accidental encounters, potential danger can be minimised by knowledge of big cat behaviour as summarised in the following section.

Practical Observations

Several practical techniques were learned by keepers on foot with both lions and tigers, in situations without bars or fences between those animals and their keepers. Their validity derives from their value as practical survival techniques. Whilst, in the following scenario, the animals (lions and tigers) were released into large reserves during the daytime, licensing stipulations required them to be caged overnight. All cages were located in what was called the 'night yard'. The movement of over 30 animals between reserves and night yard, mornings and evenings, usually required the use of 4WD Land Rovers. However, some circumstances in both reserve and night yard required an animal or animals to be moved by keepers on foot holding a 'fork', a heavy iron pole about six feet long with a two-tined forked end. The animals would treat the pole as part of the human body and it provided something the predator could cuff with a paw or bite without harming the human holding it.

Some practical lessons were quickly learned, among them to stay bipedal and upright, and to face the animals. There is no doubt in the mind of anyone who has worked closely with large land predators that adult humans' upright bipedal stance while facing the animals has a strong effect to a human's advantage, providing that one is taller than the predator's normal four-legged height of approximately 3 feet (approx. 1 metre). Moreover, the taller the keeper, the greater the effect.

This point was emphasised when children (who were, obviously, also upright and bipedal) of between approximately 3-4 feet tall, visited the night yard with a keeper (away from the public, which only saw the lions and tigers in reserves from within their cars in a 'safari park' setting). The predators would become visibly excited and focus on the children and follow them, with vigorous energy and eager movements, as closely as their cages allowed. It would have been extremely dangerous to have had the children in situations without cars, bars or fences.

By the same principle, shorter keepers were more at risk than taller keepers. All this remains true even when the predators learned that, when standing on their hind legs (an approx. six-foot body and head pivoting at the pelvis approx. 3 feet high), they towered above adult humans at between 8 and 9 feet tall.

Corbett readers would remember his tale of two children lost in a jungle well stocked with wild animals, including predators, who emerged without suffering any physical harm, and may wonder why captive predators present a danger to children. The answer is in the word 'captive' since this imposes distortions of natural behaviour. In the absence of any other animal that could stimulate their instinctive hunting behaviour, children provided this stimulus, and more so than adults since they lacked the height advantage of adults.

Whatever one's height, it was very dangerous to turn one's back towards the predator, and still more dangerous to run away, which seems to automatically trigger a chase response by the predator. Maintaining a face forward position, looking directly towards the predator, was a relatively safe orientation - although no orientation was safe with a male lion during the period of a few days or at most a week, when he was mating with a lioness. During this period, he would attack anyone or anything that approached too closely to the lioness, including Land Rovers, charging them and standing on hind legs to bite and claw the bonnet and cab areas. The only way he could be moved safely was by moving the lioness, which he would follow.

Returning to the relative position of predator and keeper: It is well known that predators tend to avoid head-on attacks and will usually seek to place themselves as close to the rear of the prey as possible. If prey observe an approaching predator and face it, the predator will usually abandon the hunt.

There are exceptions and one of Corbett's own films shows a very game tethered goat using its horns to repel the repeated frontal attacks of a leopard, until the leopard abandons the attack. Among the exceptions to the rule could be some, presumably rare, successful frontal attacks, especially when the predator had committed itself, launched the attack and the front facing position of the prey only occurs in the last few seconds of the predator's charge. Yet, I have seen a tiger launch a top speed run at a keeper when the keeper absent-mindedly walked beyond some chain-link fencing and turned his back towards the open reserve. In the last few seconds before contact, the keeper turned and faced the tiger, which, almost like a cartoon cat, tried to stop, with forepaws rigidly extended and hind legs tucked beneath a lowered rump, skidding on the grass to halt just in front of the keeper, who jabbed the barrels of his shotgun, carried with one hand at its midpoint by his side, towards the tiger's face.

The tiger, now sitting on its rump with forelegs still extended, was so close he had to pull his head back to avoid them. It was astonishing, knowing how weak and feeble humans are as compared to a running tiger, that the face-on position could stop the tiger more effectively than any physical action that could have been taken.

A professional hunter in Nepal, Peter Byrne gives an account of a West Bengal postman who for many years delivered all his mail on foot. In 1952, in accordance with the postman's increasing age, he was given a useful present – a bicycle. On one occasion while he was riding his bicycle a tiger chased him. He increased his speed which meant he was unable to look around due to the risk of falling off. Despite this, sounds behind him indicated that the tiger was gaining on him, so he braked to a halt, got off of the bicycle and turned to face the tiger. On seeing the usual human form and stance the tiger stopped, looked at the man and then walked away. (Byrne, 2002:292-293).

Although puma (mountain lion) attacks on humans are rare, cases of pumas chasing and attacking humans on bicycles are well-known in the USA. In January, 2004 a puma killed and partly ate a mountain biker at Whiting Ranch Wilderness Park in Orange County, California. Only days apart, in the same region, a 30-year-old woman from Santa Ana was pulled off her bike by a mountain lion. After a tug of war between other bicycle riders and the puma, she was rescued and taken to hospital in a serious condition (see the post "Mountain lion attacks bicyclist in California, 2004").

If, in the face of imminent danger (for example, after a sudden meeting with a big cat) one's feet seem to be glued to the ground, this might be a "blessing in disguise," a right instinct in the face of danger from a surprised but still lethal predator. This human instinct was mentioned by Corbett at the end of the story about his pet dog hunting companion, Robin, although in Corbett's case he was actively hunting a leopard and had wounded it.

Corbett's own words are: "Our reactions to the sudden and quite unexpected danger that had confronted us were typical of how a canine and a human being act in an emergency, when the danger that threatens is heard, and not seen. In Robin's case it had impelled him to seek safety in silent and rapid retreat; whereas in my case it had the effect of gluing my feet to the ground and making retreat rapid or otherwise impossible." (Corbett, 1944).

We have seen above that it is unwise to turn one's back on a predator and it is of note that, when facing a predator, it is the eyes of the potential prey which affect the predator. Predators are keenly aware if the prey can see them. Predators prefer to attack when the prey is not looking at them, preferably from behind. The use of false eyespots, in the form of simple plastic masks tied on the back of human heads, have saved the lives of many Indian villagers, particularly in the Sundarbans.

Practical advice to actors from animal trainers working for film companies, and from circus 'lion tamers' to trainees, is not to squat down or turn their backs towards big cats, or run away, all of which is consistent with the above. Tragically, there is a famous filmed case of a tourist recklessly disregarding all the rules of and advice from the safari organizers, who was killed by lions in front of his family. This happened on February 18th 1975, during a safari at the Namibia-Angola border. As a few cars full of tourists were viewing a pride of lions, one male tourist, against all safety precautions, got out of his car and walked up very close to the lions in order to film them from a shorter range. It is difficult to understand the tourist's mentality not only in leaving his car, but also in leaving his wife and two small children in it with windows open. For several seconds the intrusion of the man in the midst of the lion pride escaped any consequence, until the man squatted down.

The man crouched down with his camera to film a snarling male lion at a more effective angle. As soon as he crouched, a lioness approaching very closely from behind used her forepaws and jaws to knock him to the ground and savage him. There is graphic video footage on YouTube, filmed from another car, showing the tragic scene, in which the lioness is joined by other pride members at the man's body in full view of his wife and two children. It is difficult to say whether staying upright would have saved the life of the tourist (since he already had his back to a lioness) but certainly, bending down removed the last safeguard of human bipedal posture discussed herein (see also Jordania in this volume).

The examples given so far have emphasised that turning one's back to, running away from or crouching near big cats is lethally dangerous. Exceptions include situations in which the predator has been affectionately hand-reared from being a young cub, with much contact and care. In such cases humans can even pretend to be prey by squatting, lying down, turning their backs or running away, to stimulate mock attacks, which are launched and completed by the predator but with sheathed claws and mouthed 'bites' with open jaws e.g., as seen with Billy Arjan Singh in India bringing up a leopardess and later, a tigress, before releasing them into the wild.

As the reader will recall, the above-mentioned points relate to knowledge useful on the rare occasions that humans and big cats encounter each other in natural habitat. Such encounters are rare due to the predators actively avoiding contact with humans. This is fundamental to the purpose of this conference and such avoidance behaviour is completely incompatible with humans being seen as prey by predators.

I have been fortunate enough to have had opportunities to watch wild tigers from trees without them being aware of my presence and seen their reactions when humans, unaware of the danger, pass nearby on, say, a sandy track through the dense undergrowth concealing the nearby tiger. I have seen this twice, the first time in 1978, in Chitwan National Park, Nepal, while assisting the Smithsonian Tiger Ecology project, and then in 2004, in Kanha Reserve, India, while working for LifeForce Charitable Trust. In both cases, the tigers did not assume a crouching or stalking position or in any other way react with interest as if a prey species was nearby. They actually did the exact opposite and made every effort to avoid the humans either by remaining motionless or moving silently away, such that the humans on the ground were not aware they had been in such close proximity to a wild tiger.

The Relative Scarcity of Man-Eating Big Cats poses a Scientific Puzzle in Relation to Currently Accepted Orthodoxy

Any reader of Corbett recognizes that man-eating is anomalous, that man-eaters are rare exceptions, and nearly always man made, directly or indirectly, by depriving the animal of sufficient food, either by wounding the predator or damaging or destroying its habitat and/or prey base. I realise that I might be committing heresy from a scientific perspective but believe that at least some ‘city born and bred scientists’ simply assume that freedom from attacks by wild animals is due to our distance from wild habitat, and that if we were all living in the wild, we would be prey to large carnivores.

This unfounded assumption is then extrapolated back in time and a further assumption made that this must have been the experience of our distant ancestors (see, for example, Brain, 1981; Hart & Sussman, 2005). Such a conclusion is not in any way scientifically derived and the information herein suggests that it is based on a false assumption. Scientists with experience in the wild e.g. Louis Leakey, who experienced some unexpected and tense moments with big cats, have a different opinion.

During his archaeological fieldwork Leakey witnessed lions at night, on more than one occasion, entering tents where scholars were sleeping and, after sniffing humans' heads, leaving, making Leakey believe that there was something in human scent that discourage lion attacks (Leakey, 1967). This is consistent with many animals' reactions to human scent, which acts as a repellent to wild creatures. People asleep (lying down with eyes closed) are obviously without the safeguards referred to above (bipedalism, facing predators). The human scent, coupled with the fact that the lions were in relatively new and artificial surroundings (the tents) while free to move away to continue their habitual hunting routine, was a combination of factors that, on the occasions witnessed by Leaky at least, favoured the sleepers. However, allowing for individual variations in lion temperament (and possibly the level of predator hunger), it is not a situation that would always have predictable results, and not one in which I would personally volunteer to be a sleeper.

With regard to the tiger, of what limited scientific research there has been, Schaller's study of the tiger noted that "Although man is the most easily obtainable source of food throughout the tiger's range, he is for unknown reasons rarely eaten" (Schaller, 1967:278).

Charles McDougal wrote: "...man-eaters are abnormal tigers; normal tigers avoid man and attack only if provoked or under some special circumstance, such as when a tigress thinks her cubs are threatened. Never did they constitute more than a fraction of the total population – even in the notorious Sundarbans region, only about three percent of the tigers are confirmed man-eaters. Because stories about them make more exciting reading, they have been much in the public eye. This is unfortunate, for man-eaters have given the species as a whole a bad press." (McDougal, 1987:162-3).

A long-running project (from 1973 to, using different techniques and with different management, the present), starting as the Smithsonian Tiger Ecology Project in Chitwan National Park, Nepal (the same location in which McDougal conducted his studies) and the habitat of dozens of tigers (in the region of 30+ animals), found no recorded case of man-eating before 1980 (McDougal, 1987:444). Thereafter, various factors resulted in an increase in the tiger population. This caused numerous territorial fights between tigers and dispersal of some tigers to beyond the Park's boundaries.

From 1980 to around 1987, 13 human victims were killed and eaten around and within the Park's boundaries by three male tigers. All three had lost fights for territory with other males and two at least were definitely known to be wounded in consequence. Almost all human victims were grass-cutters (and therefore unlikely to have been upright when attacked and killed) who were obliged to enter habitat sheltering the tigers (McDougal. 1987:445).

Tigers need cover, prey and water to survive naturally. For tigers pushed out to sub-optimal habitat lacking some or all of these features, survival becomes much more difficult. Due to human activities, land surrounding Parks and Reserves is often completely cleared of forest and, all too often, paddy fields and/or village huts are situated right next to the forest edge. Whilst the importance of buffer zones at the boundary of a Park or Reserve is generally recognised, political and socio-economic factors often override conservation and man-animal conflict concerns.

As referred to above, a decrease in natural prey and/or damage to habitat leads to man-eating: Catherine Caulfield's excellent book *In the Rainforest* noted, in the context of rapidly cleared forest land in Sumatra and Sulawesi that was soon settled by human immigrants: "Wild animals, including ...tigers, have lost so much of their range that they have been forced to prey upon the (human) communities that have displaced them." (Caulfield. 1984:189)

With regard to the lion, apart from rare exceptions such as the infamous two male man-eating lions of Tsavo (1898), studies by Schaller and by Bertram from the early 1970s as well as later long-term studies by Packer (from late 20th century well into the 21st century), do not report that lions view humans as prey.

According to George Schaller, lions hunt their prey animals with a so-called "alert face", silently, with a closed mouth, and with forward-pointing ears – however they attack humans with open mouth, ears back and growling, exactly the same way as they attack their fellow lions. "As mentioned before, the cat uses the alert face in such a situation [when hunting], not a bared-teeth face as is usually indicated in museum exhibits. On the other hand … lions attack man with bared teeth. The exposed teeth represent a defensive reaction, whether in response to another lion, man, or an attacking prey animal; in other words, they contain an element of fear" (Schaller, 1972:98).

To fully understand these references it is important to distinguish between predators hunting and attacking: Hunting provides the predator with food; attacking repels or eliminates a perceived threat - to the predator itself, its cubs or its kill. Confusion can arise as both can involve overt violence and usually fatal physical damage.

The hunt concludes with the death of the prey and its being consumed. This requires much caution on the part of cats to approach closely enough to the prey to launch a sudden rush, get in contact with the prey, hold and kill it. This caution requires, as referred to above, not being seen, and absolute silence, whether vocally or by avoidance of rustling undergrowth or stepping on twigs or dry leaves. It also indirectly requires silence in the sense of avoiding detection by 'watchmen' of various species alarm calling at the sight, sound or scent of a predator.

Whilst the effort requires concentration and caution the predator does not exhibit or, as far as can be ascertained, feel aggression towards its prey. "Big cats are, for obvious reasons, silent and composed when stalking, catching and killing prey. There is definitely no growling, snarling or any other sign of aggression. The Hollywood tradition of 'pressing all buttons at once' for the greater stimulation of the audience results in scenes of big cats (dubbed as) always growling or snarling while hunting, or even simply moving. In reality such a predator would never eat … Killing to eat is a functional business to satisfy nature's most persistent and ubiquitous stimulus. As Konrad Lorenz writes in his book *On Aggression* 'The buffalo which the lion fells provokes his aggression as little as the appetising turkey which I have just seen hanging in the larder provokes mine.'" (Blake 2010:79)

In contrast to hunting, attacking predators do exhibit aggression and, once the attack is completed, it is not followed by the victim of the attack being consumed by the predator. The open mouth, bared teeth, roaring and/or growling usually intimidate the other animal and very often remove the need to follow up with physical contact because the other animal retreats.

On occasions when physical contact between conspecifics does result, it is conducted according to ritualised behaviour, which minimises physical damage to either animal i.e. much vigour, noise and side swipes from paws (usually to the shoulders or side of the head of the opponent). However, when neither opponent is intimidated, fights can escalate and serious damage or death can be inflicted on at least one opponent.

In these cases, the attacking big cat can bite the lumbar region of the spine, which severs the spinal cord and cripples the rear legs of the victim. With or without the lumbar bite, death is delivered, if possible, by biting such that the canine teeth penetrate the cranium of the victim (note the lack of a nape or throat bite as used in killing prey).

In attacks on humans, one blow from a paw is usually sufficient to either kill or 'neutralise' the perceived threat. On occasions when bites are inflicted on humans, they are not normally aimed at the neck or head region (as they would be with prey) but other areas of the body, often those which happen to be in close proximity to the mouth during the melee. Even if biting does occur during the attack and proves fatal, after the attack is over, be that on a conspecific, other animal or human, the adversary or 'threat' is not eaten. If a lion or tiger bared its teeth and growled in the captive situation but without bars of fences between cat and keeper, described at the beginning of this presentation, it was, in one sense at least, reassuring, since these are signs of defensive threat and indicate an element of fear in the animal i.e. provided one ensured the animal had an open (escape) route in the direction in which one wanted the animal to move and provided one gave it the time and opportunity to see this route, the situation could be managed without harm to keeper or cat.

In contrast, if the animal had harmful intentions towards the keeper, it did not make any threat display – no bared teeth, no growling and no fear (on the part of the predator!) Its actions would match Schaller's 'alert face' and its eyes would hold a chilling and alarming expression. The keeper had become prey. These situations had to be handled very carefully and would almost always require back-up in the form of another keeper or vehicle. So, we can complete Schaller's passage above to read that lions (and, we can add, tigers) *attack* man with bared teeth, and possibly growling, snarling with laid back ears, but hunt man with the same so-called 'alert face', silently, with a closed mouth, and with forward-pointing ears.

While attacking a threat and hunting are usually mutually exclusive types of behaviour, we know of the former turning into the latter from an example given by, appropriately, Corbett, who mentions the case of the Muktesar Man-Eater (Corbett 1954) lying up severely wounded by numerous porcupine quills, killing a woman (with a single blow of her paw) who inadvertently approached too closely to the tigress' position. Leaving the woman where she lay without touching her the tigress limped away. Two days later a man also unknowingly approached too closely to her new position and was also killed. His torso was exposed and, before moving painfully on, the hungry tigress ate a small portion of the man's back. Thereafter she became a regular man-eater.

So, from our current perspective, the initial attack on the man was a defensive attack to repel or eliminate a perceived threat. The man was not consumed as hunted prey would have been but a few mouthfuls were taken and acted as a bridge between the two normally distinct modes of attack or hunt. The tigress' wounds and hunger turned that original unplanned attack against a human threat into future planned hunts of humans as prey.

I know of no scientific, long-term study of the leopard. Like foxes, leopards are able to live in close proximity to humans and often prey on pet and/or feral dogs living around human habitation (see Gadhvi in this volume). Hence, the chances of surprise encounters with humans are increased. However, when neighbouring natural habitat is degraded or destroyed by humans such as around slum areas on the outskirts of the Indian city of Bombay / Mumbai during the late 20th century, man-eating leopards arise.

Similarly, in the western Himalayas "human activities, which are too often thoughtless and careless commercial enterprises, have resulted in naturally indigenous trees and plant species being cut down and replaced with fast-growing conifers for commercial purposes. The unnatural excess of pine needles from these trees acidify the soil to the extent that naturally occurring plant species die off, disturbing the ecosystem. One result is that herbivores move away to find food but the resident leopards (higher altitudes mean that prey and cover are too small or scarce for tigers) are territorial and cannot move so easily (they may already be in sub-optimal habitat due to not being able to secure territories in optimal habitat at lower altitudes). In consequence, these areas have recently (late 20thcentury and early 21st-century) suffered dramatic increases in the numbers of man-eating leopards and, obviously, human lives lost to them." (Blake 2010:76).

Corbett also noted that when pandemics make many unburied human corpses easily available, man-eating leopards can arise in consequence i.e. once the supply of corpses are consumed, the leopard takes living individuals to continue its recently discovered easy supply of food (see the discussion on this subject for all big cats, in Waltl, 2016).

Whilst an unfortunate human death might result from a carnivore protecting its young or kill, this is not man-eating. Experience with predators in captivity and the wild has convinced me that, surprisingly, humans are not natural prey for any land-based predator. If criticism of this claim in the context of the conference is that it cannot be proved for early man in ancient history, nor can the opposite claim be proved, nor even conclusive evidence produced. The only evidence we do have i.e., the behaviour of modern predators, supports the first claim and, quoting from Corbett's 'Author's Note' in his Man-Eaters of Kumaon: "A man-eating tiger is a tiger that has been *compelled, through stress of circumstances beyond its control, to adopt a diet alien to i*t." (My emphasis. D.B.).

Whatever poetic or artistic license Kipling allowed himself, his jungle stories are rooted in well-observed reality, accurately described, and reveal advanced knowledge and insights. Among those insights (e.g. 'For the strength of the Pack is the Wolf, and the strength of the Wolf is the Pack' – an interdependency that extends throughout nature, within and between species). Kipling's Law of the Jungle tells us: "Ye may kill for yourselves, and your mates, and your cubs as they need, and ye can; But kill not for pleasure of killing, and seven times never kill Man!" If humans are not natural prey for predators, why would keepers/actors/trainees referred to above need to avoid turning their backs towards predators? This is because humans become 'unnatural potential prey' for captive animals, the behaviour of which is (by definition) unnatural when in captivity.

Powerful instincts remain despite the predators' captivity and humans are the only other species they see of any substantial size and these, in the absence of anything else, are the only stimuli on which those instincts can focus. Captive big cat behaviour actually supports the fact that unnatural deprivation of prey can drive some individual predators to man-eating. All cases of children alone and keepers / actors / trainees turning their backs on predators, represent unnatural circumstances, in particular they indicate a lack of alternative prey to satisfy the predators' natural instincts.

Likewise, the evidence from ancient Rome at the time of the Colosseum and similar amphitheatres, where tigers and lions were kept very hungry, without any natural prey being available, and then let loose into an arena only containing helpless humans (some of whom may well have laid down and/or turned their backs towards the predators and/or run away; all very dangerous stimuli to hungry predators).

I would respectfully suggest that the conference concentrate on what is known, at least in recent history, and ask why humans are not regular prey for any land-based predator: Is this instinctive or learned behaviour?

There is no persuasive evidence for Leakey's idea of 'unpalatability' of humans to lions. Relatively few taste buds on large carnivores' tongues and the fact that they do not chew meat would argue against it being a significant factor. Moreover, lions will consume meat in its most advanced state of putrefaction and/or kill and eat their own cubs (if deformed in any significant way, not due to new males taking over the pride) and even each other, once a conspecific has died (I have witnessed all of these examples). So, large carnivores, lions especially, are not fussy about food.

Some authors, citing man-eating animals, have claimed that human flesh tastes similar to pork and that tigers, supposedly finding wild boar appetising, on becoming man-eaters, find human flesh appealing, as far as any taste distinction might be made. Weldon (2018) proposed that lions reject humans as prey as they have an evolutionary memory of the successful defence from large-bodied hominids that could defend themselves vigorously. In his original words, "body odour of humans and, historically, of hominids denotes chemical emitters who exhibit formidable defensive traits, including large body size, agility, vigilance and the capabilities of deploying projectiles and other weapons and/or marshalling group defences." (Weldon, 2018:1).

Hunters, naturalists and researchers advise that the safest way to remove oneself from an unexpected encounter on foot with a predator in natural habitat, if and when unable to climb a tree, is to keep facing the animal and walk backwards slowly until at a safe distance from the animal.

Moreover, when humans do not deliberately place themselves in close proximity to large predators while simultaneously depriving them of natural prey species, they are ignored or actively avoided. Hence, we find Corbett's account of the small children lost but safe in a jungle and his observation that "...tens of thousands of men, women and children who, while working in the forests or cutting grass or collecting dry sticks, pass day after day close to where tigers are lying up and who, when they return safely to their homes do not even know that they have been under the observation of (a tiger)." (Corbett, 'Author's Note', Man-Eaters of Kumaon.)

We also know from Corbett, other hunters and researchers in the field that a tiger's (or lion's or leopard's) growl means 'go away' and, if the warning is heeded, the human is able to go away without being harmed. If humans were prey, tigers would not growl but remain silent and adopt a hunting posture, soon to be rewarded with an easy meal of a weakling human.

Even on rare occasions when the warning is not heeded, the tiger might charge (usually with a coughing roar) and frighten the intruder away or, if contact is made, inflict some wounds but not kill the intruder immediately (although blood poisoning might do so later), and then return to cover. This is not even remotely similar or comparable to its behaviour towards prey species. To quote Schaller's scientific study again: "...persons familiar with tigers all agree that the animals are so shy and avoid man so assiduously that they are rarely seen." (Schaller, 1967:302).

Schaller again: "In general, my findings agree closely with those of Corbett, who wrote: 'Tigers, except when wounded or when man-eaters, are on the whole very good-tempered...occasionally a tiger will object to too close an approach to its cubs or to a kill that it is guarding. The objection invariably takes the form of growling, and if this does not prove effective it is followed by short rushes accompanied by terrifying roars. If these warnings are disregarded, the blame for any injury inflicted rests entirely with the intruder.'" (Schaller 1967, Corbett, 1954, Temple Tiger, story Talla Des Man-Eater.)

So, in addition to models, perhaps another category of 'titles for research proposals' might include 'Humans are not treated as regular prey animals by any large, land-based predator. Why should this be?'

Aposematism might form part of an answer, but any additional, alternative or currently unknown possibilities need to be established for a full understanding. As the conference is the result of a newly formed university department, currently named 'Jim Corbett International Research Centre', Model 6 (aposematism) and, if accepted, additional Research Proposal more in harmony with what Corbett teaches us in his books and distinguishes the current conference from other more orthodox conferences working on unquestioned assumptions.

Finally, for further study in harmony with Corbett's books, pork is a salty meat (I do not know about the relative salt content of human flesh). The possible connection between salt and man-eating I have considered on pp.75-9 of Framing Fearful Symmetries.

CONCLUSIONS

The aim of this paper is to offer behavioural perspectives of both captive and wild, free ranging big cats in the context of man-killing and man-eating. Its contents suggest two central conclusions:

(1) Humans are not a natural prey species for big cats, or, by extension, any other land-based predator;

(2) The reason(s) for this is/are yet to be established.

Reasons might include adaptation. Whether or not this is correct, a scarcity of other possibilities presents yet unexplored field, which may involve innate and/or learned behaviour, any of which could offer rich results.

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Battle Trance: From Ancient Survival to Miraculous Healing and Super Performance

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Abstract. Battle trance, which evolved from instinctive defensive and offensive behaviors for close, conspecific combat, involves socially transgressive processes like becoming-intense and becoming-animal that produce advantageous non-ordinary psychophysical states. Battle trance is an ancient technique useful in hand-to-hand combat but little understood today. *Berserkergang* (going berserk) is one of the best attested forms of Indo-European battle trance, associated with spiritual attainment, including ecstatic *amok* warriors and *juramentado*, a Muslim form of battle trance. Colonials pathologized and tried to reduce the magic and sacred qualities such fighting styles, despite practitioners' discipline, spiritual dedication, and altruistic self-sacrifice, up to the present, but the techniques for achieving battle trance remain in use in combat, spiritual disciplines, and martial arts. Today research not only validates some of the most extraordinary features of battle trance, but also demonstrates its potential for healing and outstanding human performance.

On November 7, 1944, after shelling and gunfire had killed almost everyone in United States Army Staff Sergeant William F. Leonard's platoon near St. Die, France (Staff Sergeant William F Leonard. Biography), he led the eight survivors in an uphill charge through withering automatic fire and killed two snipers. After sustaining multiple bullet wounds, he went on to destroy a machine-gun emplacement and its crew, and though stunned by a bazooka shell, he wiped out a second machine-gun nest and captured the roadblock objective.

Nepalese Gurkha Lachhiman Gurung on May 12-13, 1945, held off 200 advancing Japanese troops after his frontline position was attacked and all his companions were wounded or evacuated (Lachhiman Gurung VC Victoria Cross). When he tried to throw back a Japanese grenade, it exploded, ripping off his fingers, shattering his arm and severely wounding his face, torso, and leg. He held the line by himself for four more hours, killing 31 and singlehandedly beating back the enemy assault.

On May 21, 1951 near Munye-Ri, Korea, after Private Joseph C. Rodriguez's platoon, surrounded on three sides by enemy fire, had been unable to break out of their position, he leaped up and charged through heavy fire up the hill, destroying the guns and crews in five enemy positions (Col. Joseph C. Rodriguez, USA). When asked why he had done such a suicidal thing, Rodriguez said, "I was very angry…that they had all of our men pinned down. And I felt something had to be done. I didn't even think about it, just did it" (Joseph C. Rodriguez collection).

Such extraordinary feats can be found in the wartime records of any country. Their distinguishing features – fearlessness in the face of overwhelming force, not being aware of pain, supernatural strength to keep attacking even when gravely wounded, and sacrificing personal survival for the group and its goal – characterize a psychophysical altered state called *battle trance* (Jordania, 2011, 2014), part of the primordial human survival repertory demonstrated both by males and females.

Besides combat, this state appears adventitiously when triggered by sudden, horrific threat. Most such reports involve people's lifting vehicles many times their body weight to free others pinned beneath them, such as two sisters, aged 14 and 16, who raised a 3,000-pound tractor off their father ("Oregon Man Pinned," 2013), and a 72-year-old man who lifted a Jeep off his son-in-law ("72-year-old N. L. 'Superman,'" 2013). Scientists do not believe adrenaline acts quickly enough to account for such feats, and evidence for other likely physiological mechanisms, such as a rapid endorphin dump, remains scant (Holohan, 2012; Wise, 2009).

For combat, battle trance has been deliberately cultivated since time immemorial to maximize innate survival mechanisms. According to Jordania (2011, 2014), battle trance is an evolutionary survival strategy that bonds the group with exhilaration and feelings of strength, unity, and immortality. Battle trance comprises a cluster of extreme capabilities bridging evolutionarily ancient survival techniques and spiritual attainment that represent potentials for enhancing human performance and healing. This paper presents methods for its cultivation in combat, its decline as military technologies changed, evidence substantiating its more extraordinary qualities, and its potential for new applications to better the human condition outside combat.

The Human Need for Battle Trance

All amniotes employ aggressive displays among their own kind to dominate a rival for an immediate goal, such as access to food, territory, or a mate, and such conflicts usually end short of killing the rival (e. g., MacLean, 1973, 1990). But *Homo sapiens sapiens* engage in the organized mass killing of fellow humans. Conspecific killing is not easy in close combat, the only way humans fought for millennia, armed with bladed and blunt-force weapons in addition to short-range projectiles. The closer fighters are physically, the greater their need to dissociate from their humanity (Grossman, 1996), using processes that put them into a liminal, socially transgressive state called *becoming-intense* and *becoming-animal* (Deleuze & Guattari, 2004, pp. 242-243; Roscoe, 2007). Such dissociation from social norms enables a warrior to kill without guilt, so combatants cultivated this state prior to fighting, not relying on its being evoked in the heat of battle, and in a reverse process, many cultures developed rituals to restore fighters to their humanity after combat (e.g., Kelle, 2014; Parsons, 1916).

Over time humans' instinctive defensive and aggressive survival behaviors developed into patterned activities universally found to promote battle trance (Carlson, 2006; Lincoln, 1991; Miller, 1990; Miller, 2000; Roscoe, 2007), including: 1) taunting the enemy to raise fighters' anger before they physically engage; 2) rhythmic vocalizations, such as singing and the battle cry, to invoke the gods, inflame mood, unify the group, communicate determination, and intimidate the opponent; and 3) rhythmic group movements, such as war-dancing, to invoke the gods, promote solidarity, and intimidate the opponent (Ehrenreich, 1997; Gibson, 2011; Jordania, 2011, 2014; Kogan, 1997; Nettle, 1961; Roscoe, 2007). A venerable example is the Maori *peruperu haka* performed by the New Zealand All Blacks before a rugby game, which employs swaying, stamping, grimacing, tongue thrusting, eye widening, grunting, crying, and slapping to prepare the body for combat and frighten the enemy. Traditionally it had to be performed in perfect unison to promote solidarity, entrain the group, and invoke victory from the god

Tumataueng. Such rituals evolved into the rhythmic drilling of troops, which provided a significant battlefield advantage (McNeill, 1995).

But before regulated, massed combat styles were developed, warfare was loosely organized, with individual fighters behaving fairly independently, often engaging in single-combat challenges before or during group engagement. Greece and Rome had a strong single-combat, sacred warrior heritage (e.g., Cowan, 2007; Martino, 2008; Znamenski, 2012), but had largely abandoned it by their classical periods for regulated, massed fighting better adapted to new technologies (McNeill, 1995). Ecstatic warriors appear in the *Rig Veda*, the *Iliad*, and Assyrian sources, among others (Burkert, 1992; Kershaw, 2000; Speidel, 2002, 2004). Indo-European cultures retained an unregulated tradition featuring individual champions seeking to outdo others in glorious deeds for two and a half millennia (Speidel, 2002; Znamenski, 2012), and such heroic personal status-seeking through combat occurs other cultures, such as the Native American Plains tribes (Znamenski, 2012) and in Southeast Asia (e.g., Barnes, 2007; Turbiville, 2012). Societies with single-champion traditions produce the best descriptions of cultivated battle trance, and the best attested is northern European *berserkergang* (English rendering of Old Norse *berserksgangr*, *walking* or *moving like a berserker*, a characteristic way berserks carried themselves or perhaps fought; Dale, 2014), now commonly translated as *going berserk*, discussed below. Although the cult-specific berserkergang died out during the Viking Age, battle trance and the practices for cultivating it are still seen in war (e.g., Pieslak, 2009; Roscoe, 2007), religious traditions and their associated martial arts, and elsewhere (e.g., Farrer, 2009; Gargenbert, 2000; Wilson, 2002). Owing to its greater documentation, berserkergang will be used to illustrate the universal features of battle trance.

Battle Trance as a Sacred Phenomenon

Battle trance cross-culturally was associated with spiritual attainment and the gods of war. Berserkergang is known from northern European and Icelandic sources recorded centuries after it was practiced by Christian monks who mostly lacked combat experience and were hostile to pagan religions, so their reliability is questionable (e.g., Sigurðsson, 2004), but other contemporary sources provide triangulation. Christians stereotyped berserks as either the elite troops of famous kings (Halbrooks, 2003; Price, 2002), in keeping with their traditional high status as holy champions (e.g., *Egils saga Skalla-grímsonnar, Vatnsdæla saga, Hrólfs saga kraka*), or as outlaw thugs (e.g., *Grettis saga, Hervarar saga ok Heiðreks*). As examples of the former, berserks were assigned valued, dangerous roles in the vanguard (Duchesne, 2009; Reid, 1988; Speidel, 2002), consistent with more contemporary elite, ecstatic warriors, discussed below. A rare contemporary account reported Harald Hairfair's deploying berserks as shock troops, using the device of a dialogue in which a Valkyrie battle goddess asks a raven, Odin's familiar and battlefield scavenger:

> "Of the berserkers' lot would I ask thee, thou who batten'st on corpses:
> how fare the fighters who rush forth to battle,
> and stout-hearted stand 'gainst the foe?"
> "Wolf-coats they are called, the warriors unfleeing
> who bear bloody shields in battle;
> the darts redden where they dash into battle
> and shoulder to shoulder stand.
> 'Tis men tried and true only, who can targes [shields] shatter,
> whom the wise war-lord wants in battle." (*Hrafnsmál*, 20-21)

The Icelandic sagas reflect the same roles for berserks in the field. "Then the king cried on his bearserks [*sic*] for an onslaught, and they were called the Wolf-coats, for on them would no steel bite, and when they set on naught might withstand them" (*Grettis saga*, 2). Berserks were strategically deployed and fought in the disciplined ranks of the shieldwall (*Hrafnsmál*, 20), as well as more independently. When a war-band of berserks was ordered to eliminate enemy troops on a long ship,

> [Kveldulf] then had a fit of shape-strength [i.e., went berserk, involving shapeshifting], as had also several of his comrades. They slew all that came in their way, the same did Skallagrim where he boarded the ship; nor did father and son stay hands till the ship was cleared. (*Egils saga Skalla-grímsonnar*, 27).

Berserks were the consecrated warrior-shamans of Odin, god of magic, battle, death, and poetry, the medium of heroic fame and immortality. They were initiated into ecstatic rites to win fame and everlasting life through heroic deeds before dying fighting, part of a long line of Indo-European sacred warriors distinguished from society by such means as ritually conspicuous grooming (Kershaw, 2000; Miller, 1998) and being forbidden to farm or own land (later confused with outlawry). Tacitus described such warriors' roles among the Chatti:

> Every battle is begun by these men. They are always in the front rank, where they present a startling sight…None of them has a home, land or any occupation. To whatever host they choose to go, they get their keep from him…until old age leaves them without enough blood in their veins for such stern heroism. (*Germania*, 31)

Odin's name derives from Old Norse *óðr*, often glossed as *fury*, after missionary Adam of Bremen's *Gesta Hammaburgensis ecclesiae Pontificum* (4.26), but *óðr* also means *mind, intelligence*, or *soul* as well as *poetry*, *eloquence*, and *inspiration* (**uat-*; e.g., Davidson, 1988, 1990; Simek, 1993; Sturluson, 1987). Odin is the god of mental powers and spiritual awakening, highly suggestive of battle trance as an altered state. Thus, *berserkergang*, often rendered as *battle-fury* or *-madness*, means being possessed by Odin (e.g., Kershaw, 2000). Odin, like his berserkers, was viewed as an ambiguous god not always to be trusted; berserks in later accounts were unable in their battle madness to distinguish friend from foe, sometimes killing civilians (e.g., *Egils saga Skalla-grimsonnar*, 40). (Interestingly, such negative reports of battle trance have tended to emerge as societies turned away from the single-combat champion fighting style in favor of massed engagements [Colarusso, 2019].)

Odin determines the outcome of battles, and, with the Valkyries, selects the outstanding heroes among the slain who deserve glorious afterlife in Valhalla. On earth, heroes were immortalized through having their deeds sung in poetry so that their memories never perished, the highest aspiration of sacred-warrior traditions (e.g., Duchesne, 2009; Fortson, 2010; Gurevich, 1995; Poliakoff, 1987; Speidel, 2004). Warriors engaged in conspicuous acts of bravery, laughing at danger and scorning to protect themselves – especially in conditions of certain death – to win everlasting fame. "Their excesses meant glory: Wolf-warriors, berserks…no doubt won the 'unwilting glory' held out by the *Iliad* and the *Rig-Veda*" (Speidel, 2004, p. 193).

Odin's powers relevant to battle trance included: shapeshifting; clouding a warrior's mind with fear and confusion, or the reverse, instilling courage and clarity; weakening or strengthening the body; magical paralysis ("the fetters"); breaking or strengthening weapons and armor; and invulnerability magic. For example, Odin tells how he can blunt or turn aside weapons:

> That third [spell] I know, if my need be great
> To fetter a foeman fell:
> I can dull the swords of deadly foes,
> That nor wiles nor weapons avail….
> That fifth [spell] I know, if from foeman's hand
> I see a spear sped into throng,
> Never so fast it flies but its flight I can stay,
> Once my eye lights on it. (*Hávamál*, 148, 150; Hollander's translation)

Odin's magic was shared by his warrior-shamans:

> In battle Odin could make his foes blind or deaf or terrified and their weapons were as nothing more than sticks; but his own men went about without armour and were mad like hounds or wolves, and bit their shields and were strong as bears or bulls; they slew men, but neither fire nor steel would deal with them. This was called a berserk's-gang. (*Heimskringla*, Ynglinga Saga, 6)

Berserkergang reflected an older Indo-European war-magic heritage (e.g., Speidel, 2002) involving: shapeshifting, stunning the enemy with terror; scorning to wear armor; rendering enemy weapons harmless; and invulnerability to fire and blades. Formulaic language identifying berserks is "no iron would bite them" (*á þá bitu eigi járn;* e.g., *Egils saga Skalla-grímsonnar*, 9; *Grettis saga*, 2).

Techniques Berserkers Used to Produce Battle Trance

Berserkers prepared for battle by shapeshifting into bears or wolves, hence one meaning of *berserk*. Scholarly debate (e.g., Price, 2002; Guðmundsdóttir, 2007) about whether *berserk* means *bear-shirt (sark),* for the donning of animal skins in a shamanic transformation rite, or *bare of shirt,* for fighting without armor or bare-chested, discussed below, remains unresolved; both meanings support battle trance. Warriors were likened to bears and to wolves, Odin's totem animal (*ùlfheðnar*, *wolf-skins,* often translated as *wolf-warriors*; e.g., Davidson, 1988, 1990; Price, 2002; Speidel, 2002, 2004).

They were believed not just to resemble animals but to become them in battle trance, just as Odin could assume any form he wished:

> [Odin] could change himself and appear in any form he would.... Odin often changed himself; at those times his body lay as though he were asleep or dead, and he then became a bird or a beast, a fish or a dragon, and went in an instant to far-off lands on his own or other men's errands. (*Heimskringla*, Ynglinga Saga, 6-7)

Material finds in northern Europe depict the ritual wearing of animal skins and masks and war-dancing with weapons as a shapeshifting device (e.g., Davidson, 1990; Price, 2002; Speidel, 2004), such as ornamental plates from armor showing naked, leaping warriors alongside warriors clad in animal skins brandishing weapons. Transforming into beasts by wearing animal pelts and masks is well established in Indo-European cultures (Cebrián, 2010; Kershaw, 2000; Price, 2002; Speidel, 2002, 2004). Dancing, singing, howling, and wearing skins conferred the animal's strength, ferocity, and speed on participants, identities reflected in the terms *berserk* and *ùlfheðinn* and in personal names containing the element *bear* and *wolf*, such as Gunbjorn and Wulfgang, respectively. Berserkers were called shapeshifters, *eigi einhamr* (not of one shape) or *hamrammr* (shape-strong), with the root *hamr* closely associated with supernatural, magical powers and perhaps changed mental state (e.g., Perabo, 2017; Tolley, 2007). Ecstatic dancing in animal pelts seems to have conferred supernatural feral qualities on berserkers. When the legendary hero Sigmund and his son Sinfjotli ("Helgakviða Hundingsbana I", 36-37) donned magic wolf skins, they spoke the language of wolves and hunted like them (*Volsunga Saga*, 8), able to kill seven or more men alone. When the skins came off, the heroes remained human but with increased lethal powers. The most famous bear warrior, known from multiple sources, was Boðvar Bjarki, who, like Odin, bilocated in a shapeshifting trance. His human body was observed sleeping in the hall while a giant bear fought in King Hrolf Kraki's bodyguard on the battlefield:

> Then Hjorvard and his men [the enemy] see a huge bear going before the King Hrolf's men, always nearest to where the king was. He kills more men with his paw than any five of the king's other champions. Blows and missiles glance off him. But he bursts under him both men and horses…and everything that comes in his way, he crushes

> in his teeth, so that panic sweeps King Hjorvard's army. (*Hrólfs saga kraka,* 50).

When Boðvar was awakened from the trance, the bear disappeared. As a man, Boðvar fought in berserkergang, but less effectively than his bear persona.

Warriors used classic precursors to battle trance, such as taunting to work up anger and courage, as Diodorus Siculus wrote of the Gauls:

> It is also their custom, when they are formed for battle, to step out in front of the line and to challenge the most valiant men from among their opponents to single combat, brandishing their weapons…to terrify their adversaries. And when any man accepts the challenge…, they then break forth into a song in praise of the valiant deeds of their ancestors…their own high achievements, reviling all the while and belittling their opponent, and trying, in a word, by such talk to strip him of his bold spirit before the combat. (*The Library of History*, 5.29)

In the sagas, Skapheðinn abused Skapti Þorodsson's intelligence, courage, and appearance (*Brennu-njal's saga*, 118). In *Beowulf*, Unferth sneered that Beowulf (Am-a-Wolf), who had lost a swimming contest, would similarly fail if he fought the monster Grendel (*Beowulf*, ll. 506-528) while Beowulf charged Unferth with ineptness, cowardice, and having murdered his own kin (ll. 582-601).

Ancient European warriors routinely used noise-making tactics alone or with dancing to bring on battlet rance and frighten opponents, per Livy's account of Celtic fighters: "[T]heir songs…, their war-whoops and dances, and the horrible clash of arms as they shake their shields in the way their fathers did before them – all these things are intended to terrify and appall" (*The History of Rome*, 38.17). Berserks howled like animals: "Now bearserks'-gang [*sic*] seized them, and they howled like dogs" (*Grettis saga*, 19). According to the earliest berserk account of Harald Hairfair's victory at Hafursfjord around 872 CE:

> The berserks bellowed as the battle opened,
> The wolf-coats shrieked loud and shook their weapons.
> (*Hrafnsmál,*8; cf. *Heimskringla*, The History of Harald Hairfair, 18)

Berserk-style Rus warriors unnerved seasoned Byzantine troops by "roaring like beasts and uttering strange and weird howls" (Leo, *History*, 8.4).

Germanic warriors sang before battle to "kindle their courage…[and] terrify their foes….What they particularly aim at is a harsh, intermittent roar; and they hold their shields in front of their mouths so that the sound is amplified into a deeper crescendo by the reverberation" (*Germania*, 3). Berserks bit on the iron rims of their shields to bring on battle trance. "And as he came forward…to the ground of combat, a fit of Berserk fury seized him; he began to bellow hideously, and bit his shield" (*Egils saga Skalla-grímsonnar*, 67). According to Speidel (2004), bears clack their teeth when on the defensive, and berserks made the same sound by biting on their shields' metal rims.

The Berserk State as Battle Trance

In combat berserkergang was characterized by fearlessness, supernatural strength, and invulnerability. Stripping before or during battle signaled fearlessness (Kershaw, 2000; Speidel, 2002, 2004), hence *bare of shirt* for *berserkers*. Fighters would ostentatiously discard armor and even clothing to demonstrate courage, disdain for the opponent, love of glory, and invulnerability magic. According to Polybius, the Celts "calculated to inspire terror" among the legions by doffing their clothing and moving into the front lines naked except for weapons (*Histories* 2.28). Diodorus Siculus said that Gallic warriors "despise death to such a degree that they enter the perils of battle without protective armour and with no more than a girdle about their loins" (*The Library of History*, 5.29). Norway's king Hákon went berserk when surprised and badly outnumbered,

> Flung off his war clothes,
> Slipped off his byrnie,
> Before he began.
> The gladdest of fighters…(*Heimskringla*, The History of Hacon the Good, 32)

Good spirits – laughing at danger, especially when death seemed inevitable – was a bid for Valhalla and fame, as were heroic deeds. When Byrhtnoth, Anglo-Saxon leader of the battle of Maldon, was impaled by a spear, he broke off the shaft, leaving the point in his body, then killed his attacker with a spear-thrust through the neck and drove a spear through another foe's mail coat and into his heart:

> The earl was the blither:

> the brave man laughed then, said thanks to Metod [Christian God]
> for the day-work God gave him. (*The Battle of Maldon*, ll. 146-148)

Warriors discarded their shields or wore them on the back instead of defensively (Speidel, 2002, 2004), shown in the Viking version of the battle of Brunanburh,

> Then Thorolf became so furious [berserk] that he cast his shield on his back, and, grasping his halberd with both hands, bounded forward dealing cut and thrust on either side. Men sprang away from him both ways, but he slew many…. (*Egils saga Skalla-grímsonnar*, 53)

Two-handed sword or spear work signifies that the warrior has thrown off his shield (Speidel, 2004). For example, Asmund went berserk and sang, "'Now without shield let us ply our warfare bare-breasted, with flashing blades….' When he had said this, he gripped his hilt with both hands, and, fearless of peril, swung his shield upon his back and slew many" (Saxo Grammaticus, *The Danish History*, 1).

Even at a time when fighters routinely hacked one another to pieces, feats of superhuman strength stand out in the texts. Reported with odd details, these sources undoubtedly reflect eyewitness accounts of actual events, if not those ascribed to a particular actor. For example, Kveldulf "brandished high his battle-axe, and smote Hallvard right through helm and head, so that the axe sank in even to the shaft; then he snatched it back towards him so forcibly that he whirled Hallvard aloft, and slung him overboard" (*Egils saga Skalla-grímsonnar*, 27). Thorolf, fighting without a shield:

> slew the man who bore the earl's standard, and cut down the standard-pole. After that he lunged with his halberd at the earl's breast, driving it right through mail-coat and body, so that it came out at the shoulders; and he lifted him up on the halberd over his head, and planted the butt-end in the ground. There on the weapon the earl breathed out his life in sight of all, both friends and foes. Then Thorolf drew his sword and dealt blows on either side, his men also charging. (*Egils saga Skalla-grímsonnar*, 53)

In battle trance, berserkers were invulnerable to fire and blades. Sivald's sons "would roar savagely, bite their shields, swallow hot coals, and go through any fire that could be piled up…." (Saxo Grammaticus, *The Danish History*, 7). Invulnerability to bladed weapons was sometimes attributed to wearing animal skins (e.g., *Heimskringla*, The History of King Olav, 228*), though it is often* impossible to tell how berserkers were clad. "When the roll of Harold's army was called, many were they that had fallen, ….nor was there a man unwounded in the king's ship before the mast, except those whom iron bit not, to wit the Berserks" (*Egils saga Skalla-grímsonnar*, 9). In one epic battle two berserks Egil and Atli hacked each other's shield to pieces.

> And when Atli's shield was of no use, then he cast it from him, and, grasping his sword with both hands, dealt blows as quickly as possible. Egil fetched him a blow on the shoulder, but the sword bit not. He dealt another, and a third. It was now easy to find parts in Atli that he could strike, since he had no cover; and Egil brandished and brought down his sword with all his might, yet it bit not, strike where he might. (*Egils saga Skalla-grímsonnar*, 68).

When berserks fought each other, they tried to bypass their opponent's invulnerability (e.g., *Grettis saga*, 40). For example, Beowulf and Grendel both seem to have been berserks (Sharma, 2005). "Not blade on earth, no blacksmith's art/Could ever damage" Grendel (*Beowulf*, ll. 801-802), so Beowulf tore off Grendel's arm, mortally wounding him (ll. 816-821). In the duel above, when Egil's sword would not bite Atli, he threw it away "and bounding on Atli…. Egil went down prone upon him and bit through his throat. There Atli died" (*Egils saga Skalla-grímsonnar*, 68).

Battle Trance in Other Sacred Traditions

Battle trance is also attested in Southeast Asia's ecstatic champion legacy *amok*, which, like berserkergang, has been misrepresented and pathologized, coming to mean popularly a frenzied, senseless, destructive rage ("running amok" and "going berserk"), discussed below. "*Amok*, far from being an individual, disorganized and insane activity" – as now construed – was a "coordinated, group form of violence…unleashed through invulnerability rituals" (Farrer, cited in Reid, 1988, p. 125). It was originally a combat tactic in India's Hindu states (Barnes, 2007; Kon, 1994) involving trance possession by war-gods, which enabled warriors to fight without pain or fear until they were slain or collapsed from exhaustion. India's colonizing of the Malay Archipelago spread this combat style, which became known as *amok*, probably from Sanskrit *amokshya*, *that which cannot be loosed* (Goldenberg, 2013) or *no freedom*, signifying either the warriors' unbreakable commitment to the gods, or, since *amok* was also used as a battle-cry, that no quarter would be given (Barnes, 2007).

Amok originally meant a fight to the death, either in a mass action or in a duel (Charney, 2004). Amok warriors, unless they prevailed, expected to be killed but not before they had slaughtered as many foes as possible. Amok warriors were strategically deployed. The Javanese used an amok vanguard as shock troops to intimidate, scatter, and kill the enemy in the opening moves of a battle (Reid, 1988). During the 1624 siege of Madura, some 2,000 Madurese warriors feigned retreat, then wheeled and "ran amuck" against Sultan Agung of Mataram's 50,000 troops, killing 6,000, including 17 top commanders (Charney, 2004); Agung was later defeated by 800 amoks. The Balinese, who preferred massed formations, led attacks with amok troops, who, if they succeeded in killing the enemy leader, often decided the battle before the regular troops engaged.

Amok warriors, after elaborate spiritual rituals to create battle trance, charged slashing with blades. A rare seventeenth-century first-person account describes engaging a Makassar amok warrior:

> I plunged my lance into his stomach; nevertheless, the Makassar, as if he had no sense of feeling, advanced upon the weapon which I held fast in his body, and made incredible efforts to come at me in order to run me through; and he would infallibly have done it, if the hilt of the blade had not hindered him. I found that my best way was to retreat a little, still keeping the lance in his stomach, without venturing to repeat my thrust, till at length I was relieved by others of the lancement who laid him dead on the spot (Forbin, 1999, p. 105).

Documented more recently, elite Philippine troops, Muslim Moro swordsmen, employed suicide attacks called *juramentado* (from the Spanish, *one who takes an oath*; Tarling, 1992), involving a type of battle trance produced through ritual purification and religious preparations for a savage attack. In juramentado, sword-wielding Moro warriors could not be stopped by a .38 caliber revolver (e.g., Foreman, 1906), the regulation weapon issued to the U.S. Army and Philippine Constabulary, so they were given Colt .45 revolvers and shotguns. For example, a juramentado warrior in Zamboango, hit by seven revolver shots, kept charging and got close enough to cut the leg off an American officer (Woolman, 2002). Hurley (1938/2011) reported an attack by a Moro who had been plowing when he saw constables shooting other Moros. Without time to ritually prepare, he grabbed a sword and kept attacking even after being struck by eleven bullets and was only stopped when a 3-inch long, 30-40 caliber, 220-grain Krag bullet fired at a distance of ten feet pierced his spine (p. 327) – and still had enough strength to hurl his sword at his enemies as he fell.

With the increasing use of artillery, this ancient close-quarters fighting style became ineffective.

Demonizing Battle Trance

Berserkergang has attracted a fair amount of scholarly attention – unfortunately most of it unsound – as people have tried to account for it in reductive terms, attributing it to the ingestion of psychotropic substances, for example (e.g., Dale, 2017; Fatur, 2019; Ruck, 2016), but those explanations do not hold up to scrutiny (e.g., Geraty, 2015; Wade, 2016) since most produce effects adverse to combat fitness. Today a condition called excited delirium syndrome (EDS; Benzer, et al., 2013; also known as lethal catatonia, acute exhaustive mania, and agitated delirium [Sztajnkrycer & Baez, 2005; Takeuchi, et al., 2011]) shares some features with battle trance, such as combativeness, extreme endurance and superhuman strength, but the resemblance is superficial since it also involves hallucinations (Gill, 2014; Mash, et al., 2009; Ross & Chan, 2006) and manufactured chemicals not available to historical battle-trance populations (Flosi, 2011; Gill, 2014; Sztajnkrycer & Baez, 2005). Though the possibility of drugs cannot be dismissed, timing and dosage logistics as combat preparation would have been extremely difficult historically. Moreover, the documented ability of warriors to deliberately or adventitiously go into battle trance during combat weakens any drug argument.

When not attributed to drugs, berserkergang has been pathologized as an involuntary mental condition – a kind of insanity rather than a useful, cultivated state. It has been compared to hypomania, one of a range of poorly understood manic states of exaggerated euphoric or aggressive activity not requiring hospitalization nor declining into catatonia or death (Lee, et al., 2012). Hypomania is characterized by grandiosity, wakefulness, verbosity, distractibility, increased involvement in goal-directed activities, and elevated or irritable mood without hallucinations or delusions (APA, 1994). Other explanations have included self-induced hysteria, epilepsy, mental illness, or genetic flaws (Byock, 1995; Carlson, 2006; Foote & Wilson, 1970), but none accounts for more than a fraction of the battle trance data. The APA has conflated berserkergang and amok with equally poorly understood conditions from different cultures. Three recent *Diagnostic and Statistical Manuals* (DSMs; APA, 1980, 1994, 2013) equated a diagnosis called intermittent explosive disorder (IED) with berserkergang, amok, and other "culture-bound syndromes" (a category dropped from the DSM-V; APA, 1994, p. 845). IED, a disruptive impulse control and conduct disorder, is poorly defined (Ahmed, et al., 2010; Parzen, 2003) and characterized by unpremeditated explosive outbursts of rage disproportionate to the situation (APA, 1980, 1994, 2013). The APA's example of amok to illustrate IED involved a Filipino man who, upon learning of his wife's infidelity, killed her parents, injured her and their son, and then set her lover's brother's house on fire, which killed two children (Parzen, 2003, p. 142; cf., Schmidt, et al., 1977) – hardly the sacred states cultivated by elite warriors for group survival. The amok literature shows how the field of psychology systematically enabled the political interests of colonial powers to coopt and reduce these heroic states to intoxication and insanity (e.g., Charney, 2004; Condos, 2016; Saha, 2013; Van Rossum, 2013; Vink, 2003; Wade, 2021), a discussion beyond the scope of this paper.

The Evolutionary Trajectory and Promise of Battle Trance

Nevertheless, battle trance remains an evolutionarily useful survival mechanism with immense promise to enhance quality of life. The following examines research on the techniques for creating battle trance and on the validity for claims of its extraordinary qualities.

As noted, the human musicality – war songs, the battle cry, and war dances – used to produce battle trance may be evolutionarily hundreds of millions of years old (Fitch, 2006). Musicality in this sense means *song* (complex, learned vocalizations for communication, such as bird song and whale song) and *instrumental music* (the use of body parts or other objects to produce structured, communicative acoustical signals; p. 183). Human song probably evolved before or at the same time as speech, and instrumental music possibly dates to Neanderthal times (Cross, 2003a, 2003b; Fitch, 2006). Human percussive signals and song are thought to have developed to advertise territoriality and defend against aggressors (Fitch, 2006; Jordania, 2011, 2014; Hagen & Hammerstein, 2009; Randall, 2001) – hence their association with combat – but they also served other social interactions (e.g., Large & Gray, 2015). Human musicality includes synchronizing musical behavior with others by performing the same action at the same time or engaging in more complex forms of entrainment.

Music helps create group mind through hardwired rhythmic coordination among individuals in a collective (Jordania, 2011, 2014; See also Brown and Fitch in this volume). Music provides a sense of shared experience in a temporal framework, regulating emotions and motivational states and affecting action-readiness (Bispham, 2006), increasing the survival of hominid groups (Jordania, 2011, 2014; Kogan, 1997). Musical rhythms coordinate and entrain the movements and emotions of individuals in groups, a technique ultimately used in military drills and cadences (McNeill, 1995).

This type of intentional, ecstatic group entrainment and the characteristics of battle trance are now being validated by research, such as the discovery of mirror neurons (Cross, 2003a). Synchronous singing and dancing produce high levels of solidarity and bonding (e.g., Fischer, et al., 2014; McNeill, 1982, 1995; Swann, et al., 2009; Xygalatas, et al., 2011), which promote group survival. These techniques are notably associated with the more extraordinary feats of battle trance and spiritual performance. Their psychophysical states occur naturally in group entrainment without ingesting drugs.

The fearlessness, will and stamina to keep pursuing the goal despite bodily injury seen in battle trance may be related to feelings of invincibility from group solidarity, even when facing overwhelming odds on the one hand, or, on the other, from rage at seeing one’s fellows slaughtered and subsuming personal survival in ecstatic suicide for them and/or personal glory. Analgesia, a noted feature of battle trance, feeds fearlessness, and vice versa: when intent on a goal and highly aroused, pain may not be felt.

The perception and tolerance of pain vary significantly by mental state, regardless of the degree of injury (e.g., Kelley, 2007; Montgomery, et al., 2000; Simons, et al., 1988). Even in a normal state, people can experience serious injury without pain. More than a third of alert, rational emergency-room patients (Wall, 2000) reported no pain at the time of injury. More than half of those with skin injuries and 28% of those with deep tissue injuries felt no pain for some time. Pain onset occurred within an hour for the majority, but some felt no pain for many hours. One factor affecting pain perception is group entrainment: rowing teams (Cohen, et al., 2010; Wiltermuth & Heath, 2009) and other groups engaging in synchronous behavior (Sullivan & Rickers, 2013; Sullivan, et al., 2014) demonstrate greater pain tolerance.

Although some kinds of analgesia are linked to pathological dissociation (e.g., Cardeña, 1999), many are not (e.g., Grahek, 2001; Melzack, 1998; Wall, 2000) – and some involve deliberate dissociation, such as hypnotic analgesia (e.g., Casiglia, et al., 2017). Randomized controlled trials have shown that hypnosis for acute pain gives greater relief than other treatments (Patterson & Jensen, 2003, p. 516; cf., Montgomery, et al., 2002; Patterson, et al., 2006; Weichman-Askay, & Patterson, 2007) and accelerates healing (e.g., Garland, et al., 2017; Ginandes, et al., 2003. Since people with dissociative identity disorder can respond physiologically with a range of reactions to a single stimulus, such that one personality may be allergic to a substance that produces no effect on other personalities occupying the same body, “it has been proposed that the neurophysiological underpinnings for both spontaneous dissociative and induced hypnotic reactions are similar” (Cardeña, 2018, p. 7). It may be that berserkers who “became” bears or wolves or amok warriors possessed by the gods during battle trance produced essentially the same effect. However, combat’s intense, in-the-moment survival demands are so all-consuming that serious wounds are, to some degree, not even noticed, a “distraction” effect experimentally validated (e.g., Hoffman, et al., 2011; Patterson, et al., 2006).

Closely related to analgesia is the berserkers’ invulnerability to blades and fire, feats well documented today from self-induced states often supported by group entrainment of song and dance, especially as a form of spiritual performance, such as the body piercing, suspension, and endurance ordeals of the Sun Dance ceremony and the Salish Spirit Dance in North America (Jilek, 1982). Imperviousness to blades features in numerous contemporary spiritual performances, such as *tangka*, a kind of war magic practiced by the Minnan people who comprise most of the ethnic Chinese living throughout southeast Asia (Chan, 2014). Practitioners, acting as exorcists and trance mediums incarnating warrior gods, protect their communities by processing through the streets during festivals in battle trance. Dancing, especially with repetitive head shaking, induces a deep trance before they (or others) drive swords, rods, and other implements through their flesh to demonstrate invulnerability and imbue their bodies with the spirit-power of the items impaling them (e.g., Farrer, 2009; Hamilton, 2008). At the Thaiusam festival in Singapore, devotees pierce the skin of the forehead, tongue, and cheeks, and wear frameworks of metal rods (*kavandis*) that penetrate deeper into their flesh the longer they are worn (Belle, 2017; cf., Collins & Ramanthan, 2014; Stirn, 2003). They experience little pain and minimal bleeding. Still other Asian adepts climb barefoot unscathed up ladders made of knives (e.g., Farrer, 2009; Hamilton, 2008). Some rend their flesh with broken glass, spikes, skewers, knives, swords, and hooks (often used to pull weights or suspend the body) with little pain or bleeding (e.g., Ambos, & Sax, 2013; David, 2009; Hall, 2001, 2004, 2011; Kaarsholm, 2014).

Certain Islamic sects engage in similar performances. North African Isawiyya Moslems are noted for “eating fire and cutting themselves in ecstasy” (Brett, 1988, p. 38). Followers demonstrate instantaneous healing of deliberately caused bodily damage, such as jamming spikes and skewers into their torsos and hammering daggers into their skulls and clavicles (Brett, 1988; Crapanzano, 1973). These phenomena have been replicated in laboratory conditions. According to Hall (2001, 2004, 2011), adepts of the Sufi Tariqa Casnazaniyyah school, who pierce their bodies with spikes, blades, glass, and the like, have such complete control over pain, bleeding, and infection that their wounds heal within 4-10 seconds. Hall, trained in the practice himself, has reproduced it reliably in laboratory conditions (2004, 2011; Hall, et al., 2001), though with slower results. Hall averred that, based on EEG readings during this experiment (which involved no trance-induction methods), these phenomena were not related to “hypnosis, realization, altered states of consciousness, or trance states” (2004, p. 93; 2001, 2011), attributing the invulnerability to remote transmission by the sect leader (cf., Heath, 2011). Demonstrations had to be planned in order to succeed, suggesting some mental preparation was required; if adepts were wounded accidentally, they did not heal rapidly. In a series of laboratory case studies, a Japanese yogi endured tongue piercing without pain, bleeding or subsequent infection;

EEG readings showed a self-induced state resembling trance (Peper et al., 2006). Rapid healing phenomena have been observed among the patients of Brazilian trance surgeons (Don & Moura, 2000; Hall, 2004).

Invulnerability to fire, typically in the form of a, has figured as a sign of spiritual attainment and/or invulnerability magic cross-culturally for centuries (e.g., Ambos & Sax, 2013; Al-Krenawi, & Graham, 1999; Danforth, 1989; Kane, 1982; Pigliasco, 2010; Winfield, 2009; Xygalatas, 2012). Today it is a popular activity at Western self-development seminars bolstered by intense group bonding via collective rituals, singing, and dancing. It features shared, synchronous arousal among participants as well as observers (Konvalinka et al., 2011; Xygalatas et al., 2011). Fire-walking involves a particular psychophysiological state that otherwise appears normal (Hillig, & Holroyd, 1997/1998; Pekala, 2015; Pekala, & Ersek, 1992). Religious practitioners have demonstrated the capacity to withstand other dangerous sources of heat by rolling in hot sand (Ambos, & Sax, 2013), dipping hands into boiling oil or molten metals (Farrer, 2009; Hamilton, 2008; Waterson, 1995), passing hot skewers through the tongue, and licking boiling liquids or red-hot metal without harm (Al-Krenawi, & Graham, 1999).

Many such proofs of invulnerability are ritually practiced in a blended spiritual and martial context common in Asia (e.g., Dalton, 2011; Keyes, 1978; Moyar, 2004; Schober, 2007; Yu, 2005), especially the martial art *silat*, which includes *dabus*, a ritual performance of invulnerability, and *daboih*, a battle trance preparation used during the war against the Dutch (Gargenbert, 2000). Silat displays include withstanding blows from iron spikes, washing in sulfuric acid, slicing the tongue with machetes and regurgitating live bats without harm (Wilson, 2002, p. 265).

Two culturally specific aspects of berserkergang, shapeshifting and bilocation, have not been systematically studied, although both are widespread in legendary accounts and anecdotally attested. Shapeshifting appears in many shamanic traditions (e.g., Cebrián, 2010; Howard, 2014; Vélez, 2015; Winkelman, 2010), typically as a kind of war or hunting magic. Therianthropic figures that combine human and animal elements appear frequently in paleolithic petroglyphs, though whether such images represent altered states brought on by hallucinogens or trance rites is the subject of fierce debate (e.g., Helvenston, & Bahn, 2003; Hodgson, 2006; Lewis-Williams, 1997, 2002; Lewis-Williams, & Pearce, 2012; McClenon, 2002; McGranahan, & Challis, 2016; Soloman, 2013), nor is recent research on therianthropic experience any clearer (e.g., Blom, 2014; Kjellgren, & Norlander, 2000-2001; Van Bockhaven, 2018). According to Lindstrøm (2012) and Rossano (2009), shapeshifting – or the state of mind that conduces to animal identification – produced a survival advantage, and identification with animals may possibly be innate for some people ("Therianthropy," 2010). Bilocation remains anecdotal, but it also appears in many cultures as a power demonstrated by spiritually important people, such as Muslim, Hindu, and Christian mystics and saints (Zhmud, 2016) and silat practitioners (Farrer, 2009). The paranormal literature includes secular bilocation accounts (e.g., Auerbach, 1996; Barclay, 1973; Inglis, 1992; Rogo, 1982), defining it by the following criteria: one person's subjective awareness being in two bodies in different physical locations at the same time; each embodiment performing physical acts; witnesses perceiving themselves to be interacting with a real person; and the act of being in two places at once happening instantly, so that the individual has no awareness of having left one body to go into another; and the duration of being in two bodies at once lasting longer than most out-of-body experiences (Heath, 2011).

Indeed, paranormal studies recognize the validity of battle-trance phenomena and support the notion that such capabilities are an innate, universal, human capacity (Daniels, 2005; Kripal, 2014; Targ, et al., 2000). The branch associated with invulnerability magic and battle trance is psychokinesis (PK), any form of mind-matter interaction not explicable in conventional scientific terms (J. B. Rhine, 1934; cited in Rock, et al., 2013). Although most PK research has focused on mentally influencing objects, such as dice and random number generators (e.g., Iqbal, 2013), other studies involve biological targets (e.g., Alvarado, 2018; Braud & Schlitz, 1983; Schmidt, 2015). The effects are small but consistent and not owing to statistical error (Radin, et al., 2006). PK may very well be involved in fire and blade immunity, rapid healing, extraordinary feats of strength and speed, and bilocation (Heath, 2011). It has yet to be connected with shapeshifting.

Conclusion

Thus, contemporary research indicates that the extraordinary feats associated with battle trance are an inherent part of the human repertory. Drugs are not necessary to produce them, nor are these states signs of mental illness. As research increasingly assesses the abilities associated with seemingly superhuman feats, it is likely that most, if not all, of the battle-trance phenomena will be verified as universal human capacities, existing to a greater or lesser degree across individuals, but potentially subject to cultivation.

Originally developed from instinctive offensive and defensive behaviors and refined over millennia, battle trance may finally have reached the terminus of its usefulness in war today, when soldiers are more likely to die from remote killing technologies. However, the extraordinary abilities gained in battle trance suggest different applications, especially the capacity for self-induced analgesia with the concomitant ability to allay the psychophysiological stress that accompanies pain, and the mental ability to control bleeding, mitigate infection, and accelerate healing. With modern research methods, measurement techniques, and biofeedback processes, these abilities can be fully realized as the body's natural potential to tolerate pain and heal in response to trauma. Brain-imaging, biofield assessment, galvanic skin response, and other sophisticated feedback techniques can be used to assess, map, and cultivate such states. The identification and refinement of battle trance features can further scope the extremes of human psychophysiological potential and how to produce and enhance those faculties intentionally. Some features of battle trance, such as fearlessness and extraordinary strength and speed, are undoubtedly already being used deliberately in sport (Murphy, 1992; Kelley, 2007); others, such as the analgesic effects of trance and body transmogrification, and the inability to manage burn and penetration trauma, can be useful in healing modalities. Battle trance has great potential to improve quality of life and extend the horizons of embodiment.

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Trophic Level, Arboreal Position, and Size of Both Predators and Primates Gave Rise to a Diverse and Multi-Functional Musicality

David M. Schruth (USA)

Abstract. *The predator-prey relationship is a fundamental directional dyad underlying trophic dynamics that emerge within food-chain networks. Numerous anti-predational behaviors are possible to help animals mitigate the risk of becoming prey, including crypsis, warding, avoidance, evasion, and confrontation. Most primates leverage both vigilance and alarm calling within groups as well as infant carrying amongst protected trees to avoid being targeted and pursued by predators. Other vocalizations of primates vary greatly and many of them contain myriad manifestations of musical complexity including spectral and temporal patterning as well as diverse contouring. Smaller primates, who may inhabit attenuated terminal branches, use more subtly short melodic sequences to maintain within-group contact, but also to circumvent eavesdropping by predators. Larger primates, who may brave open ground, use calls that are more salient, rhythmic, and syllabically diverse to assert dominance outside the group and possibly towards other species. Body size also tends to scale allometrically with other (usually morphological) traits within an individual – steeply with sexual traits and more shallowly for weaponized traits. The stronger positive correlations of body size with syllable than with rhythm suggests an attractive function of melodic elements and a mildly repulsive function for rhythm. This finding is further backed by affiliative contexts for other spectral aspects (e.g. transposition) and more threat-based contexts for temporal ones (e.g. repetition). Complex rhythms appear more often in larger terrestrial species (e.g. hominid apes and some lemurs), bolstering a possibly analogous purpose, of warding-off predators, by newly terrestrialized hominins. This combination of familial arboreality and larger-group terrestriality may have spawned our uniquely dualistic musicality – as composed of both amiable melodies and imposing rhythms.*

Prey behavior, trophic security, life history, and acoustic strategies

Within their respective food webs, animals leverage a vast array of evolved and acquired tactics to avoid falling prey to predators (Fig 1). These can range from blending-in with surroundings, thereby largely avoiding sensory detection, to *aposematically* overwhelming predator senses with a barrage of unpalatability – in the form of odorous, soniferous, or colorfully honest signals (Cooper and Blumstein, 2015). Animals can also evolve *deimatic* ways of deceiving predators as part of an avoidance strategy – via exaggeration, distraction, startling, or just playing dead (Edmunds, 1974). Structural features of phenotype or niche can also be employed to make consumption or pursuit difficult. More active forms of protection may include evasion (e.g. running or flying away) or confrontation (e.g. fighting with claws, teeth, or horns). More socially inclined species (e.g. anthropoid primates) can team-up to post lookouts, warn each other, carry smaller group members away, or even collectively mob their predators.

Species of higher trophic standing may also produce more offspring [*r*] or increase gestation lengths and lengthen lifespans [*k*] – by leveraging larger body size, more group members, or higher vertical positioning – as mitigated by both population density and predictability of resources (Wilbur, Tinkle and Collins, 1974). Burrowing, island dwelling, and arboreal species – such as wild dogs, marsupials, song birds, and primates – are slow to wean their altricial young, thereby also slowing growth rates (Case, 1978) and extending individual offspring security through more concentrated nurture. Such (*k*-selected) species, particularly primates, have lower parity and longer lifespans (Jones, 2011), perhaps as a result of leveraging trees to mitigate predation. Since some terrestrial predators can climb trees to pursue and corner arboreal residents at these dead-ends, many primates have alternatively evolved means of positional avoidance that employ discontiguous, inter-substrate, and inter-tree locomotion.

Another way [typically larger] animals, and indeed many primates, can deter predators is by producing calls of high amplitude (Wich and Nunn, 2002). These ‘loud calls’ have long-distance transmission properties that evolved as a remote way to demarcate home range and maintain spatial boundaries (Mitani and Stuht, 1998). But it is uncertain to what extent these calls are directed within species, such as towards rivals or the opposite sex (Delgado, 2006), or between species, such as towards predators (Zuberbühler, Jenny and Bshary, 1999). In any case, repulsive terrtiorial calls of primates are typically produced from a position of elevated trophic standing, analogous to the loud-calling of non-primate apex predators – including large carnivores, such as lions, hyenas, and wolves (Hagen and Hammerstein, 2009).

This chapter starts where others have left off, by exploring the idea of acoustics as frequently serving to defend territories by deterring the encroachment of predators and competitors (Hagen and Hammerstein, 2009; Jordania, 2011; Hagen, 2022). This work begins by delineating forms of defense against predators ranging from aposematic repulsion (e.g. chorusing) to inconspicuous silence and camouflage (see chapters by Jordania, Podlipniak, and Alonso, this volume). Here I propose that in primates, more salient acoustic output originated as generically repulsive threats directed more generally towards a multitude of predators. I further argue that such threats, in many cases, likely atrophied towards a less actively repulsive (e.g. aposematic) and possibly even more attractive (e.g. mating) intentionality when those primates (esp. in our own lineage) became more secure with regard to predation.

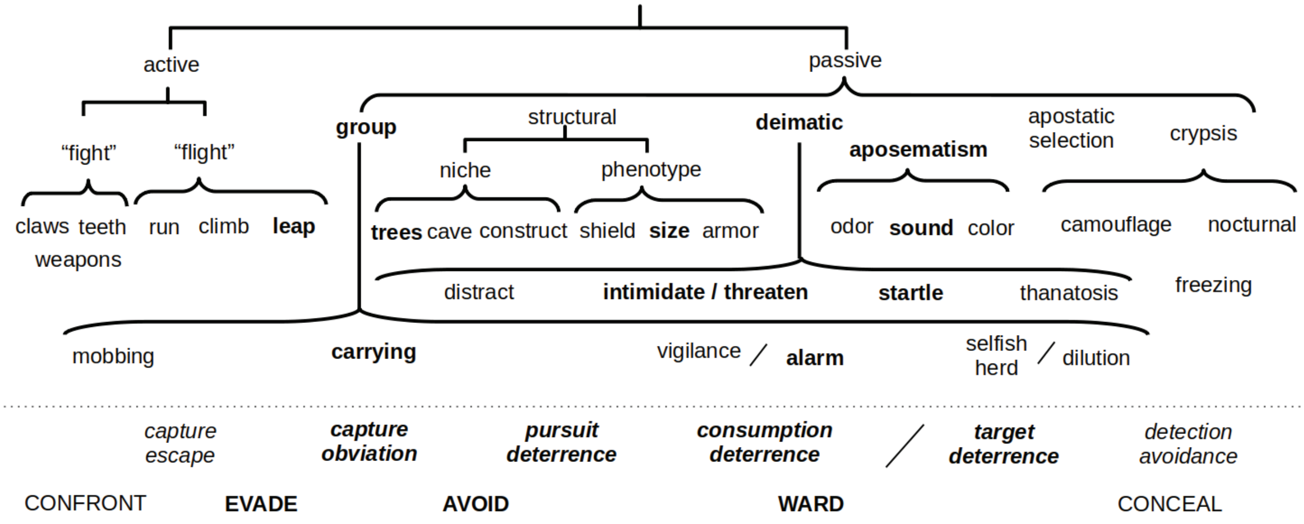

Figure 1. The many forms of anti-predational behavior can be organized into the above diagram according to related strategies – broadly partitioned into a dichotomy of passive (right) or active (left). These more exigent behaviors can further be split into fight or flight (far left) whereby prey actively counter predators by fighting back or fleeing evasively. On the far opposite extreme (far right), potential prey will conceal themselves and avert detection entirely via a variety of means, including crypsis, masquerade, mimicry, or freezing. Aposematism, covered in a previous chapter (by Jordania), appears alongside less hidden defenses such as toxicity and deimatic strategies. This chapter focuses on the intermediate categories, such as 'warding-off' and avoidance, that lie between active and passive defenses. These prominently include group strategies, which range from active fighting in the form of mobbing or more passive herd-dependent strategies, as well as the use of motor faculties (e.g. climbing) and structure (e.g. trees) to avoid consumption by terrestrial predators. Carrying, in particular, is a socially facilitated capture-avoidance behavior that often leverages structure – both passively, via intrinsic morphology, and through movement, via extrinsic vehicles. A central point advanced here is that most primates employ these intermediate strategies – favoring evasion, avoidance, and warding of predators rather than either extremes of confrontation or concealment. This manner of capture obviation may have persisted, via phylogenetic inertia, into our hominin line – emboldening and diversifying both intra- and inter- group (as well as anti-predator) acoustics to serve in both attractive and repulsive capacities.

Crypsis, avoidance, masquerade, and alarm

Many smaller primates, including pottos, lorises, tarsiers, and many lemurs, are nocturnal and augment predation avoidance via crypsis (Gursky and Nekaris, 2007). However, primates primarily obviate consumption by occupying trees (see the next section on arboreal positioning). Larger, especially anthropoid, primates evolved socially-facilitated means of protecting themselves from predators, such as nest construction (e.g. apes), as well as vigilance and mobbing (e.g. monkeys). A continuum of warding behaviors – from deimatic (bluff) to (honest) aposematic signal – may stave off imminent confrontations, to varying degrees of success. Alarm acoustics, including both tonal and atonal calls, which are directed both towards the group or the predators themselves, can play a central part of these strategies (Zuberbühler, Jenny and Bshary, 1999). Thus, the danger of many forms of impending predation can induce an array of possible vocal responses in primates.

The acoustic features of such alarm-like calls have similarities with many other calls. And some group conflict related calls, may be more syllabic. But those explicitly related to predator presence tend to be more repetitive if not also more rhythmic – an observation also applicable to bird alarm calls (Templeton, Greene and Davis, 2005). Analysis using predator counts at the genus level (Miller and Treves, 2011), compared with various musical features, suggests primates become less vocal when sharing habitats with a greater diversity of predators (Fig 2). Conversely, as certain genera became more adept at inter-arboreal avoidance via specialized locomotion through trees, they may have also been emboldened to vocalize more saliently (Schruth and Jordania, 2020). This inversely associating trend is especially strong for repetition and rhythm (bold lines at bottom of Fig 2). Thus, for species who are threatened by numerous predators – and face a higher risk of being eaten – producing only a few generic anti-predator calls should not necessarily qualify them as being aposematically capable of inducing instinctive retreat (but see Jordania and also Alonso, this volume).

Arboreal apes likely co-evolved above large terrestrial felines, using the canopy to deftly move between trees (Isbell, 1994). And modestly vocal orangutans serve as possible exception to the general emboldening effect of arboreality, proposed above. Unlike gibbons who routinely employ more acrobatic locomotion to avoid consumption by tree climbing felines, more deliberate and often cryptic orangutans have developed capacities for nest building and a correspondingly mystifying “kiss-squeak” atonal alarm call (Lameira *et al.*, 2013). Vocally, such shorter and degraded tonality characterizes the calls of orangutans, in spite of their larger size and composed seclusion. Gibbons, on the other hand, are highly vocal – creating long call sequences with high levels of rhythm and repetition (Geissmann, 2000). But even these lesser apes, whose near crepuscular songs can preempt and possibly even masquerade their [often] sympatric hornbill which has calls similar in amplitude, frequency and accelerating tempo – subside in singing output throughout the day. Thus even highly soniferous animals can exhibit a diversity of anti-predation behaviors daily. But with lesser apes, such masquerade arguably morphed into a partial feigning of flight capability.

Many other primates also employ such a vocally active role in deterring group-outsiders via generalized deimatic threats – those ambitiously directed towards competitors, predators, or both. The analysis reported here suggests that threatening contexts most often involves repetition and rhythm, and further, that mobbing confrontations are often preceded by such temporal patterning, especially if containing intervalic units. This association between repetition [of barks] and mobbing has not gone unnoticed in other animals (Lord, Feinstein and Coppinger, 2009). Thus, both mild deimatic threats and more active aggressions may be associated with temporal patterning of calls. But primarily only in the former case do (temporal) acoustic features appear to be directed at predators who contend for apically-adjacent trophic positions. Admittedly, disentangling the directionality of causal relations between predation threats and prey acoustics continues to be quite challenging.

An evolutionary progression, from small and quiet to the large and loud, should logically entail crypsis and silence from the very smallest primates. But we might also predict that more vocal, mid-sized primates, who auditorially expose themselves to a greater number of possible predators, would produce vigorous yet generalized deimatic alarm and threat calls. Likewise, we would expect the largest and least easily consumed species, who face the fewest predators, to produce more passive aposematic signals. It is important to note that the difference between deimatic and aposematic largely lies in whether the targeted prey is eventually eaten (Bates and Fenton, 1990).

More evolved aposematic signals may require higher specificity – matching certain call types directly and individually to each specific predator. In turn, it is likely also, that most predator directed calls (e.g. of mid-sized primates) initially evolved as generic cues (e.g. of exaggerated size) designed to startle or intimidate a wider array of predator classes. This latter case allows for a generalized approach to acoustic defenses against predators, and it would occasionally fail to work in all cases. In sum, generalists with many different types of predators (e.g. monkeys) likely evolved a small set of more generalized deimatic calls, whereas species with fewer predators (e.g. apes) might be more efficiently aposematic with an even smaller set of extra-species calls, corresponding to their smaller pool of predators.

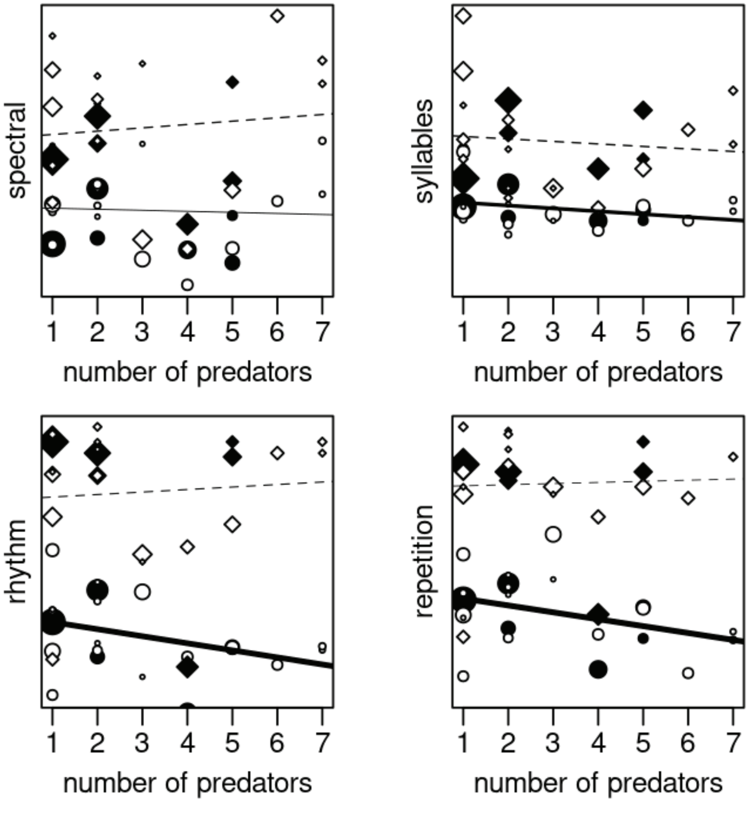

Figure 2. Duetting tarsiers and gibbons, who are primarily preyed upon by very few predators (e.g. pythons and leopards), appear in the upper left of most of these plots. Terrestrial (filled points) monkeys, such as vervets and even highly arboreal (open points) but smaller New World monkeys, use exceptional calls (max: dashed

lines) to voice alarm for many sources of predation. Although terrestrial taxa face a nearly two-fold higher predation risk and greater "silencing" [less vocally obvious upon grounding] (Schruth & Jordania 2020), exceptions persist for larger-bodied and collectively-acting primates such as hominids and many Old World monkeys. The two strongest trends (thicker lines) are decidedly downward for mean (circles) temporal patterning, but maximum (diamonds) may have positive associations, though not significant (thinner lines) here.

Arboreal positioning and intra-group calling

Primates have specialized as an order to avoid predation by climbing and leaping – moving throughout and between arboreal topological vantage points (Le Gros Clark, 1959). Their clawless and flexible embrace, enabled by use of an opposable thumb, allows not only more comfortable orthograde carrying but also the ability to grip a wide range of branch shapes and orientations. Large primates are capable of impressive inter-arboreal leaping (Druelle *et al.*, 2020) and can also produce salient loud-calls (Wich and Nunn, 2002), although those of leaf monkeys tend to be less elaborately exhibitional than the highly syllabic calls of similarly-sized (yet more acrobatic) gibbons. The difference could result from the many-fold greater number of predators that typically prey upon these leaf-monkeys than exist as threats to gibbons.

Acoustically, strictly arboreal primates prefer to use shorter more subtly-melodic transpositional calls to communicate between group members (Schruth, Templeton and Holman, 2021), without attracting unwanted attention by external threats. In the avian acoustics literature, this phenomenon of predators detecting conspecific-directed calls of their prey, is termed "eavesdropping." Eavesdropping typically focuses on the coevolutionary arms race between observation by predators and obfuscation by prey (Zuk and Kolluru, 1998). Risk of predation may reduce amplitude of calls (Reichard and Anderson, 2015), shape special aspects of acoustic structure of such soft signals (Akçay *et al.*, 2015; Vargas-Castro, Sandoval and Searcy, 2017), drive them to ultrasonic ranges (Arch, 2008), or entirely silence the songs of species (Zuk, Rotenberry and Tinghitella, 2006). An arboreal-descent version of such exposure-based muting has been termed "terrestrial silencing," and may act to reduce both call length and complexity across primates and possibly also other taxonomic clades (Schruth and Jordania, 2020).

Acoustics signals have helped to compensate for the loss of scent-based communication (Rogers and Kaplan, 1998), all while avoiding unwanted attention discussed above. In many animals, including primates, spectral display features may have co-evolved with locomotion by way of signaling aptitudes for motive emplacement (Schruth, 2021). Precise re-creation of song syllables likely served as intra-specific signals of cognition for pattern matching that could have, in branch landing species, also been useful in rapid visual gauging of distances for high impact grasping (Schruth *et al.*, 2020). As mentioned above, a pronounced contrast between gibbons and orangutans, who face similar predation threats, highlights the feasibility of this selection mechanism. Despite their larger size, orangutans are much less vocal than gibbons. Salient daily singing, by the latter, may not only reflect greater confidence in expedient inter-arboreal avoidance (e.g. to predators), but such vigorous recitation of diversely reappearing syllables may be an essential part of securing both range and mates, as signals among gibbons themselves.

Arboreal descent and terrestrial musicality in anthropoids

At some point, in our evolution from apes to humans, we can certainly surmise that our musicality became more complex and multi-faceted. While the most musical primates (e.g. gibbons, tarsiers, and indri) all frequently locomote using agile limb-landing in trees, humans are paradoxically not arboreal. Previous work on this subject speculated that this is because humans repurposed the motor-planning, homologous to the forelimb-dominant branch landing of other apes, for landing of ballistic devices in the hunting of terrestrial game (Schruth, 2005). More recent evidence, for possible connections with hominid hammering of stones, supports this hypothesis (Schruth *et al.*, 2020), through the positive associations of terrestrial hunting with both rhythmic and melodic aspects of the music of traditional human societies (Fig 3). Thus, it may not have been merely the shift to terrestriality that made *Homo* unique, but the freeing up of our forelimbs, to craft and deploy tools, which facilitated our trophic dominance over other terrestrial species. Such capacities for crafting and deploying remote weaponry vastly hastened our genus' selection towards a human-like transcendence of nearly all predation threats.

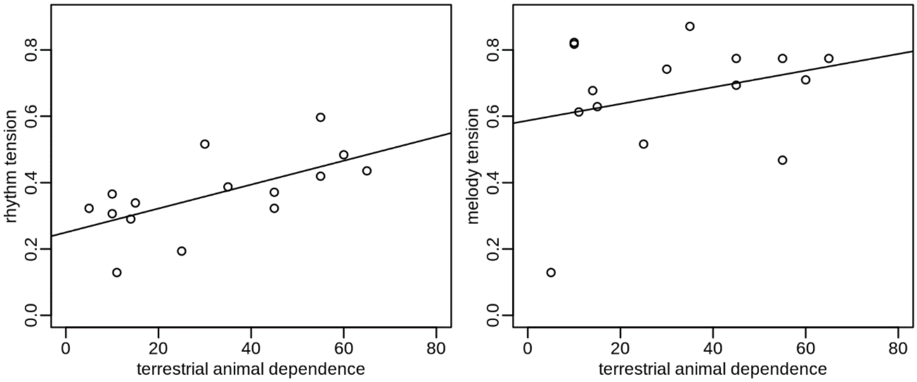

Figure 3. The significant positive associations between a *rhythmic* and melodic indexes (from the *Natural History of Song Database*) and degree of terrestrial hunting (from the *Binford Hunter-Gatherer Database*). Rhythmic display may signal collective action abilities useful, for example, in coordinated group hunting. Melodic display could signal precision spatial abilities required for crafting (and deploying) sharp weaponry (e.g. arrow heads) for use in ballistic attacks.

This shift towards increasing terrestriality also likely accompanied diminished forelimb use in hand-eye driven coordination, such as during climbing. Cognition for landing semi-vestigial limbs (those formerly used in more routine rhythmic climbing locomotion) could have been atavistically co-opted as part of an ornamental display signal. That is, as section pressures on accuracy in fore-limb climbing were reduced for increasingly terrestrial and occasionally bipedal primates, the lingering functionality of these limbs were reallocated towards other, perhaps reproductively focused, goals. Large terrestrial gorillas still deploy rapid chest-beating as possibly honest signals, perhaps of motor control for the occasional bout of arboreal clambering. Free arms, as merely accessory appendages, could have enabled other hind limb decoupled displays – perhaps even "dancing" – in lemurs, birds, and humans. Acoustic display in these species could operate to signal motor skill also useful for climbing, carrying, or crafting.

As primates became larger and more capable of coordinating as a group, thus emboldening increasing levels of terrestriality (e.g. in many anthropoids), they also trended towards declining spectral patterning in their calls (Schruth, 2022). This is strongly evidenced by the degradation of spectral definition in the calls of many cercopithecoids (Schruth, 2020). A shift to terrestriality likely also required larger individual or group sizes, or both (Willems and Van Schaik, 2017). Likewise, arboreal species tend to have more spectral features for within-group alarm and contact calling whereas terrestrial species tend to have more complex rhythms, possibly for countering extra-group threats (Fig 4). A combination of arboreal sleeping and terrestrial ballistics, protective against most predation by large terrestrial carnivora, likely elevated higher trophic standing by further reducing risks of attack from the rear or oblique angles (see also Fig 2). The calls of species with elevated trophic standing in complex and disconnected (e.g. arboreal) habitats reflect this difference in priority for anterior targeting over peripheral vigilance.

This shift towards terrestriality has been characterized previously as a tree-to-ground [sleep or nest] transition (Coolidge and Wynn, 2006; Samson and Nunn, 2015) and likely occurred gradually over millions of years in the late Pleiocene (also see Wah, this volume). A handful of key ecological factors associated with hominin life on the ground likely molded ancestral hominid behavior into a fully human form – including low temperature and light conditions as well as evening fatigue, anonymity, predation risks (Varella, 2023) and group cooking (Wrangham, 2009). These more recent (mid-Pleistocene) pressures, associated with nightfall over more open habitats, were alleviated by new forms of evening sociality empowered by the invention of fire – such as eating, singing, dancing, storytelling, and associated rituals (Varella, 2023). The central focus of this chapter explores a preexisting duality of *habitat* – both arboreal and terrestrial – of early hominins that existed several millions of years ago. Any related ideas on *finalizing* our human terrestriality through the controlled use of fire (<1MYA) only serve to complement those proposed here on *initializing* such a transition. And both certainly had profound effects on the structure and dynamics of groups.

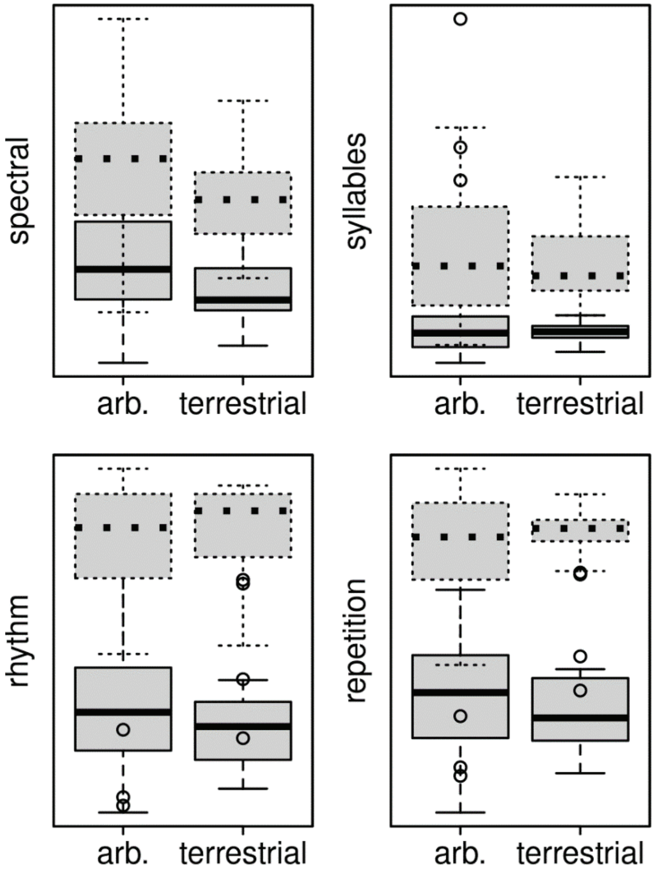

Figure 4. Spectral, but not rhythmic, musicality tends to decrease upon transition to terrestrial habitats. Only maximum (dashed) temporal aesthetics (e.g. *repetition* and *rhythm*) appear to increase in terrestrial species. The slight increase in *rhythm* is further accentuated after considering both body mass and climbing frequency. Four macaques, three great apes, and *Lemur catta* (top-most diamonds in Fig 5) primarily drive higher maximum *rhythm* scores here.

Group functionality of acoustic musicality

Music has been observed to elicit attractive as well as repulsive emotions (Nielzen and Cesarec, 1982) and could have evolved to facilitate group dynamics (Hagen and Bryant, 2003). This dichotomy is also observable across the animal kingdom with calls that can range from affiliative to threatening (Orwen and Rendall, 2001). Intra-group calls can help members localize conspecifics, orient and reunite with one-another, and help warn of impending danger (Arnold, Pohlner and Zuberbühler, 2008). Extra-group calls may help to advertise size, muscular agility (Schruth *et al.*, 2020), as well as to let predators know they have been detected (Zuberbühler, Jenny and Bshary, 1999). A class of calls that span both of these categories includes mobbing calls – that simultaneously serve as alarm, threat, and battle cry – to facilitate rounding up group members to collectively stave off an attack from predators or other groups.

Hominins likely experienced profound social and musical changes that coincided with walking. Bipedal pressures on modern hips selected for more compact brain folding and also more altricial offspring but therefore also necessitated social [mother-infant] bonding (Dissanayake, 1992). In humans, rhythm has been hypothesized to serve as a possible catalytic vehicle for inviting in new members into the group and perhaps to facilitate making music collectively (Savage *et al.*, 2021). Accommodation for additional group-display participants (in very small groups) seems to be slightly higher for rhythm than other forms of musical patterning (Schruth, 2022), but may also serve in a less welcoming extra-group directed capacity (Hagen and Bryant, 2003). Humans are unusual in our extreme use of rhythmic musicality, perhaps due to our unique bipedality (Mithen, 2006) or groupishness (Brown, 2000). Evidence from the vocalizations of a larger swath of primate species suggests that larger group sizes tend to be less rhythmic overall (Schruth, 2022), hampering the plausibility of its use in coordinating numerous individuals. However, the fact that larger bodied species from more sizable [and usually terrestrial] groups also tend to exhibit at least one highly rhythmic call (top of Fig 5), supports rhythm as serving in a more directly threatening capacity across primates (also see Fitch, this volume).

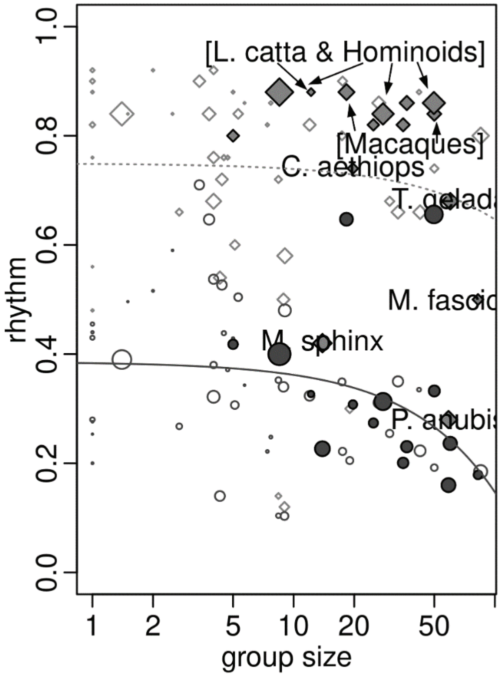

Figure 5. Group size correlates inversely with rhythmicity across primate species. Scores of the most (diamonds) and average of (circles) rhythmic calls highlight a negative correlation across the order – excepting larger bodied terrestrial forms (top) which have higher max(*rhythm*). Circles are scaled by *body mass* and filled according to *terrestriallity*. The exceptional *Papio anubis* (lowest diamond) climbs the least (<3%) of any primate here except the Japanese [island protected] *M. fuscata* (near top).

Size and extra-group signaling allometry

Recent work using allometric analysis, or the study of changes in the sizes of isolated traits in relation to [usually] overall body sizes across species, has delved into interpretation of the differences between these associations – assessed through their regression slopes. For example, many exaggerated traits lie along an ornament vs weapon continuum (Kodric-Brown, Sibly and Brown, 2006) whereby steeper slopes correspond to sexually selected ornaments and shallower ones correspond to weaponry. The former corresponds to within species signals and the latter may further extend to signals out of the group, perhaps including predators. If we extrapolate this reasoning to non-morphological traits (e.g. life history, <1:1 allometry), we might expect even shallower slopes (e.g. syllable and rhythm in Fig 6). Since such acoustic features (e.g. of human musicality) are not typically compared outside our own order, we may only speculate here that the down-shift in allometric steepness between syllabic and rhythmic patterning might parallel the down-shift from ornamental to weaponized functionality for morphological traits (Fig 6). This only mildly positively associated trend of rhythm with body size passably supports the deimatic hypothesis introduced above. But the decisively positive slope of syllable could also admittedly be interpreted as validating both hypotheses involving sexual choice for ornamental intelligence (Miller, 2000) and those for musicality as a linguistic precursor (Brown, 2000; Bryant, 2014).

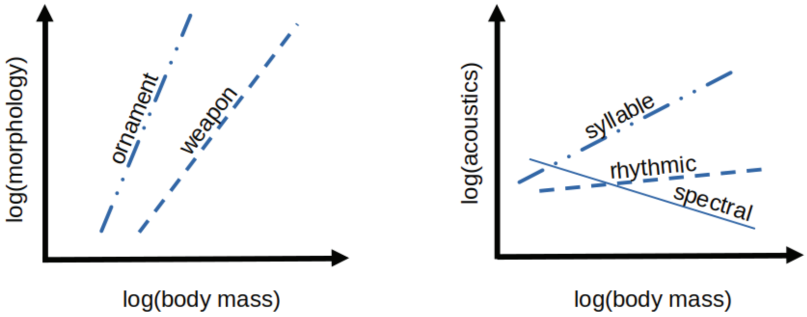

Figure 6. Allometric slopes are steeper for ornaments (dashes+dots) compared with shallower ones for weaponry (dashes) for most morphologies (Kodric-Brown, 2006). By behavioral analogy we might surmise a parallel functionality for the different slopes of primate acoustic data (right). Here syllable may approximate ornament whereas rhythm may be more weapon like. The extremely shallow slope of rhythm implies that there is only very little (size-based) honesty backing the increasing levels of rhythm, though it could proxy associated group-coordination effects. Spectral features (thin, downward-sloping line) have negative allometry with body size, suggesting an intra-group communication functionality in the face of numerous predators. An extension of the deimatic hypothesis suggests that actively functional [anti-predator] threats may act as weaponry – while more passive, exaggerated, or seemingly vestigial traits could act as aposematic signals.

Postitional and musical diversity in transitional hominins

The transition from [fully] arboreal to [partially] terrestrial life likely spanned millions of years leading up to the Pleistocene (Reed, 1997). The continued use of daily climbing is evidenced by Pliocene often remains of the semi-arboreal genera of *Ardipithecus* and *Australopithecus* (Kozma *et al.*, 2018). And hunting of terrestrial prey could have co-opted the limb landing abilities of our common ape ancestors who were capable of suspensory swinging (Schruth and Jordania, 2020). But increasing temperatures and the reduction of body fur likely complicated the handling of increasingly large-brained and altricial (but instinctively clinging) infants (Stanley, 1992). Further extension into obligate terrestriality may have fully freed up the forelimbs of hunters to allow for specialized dispatching of remote ballistics, perhaps as a primary means of subsistence. As human infants remained altricial and human walking expanded into more rapid and precarious forms of bipedality, spatial aptitudes for groundward-directed single-limb emplacement on unpredictable terrain (e.g. mangrove roots) necessarily proliferated. In sum, the spectral acoustic displays of apes likely perpetuated in modern humans as signals of limb landing ability. Such selection for landing adjustments in hominins likely manifested as both fore and hind limb accuracy – in both crafting and deployment of ballistic hunting tools as well as for onerous carrying of fragile payloads in bipedal locomotion generally.

A newfound stability in terrestrial life by hominins coincided with a reversal of the predator-prey relationship – between these primates and the terrestrial threats that had originally motivated arboreality in previous epochs. These audacious acts against ground predators must have eventually morphed into proactively hunting them for food. And by usurping the dominance of large cats, hominins consequently inherited an apical position over their terrestrial food chains. But long before they worked collectively in groups for the purposes of terrestrial *offense*, team hunting may have been preceded by millions of years of coordinated *defense*, for example in warding terrestrial predators (e.g. hyenas) away from arboreal kills and sleeping trees. Large African felines appear to have since developed aversions to any resemblance of bipedal hominins, especially when they stand tall (see Blake, this volume). Thus, any such coordination for targeting outsider threats in increasingly bipedal groups – initially used defensively, by semi-arboreal hominins, for scaring-off predators – may have eventually evolved into a more coordinated and ritualistic (therefore human like) musical performance.

But, as evidenced from other primates, a rising rhythmicity and possibly declining intervalic virtuosity could have also foreshadowed the decline of singing in terrestrial humans towards only a more episodic and ornamental occurrence. These temporal bookends, from known fossils to modern human societies, also suggest an intermediate evolution through hominins who were terrestrially social but also retained a lingering arboreality. For example, even many modern human societies are known to still climb trees regularly to obtain high energy food items, such as honey (Kraft, 2014). A daily circadian cycle of security, both in trees at night and in groups by day, may have been echoed by an equally great diversity of moods and forms of musicality. In short, our unrivaled panoply of musical complexity, composed of both affiliative melodies and warding rhythms, were likely selected by the numerous daily contrasts in positional, predational, social, spatial, and sensory proximity.

Conclusion

Primates can respond to predation pressure in five primary ways: concealment, evasion, avoidance, confrontation, and warding. Concealment, of both visual and auditory cues, is a strategy typically employed by smaller and nocturnal primates who face numerous predation threats. Evasion can be a regular option for more solitary living primates who may also be diurnal and therefore more easily spotted by predators. Primates primarily leverage trees to evade most predators – climbing them to avoid terrestrial ones and vaulting between them to avoid the climbing ones. Both of these forms of anti-predation strategy do not typically entail highly salient vocal output. Instead these species, ranging from mouse lemurs to sifakas, may only produce close calls that are short and atonal or more patterned tonal calls that are hidden from predators in ultra-sonic frequency ranges.

Primates primarily leverage arboreality to not only assist with evasion, but to also avoid becoming prey over the long-term. For this strategy to work, primates must habitually avoid eavesdropping by potential predators. This may require frequently deploying shorter, more subtly melodic phrases to attract group members, with only the occasional (and typically temporally patterned) loud calls to signal alarm in emergencies. A greater diversity of alarm calling, perhaps with higher specificity to individual forms of predation, tends to occur in mid-sized primates. Calls with more intervalic content, especially those produced by arboreal forms living in larger groups, can even serve to exacerbate confrontation in the form of mobbing. Rhythmicity, on the other hand, has a strongly inverse association with group size and predational diversity, despite the fact that larger species produce more rhythmic (than other forms of) musicality.

In our more recent ancestry, highly salient extra-group directed (especially rhythmic) sounds could have also been used in preventative repulsion – to ward-off external threats (Fig 1, center-right) with potentially sacrificially intimidating mechanisms (see Wade, this volume). In hominins, such sounding was likely enhanced artificially with percussive instruments to impart a sense of larger, more rapid, more numerous, and perhaps more formidable targets (see Brown, this volume). But, like the salient acoustics of primates generally, the calls with the greatest diversity of spectral contouring are assertable by those possessing high levels of trophic security – notably in (other) species who have so few natural predators, such as tarsiers, gibbons, and indri. In such rare cases, increasingly vestigial alarm calling could have instead been repurposed as salient displays.

This alternative morphing into only mildly confrontational threats may have acted to passively ward off any lingering predators that still competed for top positions in local food webs. Thus, the more active and vociferous alarm calls of apical species conceivably morphed into increasingly passive and ritualistic usage as these species, such as hominins, began to approach trophic invulnerability, in spite of potentially smaller individual body masses. This subtle shift in acoustic warding, from deimatic alarm to aposematic signal, may have honestly reflected more subtle cognition-facilitated abilities of (inter-substrate and inter-personal) coordination with trees and groups rather than more obvious physiological attributes of individuals.

Lastly, a lingering diversity in positional security – manifesting daily as both protected arboreality and vulnerable terrestriality – may have given rise to our uniquely diverse musicality, which evolved over the multi-million year transition from the trees to the ground. That is, primates' exhibition of a variety of different vocal behaviors, ranging from silence to loud calls, corresponds to various anti-predational strategies, ranging from crypsis to confrontation. And likewise, transitional hominins, who likely exhibited a wide range of vulnerably related to extreme daily positional flux, may have spawned an even broader range of musical expression that was integrally melodic and rhythmic alike.

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Evolution of Prey Behaviour in Impeding Predator Mobility as Mechanism of Defence: A Case Study of Interaction Between Carnivora and Domestic Dogs, Recent Evolutionary Behavioural Changes Observed and Inferences from Rajasthan, India

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Abstract. Predator-Prey interaction is one of the most important ecological phenomena that determines the outcome of their respective struggle for survival. Anti-predator adaptation mechanisms developed through evolution and interaction that enable a prey species to thwart predator action or secure escape from potential predators for any species. Important adaptations include Mobility, Concealment, Camouflage, Apostatic selection, Aposematism, and various other forms of deterrent action. This brief case study attempts to explore the phenomenon of behavioural evolution in prey (domestic dogs) in ecological time, i.e. within their lifespan, resulting from vulnerability to attack from Predators (Leopards) as observed and reported in some villages in Rajasthan, India and potential inferences from it pertaining to the instinctive behaviour of Carnivora while hunting prey and subsequent selection on behaviour of prey, especially arrest of spring and impairment of motion being predator-action deterrents.

Discussion

Prey animals are able to adopt behavioural adaptations, in ecological time (within their lifespans) in response to predator action, thus predation is a major selective force in evolution (Lima and Dill,1990). While Nocturnality, Camouflage, Masquerade and Apostatic selection are designed in prey to negate the efficacy of the sense of sight in predators, various other mechanisms such as chemical deterrents, ability of flight, defensive physiological features, distraction, aposematism, enhanced vigilance, Autotomy and even suicidal altruism amongst numerous others are used in prey defence against predator action (Caro, 2005, Cott, 1940, Ritland, 1995, Edmunds, 1974, Eisner et all, 1974, Ruxton et all, 2004, Corlett et all, 2011, Derby, 2007, Inman, 2005, 2011).

A potential case can be made out for a combination of Crypsis (avoidance of detection) with enhanced vigilance and a lesser-discussed phenomenon – that of impediment to predator action reducing risk of predation, as observed in a recent behavioural pattern in the Domestic Dog (Canis lupus familiaris) in villages of the Desuri region of south-central Rajasthan, India in the face of frequent predation by the Indian Leopard (Panthera Pardus Fusca), as being a defence mechanism getting devised in ecological time by a prey animal in face of threats by a predator.

The Desuri region of South-Central Rajasthan is an area that has been historically rich in Flora and Fauna, with the Aravalli range of mountains running adjacent to it. The fauna of the area includes the Indian Leopard, which is currently the apex predator, as the Tiger, although present in the state, has not been found in the region in the past several decades. The wildlife of the area after seeing a depletion in the 1990s and 2000s has seen an increase over the past decade due to effective conservation. Challenges resulting from habitat loss and fragmentation of forests combined with increasing human signature remain and are forcing wild animals into closer interaction with humans in a largely human-dominated matrix.

Observation and report from locals in villages near the Narlai region near Desuri, which has seen an increase in the leopard population which frequents villages in search of prey, presents an interesting case which may throw light on the subject of this discussion. It has been observed that domestic dogs in villages, after dusk and in night hours are tending to climb up and remain on the rooftops of thatched huts.

It has been reported that this phenomenon has been observed being developed in recent years after village dogs became the chief diet of local leopards, thereby being suggestive of having been adopted by dogs in their ‘ecological time’ (within their lifespan).

It is reported that the phenomenon is seen en masse in the dogs and happens regularly at specific time of darkness, which is the primary time when the leopards are on the prowl looking for prey.

The reason does not seem to be solely concealment. Perhaps the rooftops result in a combination of concealment and lack of conducive situation for the leopards to launch their spring due to lack of movement, which seems to be an important instinct in carnivora to launch their death-grip over prey. The lack of movement seems to often desist the predator from launching its spring, resulting in better survival chances for a potential prey.

Lack of movement and deterrence (and importance) of 'spring' of carnivora as a significant factor in launching a successful attack:

– Leopard depredation on domestic has been on the rise and several cases are captured on video. It is often seen that as the leopard approaches a sleeping dog, it waits right on top of the dog till the point in time the dog awakens and launches into a paroxysm of movement, upon which in a split-second the leopard is able to launch its kill instinct and carry off the prey in most cases;

– Instances have been captured in wild lions and leopards having their kill instinct being arrested due to lack of movement, or lack of flight by a potential prey. Carnivora hunting very young ungulates, which instead of flight approached the incoming predator, have been seen to have got their spring arrested and often end up confused as to what to do with the potential prey, often spending considerable time toying with the prey before one or another movement led to its kill;

– Jim Corbett in the final sequence in the Chowgarh chapter in Maneaters of Kumaon (OUP, 1944) specifically invokes this phenomenon- lack of movement arresting a possible spring by a predator. (Corbett, 1944)

— It is often seen in cases when staff of Forest department of a state in India is compelled to trap a 'problem' leopard- one that either takes to cattle-killing or even human attacks, using a goat as a live bait to trap a leopard in a cage, that once the leopard enters the cage and the door shuts down with a loud sound, combined with the nearness of the goat, this causes interference in the spring action of the leopard and subsequent abandonment of the kill sequence by the predator. Often the leopard and the live goat, within a few feet of it, are transported back without any physical contact between the two animals. Cases also been recorded where a leopard and dog get trapped in wells, toilets and other confined spaces after a chase, with the leopard abandoning its attack mode and sitting near its prey animal without any predator action, suggestive of interference with spring action causing abandonment of a kill sequence.

– It has been observed in cases of Antelope versus African wild dogs captured on video, that the Antelope endeavour to secure their survival by climbing on to edges of cliffs, which make it difficult for the wild dogs to launch their attack, being uncomfortably and precariously positioned on top of the cliffs. This suggests that causing arrest of conducive attack movement is a potential measure of prey defence;

– Videos emerging from many forests around the world, available on the internet, show carnivora chasing behind moving motorbikes, perhaps mistaking it for an animal in flight, which further shows how the phenomenon of rapid movement of flight, causes an involuntary launch of chase/ hunt sequence in carnivora.

Potential defensive advantages to the dogs in being atop houses as against on the ground (see Blake in this volume);

– Enhanced vigilance – A leopard climbing up a rooftop would tend to stand a greater chance of making a sound, as against a leopard that approaches a dog stealthily on the ground;

– Concealment – A dog on rooftop stands a greater chance of staying out of sight than one on the ground Enabling better anti-predatory behaviour;

— Dogs on rooftops stand a greater chance of warding off an attack by a leopard, whereby a leopard unsuitably positioned on a rooftop is more likely to yield to a counter by one or a group of dogs than one comfortably positioned on the ground.

It could be argued that the dogs in this case have developed this defensive instinct in ecological time as a mechanism against predation by leopards, as the leopard on rooftop would not have the most suitable ground to launch its spring. It is contrary to the action of leopard securing prey such as monkeys from trees, which is an action that happens on natural footing of a tree, which presented itself for ages as a setting for predator-prey interaction, thereby having become a part of mutual evolution.

Lack of movement interferes with the pattern of hunt in carnivora, and often arrests the final spring which procures them their prey. In the present case, the rooftops present an unconducive ground on which to launch a spring of attack. Thus a combination of staying out of sight, enhanced vigilance, enhanced possibility of detecting a predator, enhanced possibility of defence against a predator as well as a situation causing lack of movement for the predator to launch its spring in this case have contributed to adoption of a unique defensive behavioural pattern by a prey species.

It can also be argued that defence strategies can be formed in potential prey over a short span of time and take into consideration local conditions that can be used to advantage, in this case the use of huts by dogs, thereby being a case of behavioural evolution in ecological time by a prey animal resulting in a combination of enhanced vigilance, concealment as well as arrest of spring-action of a predator in being a potential blanket of security for a prey animal.

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From Flight to Fight: How Predator Pressure Shaped the Evolution of Hominins and the Origin and Development of the Human Society

Preetum Gheerawo (Mauritius)

Abstract. Early humans have been successful in their defence strategies against large lethal predators. The proof of this statement is that we, the descendants, are still here, and have been thriving, considering expansion during our evolution period, both in numbers and in geographical range. This paper shall therefore, firstly, focus on how the evolution of early hominins among predators, over geological times, fashioned them to avoid the fate of remaining a basic prey, among the species at the bottom of the food chain; but on the contrary, how early humans defence strategies against predators evolved to reverse the hierarchy and set the stage for anatomically modern humans, Homo sapiens to became the top apex predator of the planet where there is no need for defence against predators despite our inborn fear of them. The period coinciding with the reversal of hierarchy shall then be inferred as the beginning of the Anthropocene.

It would be subsequently argued that humans' overwhelmingly successful evolution strategy did not occur through a direct classical form of natural selection against predators that is, it was not the survival of the fittest, but survival of the smartest. But all these would not have been possible if humans and their ancestors did not inherit the common trait of living highly social groups as a benefit, from ancient primates. For this statement, I base myself on the hypothesis derived from a study on non-human primates that strongly suggests that their evolution towards increased sociality and group size occurred in response to predation pressure. I shall thereby expand this view to hominins (with a higher degree of encephalisation) and shall suggest that predation pressure was the driving force affecting the not only the evolution of our ancestors but also the behavioural ecology of anatomically modern humans, laying the foundation for human society and the origin of civilisation.

However, as an a posteriori remark, not in context of this paper, victory over predators is at the expense of our domination over other species becoming such disproportionately large, that we are increasingly becoming a menace to our own species, let alone to the whole biosphere.

METHOD

The approach of this paper shall be to study, through the fossil records and recent history, why we, humans, have an inborn fear of predators and to investigate if this fear is justified or not.

These characteristics which involve defence against predators and which would be under investigations are: bipedalism, encephalisation, socialisation, tool use & modification, domestication of fire and the dog and further sexual dimorphism, group size and benefits of sociality.

Finally, in response to the call for abstracts, there was a series of models[1] of human defence against predators proposed by the International Conference Committee. So, at the end of this paper a detailed analysis of this paper's main points on how and why human ancestors won the struggle for survival against predators shall compared to the models proposed. Thereby, models shall be eliminated either wholly or partially, according to the characteristics of humans or their evolution, using matching evidence from the fossil and archaeological records, until one major model shall prevail, intermingled with shades of other retained models.

INTRODUCTION – Brief history of predation on hominins

The discovery of the Taung Child (Australopithecus africanus) by Raymond Dart in 1924 had seriously suggested an African origin for the human species (Dart, 1925; Thackeray 2016), while earlier, a European, or subsequently, an Asiatic origin had been privileged (Brodrick, 1948). As such in Darwin's lifetime, in the 19th century, and for very long afterwards, it was still conceivable that humans had evolved in a relatively predator-free environment (Darwin,1888), perhaps inferred from amongst other considerations that Germany (discovery of Homo neanderthalensis fossil skull cap in the

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[1] Refer to "Call for abstracts" by the J. Corbett International Research Centre, Grigol Robakidze University as listed in the Appendix.

Neander valley in 1856 (Fuhlrott & Schaaffhausen, 1857; Trinkaus, 1993)) was devoid of major predators at that time.

However, Africa is renowned as the land of large predators, and as it became accepted that hominin evolution started there, it was not surprising to learn, much later after its discovery, that the Taung Child had been, most probably, the victim of a large bird of prey (Berger, 2006); talon marks deep inside both eye sockets reveal how the little Australopithecine met its fate. This appears in stark contradiction with the 'killer ape hypothesis' that Dart proposed later (Dart, 1953), but also rules out the proposal that early humans had evolved in a predator free environment.

Other hominin fossil discoveries in Africa reveal a far more terrifying predator: the African leopard (Panthera pardus), a silent but efficient man-killer, whose infinite patience during its stealth and lightning-fast fatal strike, in pitch dark nights, is second to none (Corbett, 1951). A hominin fossil in particular, the Paranthropus robustus specimen referenced as SK-54, from the late Pliocene/ early Pleistocene of Swartkrans, South Africa, exposes the merciless fatality of a leopard assault: deep canine tooth marks on the skull top which matches exactly the inter-spacing and dimensions of an adult specimen's canines (Pickering et al., 2004; see also Brain, 1981). Yet more proof of predation on hominins can be found in other sites in Africa later in the Pleistocene and the question was asked if hominins were just a "…food resource for carnivores…" (dubbed as "predators' fodder") at the beginning of their evolution (Daujeard et al., 2016; Brain, 1981; Hart & Sussman, 2011).

Leopards are nowadays the most widely ranged large carnivore (Jacobson et al., 2016), though they are now classed by the IUCN as vulnerable or endangered, depending on the sub-species, and in the Pleistocene, they were in greater numbers but they were not the only carnivore around (Van Valkenburgh, 2016). If one ever thought that our early ancestors left Africa to flee from deadly predators and came to Asia or Europe to seek a haven, this would be considered as big mistake, for their new abode was home to not only leopards, but giant hyaenidae, bears, lions, and wolves among others (Ibid).

Evidence from fossil records also show several cases of predation on hominins by hyanidae, bear and saber-toothed cats in Eurasia as from 1.8 m.y.a. and also by leopards (Hart & Sussman, 2011). Further, recent data show that hominins would have always been on a leopard's diet if we consider that a H. neanderthalensis fossil of the middle to upper Palaeolithic of Spain was also found to bear the canine marks of a leopard, namely the parietal skull bone numbered CN42174b, found in the Cova Negra site (Camarós et al., 2016). Leopards are hence said to have contributed, through their predation upon hominins, to the fossil records, as they have the habit of discarding the bones and skull at the same location after consuming their meal. So, hominin fossilised remains have sometimes been discovered in association with other ungulate remains in what appears to be leopards' trash pits (Sauqué et al., 2014).

Since our contemporary history also contains terrifying narratives of deadly leopard and other big cats' unprovoked fatalities upon humans, in other terms, predation for food, a premature conclusion would be that as terrestrial primate species, humans and their ancestors have always been subject to being chosen as food by large predators. This occurrence which earned the name and fame of 'man-eating', was popularised in our collective intellectual, as a combination of fear and thrill, mostly by Col. J. Patterson (for lions P. leo, in Africa (Patterson, 1908)) and legendary hunter-conservationist Jim Corbett (for tigers, P. tigris and leopards, P. pardus fusca, in North India (Corbett, 1946; 1951; 1957)) in their best-selling books of the 20th century.

Man-eating in modern history

Records of man-eating in modern history begin in the old world where there was a deeply rooted fear of the Eurasian wolf, Canis lupus, in the psyche of humans that ran through countless generations and even found its way into literature and pop culture: The myth of the big bad wolf in Little Red Riding Hood or the Beast of Gevaudan (Smith, 2016) are just illustrations. But in the stark reality, nothing was more horrifying than the blood-curdling howl of wolves after dusk in the dark woods in the vicinity of a rural village somewhere in a European back country. It was rightly so, as cases of wolf predation on humans had alarmingly large figures from the Middle Age up to end of the 18th century, with France the most hard-hit country, such that the wolf became notorious as 'man's worst enemy' (Trinquier, 2009).

In India, aside to big cat man-eaters, stated earlier, the smaller sub species of the Eurasian wolf, C. l. pallipes, also inflicted a heavy toll on the expanding rural population in the Northern states of Bihar and Uttar Pradesh, and the number of casualties from wolf attacks, mostly cases of child-lifting, though not as notorious as those of tigers and leopards, surpassed the latter's combined human death count for several years (if not decades) at the end of the 19th century and the beginning of the 20th century, with a peak of 624 victims in 1878 in Uttar Pradesh alone (Rajpurohit, 1999; Burton, 1991). But it remains difficult to ascertain why in India, attacks of man-eating wolves were not widely reported as were the cases involving a man-eating tiger or leopard. In more recent times, there are cases of child-lifting by wolves from time to time in India. But these are seldom reported. Only when there was a spike in the number of attacks in 1996, though not as severe as a century earlier, that newspapers threw them in the limelight.

But a clue can be found in what differentiates the human collective reaction to predation by wolves on one hand and tigers/leopards on the other hand. In the late 19th and early 20th century in rural North India it happened that during a man-eating tiger outbreak, a single tiger, who, through wounds and old age could not sustain itself on its normal prey (Corbett, 1946), would often confine whole villages and communities under siege, behind fast-shut doors of their houses even during daytime, causing a severe check to their livelihood, travel and communication. Such tigers would often kill livestock and during its beat, would compel the inhabitants to live under constant terror and threat of death, sometimes for several years (Ibid).

This occurred at the time when the local economy in rural India, because of population growth, became heavily dependent on an increase of cultivation land. This was summarily done at the expense of jungle territories and subsequently brought about an increased competition for resources with wild ungulates until the latter's range and habitats started overlapping with human settlement and their agricultural land. In return, this brought large carnivora in proximity of human territory boosting the clash between humans and predators. This had been well observed by Corbett and in his essay Wildlife in the village: An Appeal dated 1931, he concluded that it was not the carnivora that were growing in numbers when the conflict was rising, but when humans started to disrupt the balance of Nature and contested for the same resources, this had compelled large predators to come into proximity and clash with humans (a copy of Corbett's essay published in D. C. Kala's biography of Corbett (Kala, 2009)).

One result of the conflict was the forced daytime curfews imposed by man-eating tigers as stated above. But also other causes arising from the proximity of carnivora with humans brought about man-eating leopards who cause severe restrictions on the population daily after dusk till dawn (Corbett, 1951) but with less significant secondary consequence on human activity. In Africa, during the construction of the Uganda-Kenya railway track in the late 19th century a pair of man-eating lions (under the name 'Tsavo lions') forced hundreds of workers to work under the supervision of guns during the day and shelter themselves behind bomas (thorn enclosures) during the night, when it appeared that tribal ancestral aposematic tactics employed by the native workers such as group singing battle trance did not deter the lions' attacks (Patterson, 1908).

So, in this paper, I shall first suggest that, as an observed rule from the cases listed above, it is the rural population who are more vulnerable to attacks by large predators and secondly, it is when man-eating animals bring a halt to economic activities that their depredations attract attention from the authorities and become exposed. This is the case mainly for tigers as they operate chiefly during the day. Otherwise, attacks on humans go unnoticed, such that the official toll of depredation by wild carnivora on humans recorded by the authorities will always be an underestimate.

In that regard, in India during active man-eating spells across large geographical areas and by several animals at the same time, as mentioned above, the consensus reached was that carnivora had increased in numbers. As such war was waged against tigers in particular, by the government who would often employ bounty hunters. However, many of these latter would often either lose the battle against the man-eaters they were hunting or abandon their assignment after repeated failures to bag the animal, such that the human-kill numbers would nevertheless be on the rise. As such, at the peak of the human-tiger conflict, the outcome seemed to be a question of as who of man or tiger would survive (Dunbar Brander, 1923:85). It was even said that the population lived and had its being under the shadow of man-eaters when a man-eating tiger was prowling about (Corbett, 1946).

Taking the latter statements, at face value, the conclusion would be that humans are still under the 'rule of the tooth and the claw', just like our long past ancestors, who had to shelter themselves in caves (Ibid) to avoid predators at night. This could have been true at the dawn of hominin evolution also when originally the earliest members who were still semi-arboreal crea-tures were finding refuge from ground predators in trees as well (King, 2022). But as we shall see this is no longer the case, and the hierarchy ranking predators above humans in the food chain has been reversed during the course of human evolution.

Reversal of hierarchy

In fact, what appeared to be a lost cause for the survival of humans, predominantly in parts of Asia and Africa, was never so. The survival of humans was never at stake and man-eating is almost always an accident and very isolated and rare. In retaliation to human killings, large carnivora were soon depleted in numbers as they were never able to evolve fast enough to compete proportionately against an increasing number of humans, let alone against their improving guns.

A priori, it looks difficult to ascertain a precise period for the reversal of hierarchy between large carnivora and humans. The scenario is much different not only between separate parts of the world but also at different periods in the human evolutionary history. Taking the examples of North America and Australia, previously several research done on the extinction of the megafauna, large animals which had a slow reproduction rate, only showed that there was a correlation with the arrival of humans on these continents, without substantial proof of extermination by humans.

However, a very recent publication suggests a direct evidence for the annihilation of the large animals of North America by humans. Study of the residues on the preserved stone tips and tools (referred to as the Clovis industry) of the first American people, who came via the Beringia ice bridge at the end of the last Ice Age, revealed the identity of those extinct large beasts that were roaming the continent previously (Moore et al., 2023). The demise of those large animals caused a definite change of pattern of the landscape of this continent and it coincides almost exactly with a quite accurate dating of the Clovis flint tips and hence with the arrival of humans, around 13 to 12 k.y.a. (Waters et al., 2021).

By extension of the above argument, large animals of Australia suffered a similar fate at the hands of humans. The sixth continent was largely inhabited until about 47,000 years ago (van der Kaars et al., 2017). Prior to that, Australia had an ecosystem dominated by megafauna which included large marsupial predators. The latter, including almost all the megafauna went extinct within a few thousand years after the arrival of humans (Ibid).

In Africa, in the pre-European settlers days (and even today), the indigenous human tribes coexisted well with large predators (Broekhuis, 2020, see also Marshal Thomas in this volume) and as we shall see, there was no need for the natives to defend against them or to attack them; whereas in Europe, pure and simple extermination occurred, such that the continent was nearly devoid of large predators since the end of the 19th Century (Boitani & Linnell, 2015). This is a fitting example of the capacity of humans to alter an ecosystem or wild environment and in this paper I shall suggest that this is a mark or characteristic of reversal of hierarchy.

The same setting as Europe would almost certainly have occurred in Asia too, had it not been for the largeness of virgin territory (mainly Russia but also China) and to the rise in Ecological Conservationism by pioneers like Corbett and others, in minor Asia. So, the need for defence against predators was very significantly lessened by the mid 20th Century in Asia.

If proof was needed to ascertain how effective humans can be in modifying an ecosystem or wild environment, then Africa is the perfect example. At the end of the 19th century, by the period when colonialism had been firmly established in Africa, ivory hunters and other big game trophy hunters from Europe and the USA came in large numbers and a mass indiscriminate extermination of wildlife ensued. In just a few decades up to the middle the 20th century, the renowned land of iconic large animals including predators, had largely been reduced to relatively small pockets of game reserves and wildlife sanctuaries, which survived thanks to the largeness of the territory, within development areas and modern settlement built around them (Di Marco et al., 2014).

While earlier the comparatively lesser-advanced native or autochthonous population and their livestock and cultivation, who were later constrained to live in or around those wildlife reserves, had been cohabiting relatively well with wild animals, they were then becoming increasingly prone to wild animal conflict as competition for grazing and agricultural land grew. So comes the various fearsome accounts of man-eating lions particularly. The most severe case being when between 1932 and 1947, three generations of lions killed some 1,500 indigenous people in the Njombe District in southern Tanzania during a severe period of drought, the latter most probably occurring as a result of human-induced activities (Kerbis & Gnoske, 2001).

Therefore, from what has been exposed in this section, it seems, based on relatively recent history (47 k.y.a.) till recently (last century) that the reversal of hierarchy had already occurred prior to the Paleolithic and therefore, investigation about early hominins and human ancestors would be able to reveal more about it.

Further, a clue has been obtained about successful defence against predators: it is technological advancement that differentiates humans; from those who are capable of dominating their environment and those who initially do not have the means to do so, including defence from predators (or attack) rather than being preyed upon. When the latter eventually acquires the necessary technology through dispersal of culture, they shall in turn also be equipped to carry out their defence (or attack) against predators effectively. So, in this paper, I shall also expand this observation as from the early evolution period of hominins and to start with, I shall briefly go back to the dawn of evolution of primates.

How did the earliest primates cope with predators?

One of the earliest and most complete fossil primates, Darwinius masillae (a juvenile holotype specimen nicknamed Ida) from the Eocene of Germany (roughly around 47 m.y.a.) most probably at the very dawn of evolution of primates, revealed that they already had fingernails instead of claws; and prehensile limbs, with opposable thumbs [and toe] but also with the frontally placed eyes (Franzen et al., 2009).

Apparently, these indicate that a basal primate in the stage of evolution of Ida was a '…[small] arboreal quadruped neither specialised for slow climbing or leaping…' (Ibid), but I would rather propose that the evolution of fingernails from claws together with the prehensile limbs and the binocular vision was acted upon by natural selection to favour primates' flight from predators instead of fight. So, since it was not adapted for fast climbing and leaping, I hereby suggest that this was achieved most probably by fast locomotion along horizontal branches helped by their prehensile limbs; but also shifting among branches, where judging distances to the next branch, helped by their binocular vision, is essential for survival. This type of locomotion is referred by primatologists as brachiation (like 'Tarzan' in the original cartoon version).

Here I also imply that claws would have been of no use but rather a disadvantage as these are suggested as an adaptation for fast vertical climbing (Cartmill, 1972) which were already possessed by some predators (e.g. semi or fully arboreal varanids) who were therefore non-adapted for fast horizontal locomotion in trees. But this appears to be not the only advantage of primates in defence against predators.

It also seems that evolution towards sociality in diurnal primates occurred in response to predation pressure (Van Shaick, 1983) and that primates have therefore evolved larger brain capacity (encephalisation) compared to other animals of the same size, possibly as an adaptation for living in complex social groups accounting for their high degree of sociability (Reader & Laland, 2002; Dunbar & Shultz, 2007; see also Fitch & Zuberbühler in this volume), which shall later be shown to be also a characteristic of the hominin/human lineage. I will thereby affirm later in this paper that the high degree of sociability accounts for cooperation in defence against predators, which we observe in living primates, including humans.

I have seen this character among the Northern grey langur (Semnopithecus entellus) in India, where a few individuals (usually males) dedicate themselves for the group's safety. They sit atop high tree branches or on a high vantage point on ground and act as guards for the group, watching for predators while their conspecifics are feeding on the ground and giving the typical alarm call even when a predator or even a human is sighted. This langur alarm call, which are also useful to ungulates for predator detection, had helped Jim Corbett several during his man-eater hunts where langurs acted unconsciously as his watchdog, if not his guardian angel. Further, male langurs also cooperate for defence by mobbing relatively smaller predators who are potential dangers to their tribe members, as we shall see later.

This specific characteristic of cooperation for defence which is quite successful in non-human primates, ascertained by their evolutive radiation in diversity of species and in range, and also shown in the fossil records, shall be expanded in details to the human lineage later. But first the hominins basic defence strategies should be investigated as it appears, based on their relatively larger body mass, that they would be slower in reaching arboreal safety and therefore be quite vulnerable to ground predators.

What made hominins seem a vulnerable species when they evolved towards ground dwelling?

When primates evolved over time and diversified, among the super family Hominoidea, one family, the Hominidae (great apes) grew larger in size and diverged from the other, the Hylobatidae family – lesser apes e.g. gibbons - which are smaller in size than their immediate cousins (Mc Nulty, 2016). Also, the gibbons retained their tail, while great apes lost their tail, "…which is less necessary when climbing deliberately and hanging from branches, rather than scampering along the tops of high branches, but it is also less effective in balancing large body masses …"(Wilson, 2021). Thus, they started to dwell on the lower branches of trees closer to the ground, in accordance probably due to what I shall refer to as the 'splat effect' – the heavier you are, the greater damage comes if you fall from higher up. Gradually over time, semi-arboreal and even fully terrestrial characters appeared in some Hominidae species as they occupied this new ecological niche possibly also as a result of natural selection acting due to a combination or succession of causes which are still unclear.

Today, the most arboreal of the Hominidae family come from the Ponginae subfamily, namely the orangutans, while among the three extant tribes derived from the other subfamily, the Homininae and which evolved exclusively in Africa, the Gorillini tribe (two extant species of Gorilla) is mostly terrestrial, while the Panini tribe (extant chimpanzees and bonobos) is semi-arboreal (Crompton, 2016). The third tribe, the Hominini, (which we refer to as hominins in this paper), of which the Homo genus forms part, distinguish themselves from the other tribes in being more terrestrial than arboreal but especially in being bipedal, having adapted its post-cranial skeleton over the course of its evolution for upright plantigrade walking (Harcourt-Smith & Aiello, 2004; Harcourt-Smith, 2007, 2010).

But, while some hominins retained the primitive phenotypical morphology of having opposable big toes in the lower limbs such as Ardipithecus ramidus which clearly displays climbing and bipedal duality (Prang, 2019), later hominins such as Australopithecus afarensis lost the ability of grasping feet, displaying a significant reduced capacity for fast climbing of trees (Ward et al, 2011; De Silva & Throckmorton, 2010; Stern & Sussman, 1983), for the avoidance of and defence against ground predators; even though the structural morphology of their forelimbs reflected a "… continued reliance on arboreal climbing at least part-time…" but this may well have been a primitive character which had been retained (Ward & Hammond, 2016), for which I shall support the argument that A. afarensis, particularly the females (or group of females), were sheltering in trees against predators at nightfall (Coss, 2021).

This origin of the specific character, termed as terrestrial obligate plantigrade bipedalism which today is possessed only by humans in the Animal Kingdom, is very difficult to ascertain from the scanty records of post-crania fossils of hominins. But in the paleoanthropological records as observed in the Laetoli footprints, the oldest hominin tracks ichnosite, discovered in the late 1970's, of the mid-Pliocene of Tanzania (Leakey M., 1978) and recently dated around 3.6-3.5 m.y.a. (Mc Nutt et al., 2021) were associated to A. afarensis (White & Suwa, 1987) and provide a direct evidence of "… human-like bipedalism…" of these basal hominins (Leakey M., 1978; Raichien et al., 2010).

Later, the genus Homo diverged from and evolved separately from Australopithecines. Its oldest described species is Homo habilis which appears in the fossil records in the early Pleistocene around ~2.6 - 2.3 m.y.a (Leakey et al., 1964), though some recent study suggests that the homo genus dates from the late Pliocene as from 2.8 m.y.a (Callaway, 2015), though this accuracy is not too important here. But from what has been inferred in A. afarensis, it appears at first that by being also fully terrestrial obligate bipedal rendered the first Homo species very vulnerable to predation especially since in being poorer climbers compared to A. afarensis and slow runners compared to other prey species, they appeared to have a much significantly reduced ability to flee ground predators.

Further, the Homo habilis holotype, a partial mandible referred to as OH7, is differentiated phenotypically from other contemporary hominins (such as A. afarensis) by its gracile teeth structure likely as a result of shifting diet to higher quality foods, as shall be explained later, and a very substantial reduction in canine size (Blumenberg & Lloyd, 1983), another loss of a means of direct defence and aposematic intimidation.

Yet, another disadvantage with regards to a predator's strike came for humans and potentially its ancestors too (to date, we can only ascertain this fact in anatomically modern humans), that is the loss of body hair and thinning of the epidermis (skin) at some stage of their evolution.

Several theories have been suggested and some of them seem quite probable and plausible, given that they contain inter-linked arguments. One of such proposes the loss of body hair and thinning of the skin in humans as a result of locomotive adaptation to become a terrestrial obligate biped, for example, compared to one of our closest relatives, Pan paniscus, the bonobo (Zihlman & Bolter, 2015). In another research which supports bipedalism through the hypothesis of transportation of non-clinging human babies, it is further suggested that "…forest fragmentation in hominin paleo-environments created conditions that were favourable for tick proliferation, selecting for hair loss in hominins and grooming behaviour in chimpanzees as divergent anti-tick strategies…" (Brown, 2021).

While regular prey animals such as ungulates can easily survive a body bite or clawing from a predator due to their relatively thick skin covered with fur, anatomically modern humans, H. sapiens, suffer consequent damage from an initially non-lethal body clawing, let alone a body bite, as the wound is deeper and leads to infection which can easily spread to the whole body and cause death even if one ever managed to pull away from the grip of the predator.

To put it quite simple, early hominins who were not adapted for fast climbing and sprints, without claws and teeth to display aggressivity or basic aposematic tactics for defence, seemed a very vulnerable species to predators. But we know that is definitely not the case, if we consider the other specific traits that are characteristics to the Homo genus, as shall be shown.

But how then did the early hominins and later humans survive against predators?

A minor part of the answer to this question lies in the fact that early hominins in Africa, particularly Australopithecines of the mid Pliocene as mentioned earlier, although bipedal, were still using trees as a refuge against predators, bar the leopard, as ascertained by some fossil evidence, for which references have already been given in previous sections. Also, by extension from what had been concluded for primates, in general, early hominins had the advantage of living in social groups and cooperated for defence.

For another part of the answer, as regards to early hominins, we can refer to archaeological records which recently revealed the first modified stone tools assemblage of the mid-Pliocene around 3.3 m.y.a., named the Lomekwian industry, and again most probably associated, through bio-stratigraphical analysis, with Australopithecines while an earlier consensus was that the use of tools was an exclusivity of the genus Homo. This pushes tool selection (or gathering), use and modification in hominins back by at least 600,000 years earlier than previously thought (Lewis & Harmand, 2016). So, there is a distinct possibility that the case of absence of arboreal safety in Australopithecines (e.g. during foraging in the open savannah) was compensated by the use of a proto-primitive tool arsenal that gave them some advantage in defence against (or why not attack?) predators.

The bulk remainder of the answer to the question shall be given by considering the characteristics that are unique to the genus Homo:

Obligate bipedalism

This has already been discussed as a disadvantage in flight from predators. But it has a greater advantage in defence against the latter as we shall see. And in parallel, I would like to quash suggestions that bipedalism in the first terrestrial hominins occurred as a result of natural selection as an advantage of the upright stance in predator detection and avoidance over the tall savannah grass (Dart, 1926), or as an aposematic means of intimidation and defence against predators (Jordania, 2011).

The point is that bipedalism in primate apes appears to have originated much earlier than previously thought, although it was a primitive form of bipedal tree branch locomotion in arboreal hominoids since at least the mid Miocene of Eurasia (around 10-11 m.y.a. Böhme et al., 2019). Until this character is proven to be a form of evolutionary convergence, I shall therefore suggest that, although they evolved separately from their Eurasian cousins, most probably, African apes, and later the earliest hominins (preceding Australopithecines) who diverged from them, were already displaying that particular form of tree bipedalism when they first became more terrestrial than arboreal in the mid Pliocene such that the evolution of the transition between quadrupedal to bipedal would not have necessarily occurred directly in a quantum leap from arboreal to terrestrial. This hypothesis finds its test in extant species of the Panini tribe (closest relatives of hominins, e.g. P. paniscus), although mostly quadrupedal, who also display bipedal duality in trees, but also on the ground (D'Août, 2004).

Notwithstanding the previous point, we can also note that the height of basal bipedal hominins, such as A. afarensis, is estimated, through a detailed analysis of its post-crania fossil bones, to have been no more than about 4 feet tall (Jungers, 1988). Comparing this data with ungulate preys of the African savannah (Nicolls, 2017) we see that among the extant widespread abundant species, the Thomson's gazelle (Eudorcas thomsonii) and the Impala (Aepyceros melampus), based on shoulder height only (and not on a vigilant erect head posture) would have been dwarfed by A. afarensis. Otherwise, most ungulates stand at 4 feet or better at shoulder height (most abundant are wildebeest and zebras) and their height is not an aposematic deterrent against predator attacks, nor they rely solely on their elevated vision to detect perfectly camouflaged predators but mostly on group vigilance during foraging (Szemán et al., 2021; Shorrocks & Cokayne, 2005).

Therefore, it seems, at least in my opinion, that A. afarensis did not evolve towards obligate terrestrial bipedalism as a benefit from aposematism for defence, whether as an advantage for scanning danger above the tall savannah grass, or using its erect posture as intimidation or deterrent against predators.

But most importantly to answer our question, the fact lies in that bipedalism freed the upper limbs in obligate bipedal terrestrial hominins like A. afarensis (Young, 2003). With their curved fingers and opposable thumbs that were initially adapted for tree branch hold, which they inherited from their arboreal hominoid ancestors (Moyà-Solà, 1999), the first terrestrial hominins had the advantage of what were coined as precision grip and power grip (Napier, 1956, see also Moyà-Solà, 1999; Young, 2003) to pick, grab and carry objects, and use them for defence (but why not attack as well?); like throwing stones or clubbing with a stick or a bone (Young, 2003). This is a form of aggressive defence behaviour associated with bipedalism, not an aposematic one (based on the definition that aposematism is connected with display of audio, olfactory and visual communications with secondary defence mechanisms (Wallace, 1877; see also: Poulton, 1890; for a novel review see: Rojas et al., 2017)) and I shall thus oppose views that suggest bipedalism associated with the use of the upper limbs to throw up in the air as an aposematic (increased height) intimidating display for defence.

Therefore, I shall formally assert that precision grip (for throwing) and power grip (for clubbing) helped the first terrestrial bipedal hominins, e.g. A. afarensis, to carry a stick (or a bone) and use it to club for defence and pick and throw stones (round ones are easier for a firm hold); and shall agree with the hypothesis that stone throwing was achieved by such hominins not only with accuracy but also with higher velocity (Roach, 2012). I also note that this specific behaviour is observed also in extant wild non-human primates, for instance, P. troglodytes, who despite being mostly quadrupedal, temporarily adopt the erect posture when throwing stones for defence (Goodall, 1964), albeit with less velocity (Roach, 2012).

Expanding the above to hominins, in general, it has been inferred by others that it was the adaptation, but also evolution, of their post-crania skeleton for obligate terrestrial bipedalism, thus freeing the upper limbs for manipulation of stones for fast and accurate throwing (Fifer, 1987; Knüsel, 1992; Roach, 2012); and sticks (or long bones) for a tight grip and high striking power (Young, 2003). Both methods which were therefore meant for defence against predators but also for attack, either to drive them off their kill; and for other purposes such as hunting, or to fight off conspecifics, are characters, intrinsic and indissociable to each other, belonging essentially to obligate bipedal terrestrial species of Australopithecines and later, evolved better in those of the Homo genus (Young, 2003; Roach, 2012). These statements for which I am in agreement.

This appeared a quite successful defence (and attack strategy) since the first terrestrial hominins are seen, according to fossil records, to expand in range and diversity across Africa right through the end of the Pliocene until the Pleistocene when the first members of the genus Homo emerged as they were very well equipped and apt to defend themselves successfully against predators.

So, I find it difficult to give credit to theories which suggest that bipedalism occurred in hominins to have a better view above the moderately tall savannah grassland to detect crouching predators (Dart, 1926) or as an aposematic intimidating display tactic (with height) against the latter (Jordania, 2011).

We can therefore philosophically reflect that the first primate that elected to gather and raise either a stick or throw a stone towards a predator in defence or in retaliation to an attack, rather than attempting to intimidate or merely flee and seek refuge in a tree, was perfectly unaware that it had laid the foundation stone for the radiative evolution of hominins.

Encephalisation, Tool Modification and Increased Sociability

The earliest member of the Homo genus, H. habilis appears in the fossil records in the early Pleistocene (2.6 to 2.3 m.y.a.). With H. habilis a significant encephalisation (increase in cranial capacity) of the order of 25-50% was noted compared to contemporary hominins such as A. afarensis and A. boisei (Tobias, 1987).

H. habilis fossils had been discovered in the Olduvai gorge in Tanzania in 1960 and Louis Leakey, the discoverer, made the originally controversial claim (that is today widely accepted) in that he thinks strongly about linking H. habilis, through bio-stratigraphical analysis, with the stone chopping tools (dated 2.6 m.y.a.) discovered in the same sedimentary strata a few decades previously and later described by his wife (Leakey M.D., 1966), in association with fossil animal bones which display clear marks of butchery (Leakey L.S., 1964). This likely explains the change in diet already noted with the evolution of the tooth structure of H. habilis in that there was a shift more towards flesh consumption, and as such entering in direct competition with predators.

Further, it has been strongly suggested that these stone tools were not only used for direct foraging such as removal of skeletal flesh on animal carcasses for consumption but also for other cutting purposes (animal hide and tree branches) and most importantly, for sharpening wooden spear tips which were most likely used for hunting (Milks, 2020). This research by Milks further suggest that those archaic humans were already ambush hunters (not necessarily skilled hunters but with a fairly low rate of success) and aggressive scavengers (‘power scavenging’ in the cited reference) by driving predators off their kill by force to steal the carcass (Ibid).

But these stone chopping tools, which form part of what is known as the Oldowan culture, also display a substantial improvement in technology, precisely in terms of tool modification for specific use, compared to the previously cited Lokmewian tools (de la Torre, 2011) and it appears that this progress in skill and expertise is in correlation with encephalisation (Rightmire, 2004).

In Europe as a result of the first human dispersal (referred to as ‘Out of Africa 1’ in several publications), but also in Africa where the genus homo continued its evolution and diversification in the middle and late Pleistocene, more recent but also more sophisticated and specialised tools than the Oldowan ones were unearthed in many archaeological locations.

The most distinctive among those tools is the Acheulean handaxe (named after a place called Saint Acheul in France) discovered in sites across latitudes from England to South Africa but also across longitudes from Algeria to China and they vary in dating from 1.8-1.7 m.y.a. to 300-200 k.y.a. This typical primitive cutting and thrusting tool is piece of flint that is “…produced by the bifacial reduction of a block or large flake blank around a single, long axis. They have a cutting edge in the secant plane, and range in shape from lanceolate through ovate to orbiculate…” (Corbey et al., 2016) and could be fitted to the end of a foot-long wooden (or straight bone or antler) handle for grip comfort and hammer-like striking power (Key et al. 2021).

This shows a quite significant improvement in the engineering and technology to produce such tools and is generally credited to the species Homo erectus (in some studies, H. ergaster for fossils in Africa) and H. Heidelbergensis (in some studies, H. rhodesiensis for fossils in Africa) (Ibid). These two species of archaic humans display a substantial encephalisation of the order of 50% to 100% compared to H. habilis (Rightmire, 2004) and we cannot now but confirm Rightmire's previously-cited hypothesis to correlate such an increase in cranial capacity with the associated parallel upgrade in technology.

Further, another consequence of encephalisation, as observed in Anthropoid primates, is a strong correlation between increase in brain capacity and group size (Barton, 1996; Dunbar, 1998) and when this view is expanded to hominins (Aiello & Dunbar, 1993; see also Dunbar, 2009) it appears that there is some proof for the link between encephalisation, group size and hence an increasing order of socialisation.

I am, therefore, inclined to think that an increased degree of sociability, both intra and inter group, led to the dispersal of culture of the Acheulean industry, as referred to by archaeologists, spread in so many places over such a large geographical range and among several species of Homo as probably an analogy of our nowadays social media. So, I am therefore inclined to agree with a study that suggests that there needs to be at least verbal (or oral) communication between conspecifics (not restricted to tribe members only) for such a type of dispersal of culture (in tool modification for instance) to occur across generations, hence the origin of teaching through visual display and language (Laland, 2017), and this is in line with an earlier research which suggested that visual communication and language originated to facilitate cooperative hunting (Washburn & Lancaster, 1968).

So, here I shall link these all up and propose that, with an increased cranial capacity, as we have seen, came improvement in technology but also increased sociability, the spread of culture and language, and shall later, further suggest that these led to compassion and increased cooperation among tribe members, including cooperation, not only for foraging, but also in defence against predators.

Thus, in line with the context of this paper and with what has also been observed in non-human primates, as mentioned earlier, we can safely conclude here that if humans have evolved and been able to dominate their environment without contest, including effective defence against predators, encephalisation plays a significant part in it.

Domestication of fire

In his book The Descent of Man, Darwin argued that the greatest discovery of humans, apart language, was the use of fire (Darwin, 1888). However, if speaking strictly about the use of fire, this is not a characteristic exclusive to humans and their ancestors. Birds of prey such as some raptors (e.g. Black Kite (Milvus migrans), Whistling Kite (Haliastur sphenurus), and Brown Falcon (Falco berigora)) in the tropical Australian savannahs do use fire for foraging, by collecting glowing sticks from a bushfire (wild or human-induced) and dropping it to another distant bushland to start another bushfire to hunt insects and other little animals that are driven out from their hiding places (Bonta et al., 2017), hence displaying at least some indirect ability to modify an ecosystem, just like humans are well able to do.

So, in the context of this paper, I shall rather discuss about the domestication of fire, which would rather relate to the ability to start a fire and its controlled use for foraging (includes cooking) and non-foraging purposes, particularly for defence against predators at night, as being a character unique to the human lineage; and shall exclude the use or spread of wildfires and those of volcanic or of lightning origin. If archaeological records show the earliest use of fire to date around 2.0-1.9 m.y.a. associated with H. erectus, the evidence for its controlled use is "…scant and inconclusive…" (Roebroecks & Villa 2011). So, in this paper, emphasis will only be laid upon the controlled used of fire for defence of the community of archaic and modern humans.

Evidence of the most ancient controlled use of fire as at date comes from the site of Gruta da Aroeira (Torres Novas, Portugal) and is dated around 450 k.y.a. (Sanz et al., 2020). The taphonomy of this site revealed that "… preserved hearths containing a combination of combustion residues, including ash, charred plant or animal remains, thermally altered sediments, and burnt artefacts provide direct evidence of the controlled use of fire…" (Mentzer, 2014). A partial fossil archaic human skull discovered at this Acheulean assemblage of the Iberia peninsula is said to have been possibly H. Heidelbergensis or even a sub-species of H. erectus (Daura et al., 2017), and in my opinion another potential candidate could be H. antecessor, another European archaic human species.

As stated earlier, archaic human species could defend themselves pretty well during the day with the arsenal of weapons at their disposal. But at night, just like Corbett wrote in his books, the prowling predators such as the leopard have every advantage. So, from the earliest simple use of fire by H. erectus, it would seem that for any subsequent homo species with reduced ability to climb and sleep in trees for comfort and safety at night, fire would have, aside from foraging, been used for night protection of the tribe, as a deterrent against predators (Sabater et al., 1997; Wrangham & Carmody, 2010). This hypothesis has been tested by studying data from contemporary tribes of the San people of the Kalahari Desert, namely the !Kung tribe of the Nyae Nyae area, where lion and leopard casualties on the tribe members occurred almost exclusively in the absence of night fire, hence the conclusion that, "…by consideration and comparison of other demographic data…, fire appears to be a powerful deterrent of predators…, contributing to a significant reduction in extrinsic mortality rates…" (Wrangham & Carmody, 2010).

It is also interesting to note that some tribes of Africa have further protection where their huts are built, and their livestock are penned, inside thorn enclosures known as 'boma', at night which are proven lion-proof fences (Lichtenfeld et al., 2015).

The dog as a means of defence against predators

It was suggested and nowadays widely accepted that the first dogs (Canis familiaris) to form part of a human tribe originated from the domestication of a particular species of Pleistocene wolf (Serpell, 2021). Since there is no evidence in fossil or archaeological records that shows that archaic human species or even early H. sapiens had domesticated animals let alone the dog, it seems that the dog is a very recent adopted member of anatomically-modern human tribes, but also a late supplement to the assortment of defence mechanisms that they already possessed against predators.

In this paper it shall not be argued on when or where dogs started to occupy a sustainable relationship with humans as a variety of dates and places have been proposed by several research papers and a rough average or estimate would be around 25-20 k.y.a. (from an upper of 40 k.y.a. and a lower of 12 k.y.a.) in Eurasia. But what is important is that the domestication of the wolf into dogs preceded by many thousands of years the domestication of ruminants and other herd animals (sheep, goats, pigs, cows, fowls, etc…) (Ahmad et al., 2020).

It could then be argued as to why humans welcomed an intimidating predator and a potentially fatal antagonist (much later in the Little Red Riding Hood folklore), in the form of Canis lupus, in their camps earlier than the relatively tame herbivore which would have been far more useful to them as a food resource? One possible but most probable answer is that "…at some point in the process [of domestication of the wolf], humans also began to recognise the benefits of living with resident, semi-domestic wolves, either as guards or as hunting partners, thereby cementing the relationship…" (Serpell, 2021).

It could also be argued that the origin of dogs among early human tribes lie in the adoption and socialisation of wolf pups as pets (referred as cross-species adoption), since they are such cute and adorable little creatures; but the most plausible reason, for which I am in agreement with, remains that humans found dogs most useful in guarding their territory, namely in alerting against marauding predators, especially at night (Ibid; Sepúlveda et al., 2014). I, therefore, firmly back this conviction since in being a highly territorial and social animal by nature, the wolf protects its pack members and vice versa, against enemy intruders and to quote Rudyard Kipling, 'the strength of the pack is the wolf and the strength of the wolf is the pack' (Kipling, 1988). So, the descendants of the wolf kept these characteristics when they became domesticated, which we still find in our dogs of today and those who earned the title of 'man's best friend' are still highly useful in alerting against, in defence against or even attacking prowlers, that represent a menace to man, his property and his herd of livestock, thereby providing a serious confirmation to the proposed hypothesis.

H. heidelbergensis, the reversal of hierarchy and the beginning of the Anthropocene

Discovered in a Palaeolithic site at Boxgrove in the UK and dated around 500 k.y.a., is a unique, well preserved, remains of a primitive horse's shoulder blade (scapula) with an almost perfect rounded pierced hole in it, most likely made, during the hunting and killing of the animal, by a wooden spear thrusted by some propelling device (Pitts & Roberts, 2000:267). Also discovered in the same sedimentary strata nearby, is an Acheulean 'horse butchery' site (Pope et al., 2020) where some fragmented hominin remains were also found and attributed to H. heidelbergensis (Roberts et al., 1994; Stringer et al., 1998; Hillson et al.; 2010). So, while we had earlier expressed doubts about H. habilis being a skilled successful hunter, it would seem that H. heidelbergensis was a competent hunter.

This assertion is further strengthened by the discovery of yet another Palaeolithic archaeological site at Schöningen, Germany, dated some 400 k.y.a. and associated biostratographically to H. heidelbergensis, where this time a number of wooden spears amongst others have been found (Thieme, 1997). Moreover, the exceptional quality of preservation of the site reveals not only the spears but also for the early elaborate use of bone tools and sophisticated hunting strategies (van Kolfschoten et al., 2015; Hudson et al., 2018; see also Voormolen, 2008). The latter has been inferred from the very large faunal assemblage of the site consisting of a large quantity of butchered remains of mainly primitive horses (Equus mosbachensis) but also in significantly lesser amounts, other herbivores such as Auroch (Bos primigenius), bison (Bison priscus), and red deer (Cervus elaphus) (Lehnig et al., 2021).

Down in the opposite latitude, in South Africa, stone tipped spears dating around the same period were found and these too were attributed to H. Heidelbergensis, and it pushes back the date of usage of stone-tipped spears, formerly ascribed to H. Neanderthalensis and/or archaic H. Sapiens by at least 200,000 years (Wilkins et al., 2012). (Please note that in this paper I am not discussing H. Heidelbergensis still being disputed if it is a waste basket taxon (Buck, 2020) and cited in other papers with a different taxonomy associated with those stone-tipped spears, but I am referring strictly to my own conviction and the cited article of 2012.)

It had been inferred earlier that the change of diet in hominins as from H. habilis to later archaic humans had brought about direct competition with predators and yet earlier we had been pondering on a date to ascribe to the reversal of hierarchy between humans and carnivora for the title of supreme apex predator. Well, we may have a clue with H. heidelbergensis since there is some probable evidence that they were actually also killing lions and perhaps other large predators.

In a Pleistocene archaeological site of Spain, situated at Gran Dolina, evidence of butchery on fossil bones of a recovered Panthera leo fossilis specimen (formerly P. Spelea (described by Goldfuss, 1810), and known by the vernacular name of European cave lion), indicate the possible anthropogenic relation between archaic humans and what we thought of as an apex predator, the lion (Blasco et al., 2010). In our contemporary time, the hunting of lions with spears was (and is perhaps still) practised by the Masai people of Kenya and Northern Tanzania as a tribe ritual mainly (Hazzah et al., 2009) and it is difficult to ascertain if the hunting or killing of a dangerous predator was done for the same reason by H. Heidelbergensis. However, the evidence of butchery might lead to the conclusion that the killing was done for food, or could it have happened in defence, and the flesh consumed after?

Nevertheless, since the killing and use of flesh and parts of P. leo fossilis as well as other large carnivores was also practised by H. Neanderthalensis in the late Pleistocene and anatomically modern humans in the Palaeolithic in Europe (Kitagawa et al., 2012; Romandini et al., 2018; Cueto et al., 2016), the conclusion came that it was humans (and/or Neanderthals) who were responsible for the extinction of the mega carnivora of Europe by the Upper Palaeolithic (Kitagawa et al., 2012, Cueto et al., 2016). This view can therefore also be extended to the extinction of the megafauna of North America and Australia by humans as mentioned previously.

Also, some very elaborate tools found in association with H. heidelbergensis, as mentioned earlier, were not for foraging purposes indicate that they were skilled craftsmen too. They were among the first archaic human species to possess some form of social intelligence and were apt to cooperate not only for hunting but for foraging in general, and also for feeding and even breeding (Vaesen, 2012).

So, in this paper I shall affirm that the reversal of hierarchy between predators and Homo species had occurred in H. Heidelbergensis. In my opinion, they were fearless hunters and toolmen who were the first to possess the ability to modify their environment by reversing the order set by Nature (or natural selection), in this instance, the food chain, where the natural hunter became the hunted. Later Homo species such as anatomically modern humans inherited those skills and perpetuated this culture around the planet.

Of course, it could be argued that other species also have the ability to modify their surroundings. We have already mentioned the case of bushfires set intentionally by raptors and in other examples, we observe elephants (e.g. African bush elephant, Loxodonta africana and African forest elephant L. cyclotis) who can significantly alter savannah and forest landscapes by destroying trees (see for e.g. Guldemond et al., 2017); or beavers (e.g. the

Eurasian beaver, Castor fiber) who can change the course of a river and its neighbouring flora that can affect the surrounding ecosystem. But there are several checks that prevent them to expand their annihilation in a larger scale, geographically, and the most significant reason is predation including humans and its related induced causes, which they have not been able to reverse.

Only humans have today completed the reversal of hierarchy which first occurred around the Upper Palaeolithic, when from the hunted (or initially as the prey) they became the hunter (ultimately the supreme predator). I shall also put forward this geological age for the start of the Anthropocene epoch, a mass-extinction cut-off in which humans have started to inflict irreversible changes in their environment that shall be observed in geological strata very much later by future palaeontologists and geologists by the differentiation of species' fossils before and after the cut-off.

Predation pressure, cooperation, compassion among tribe members: Building a model for the origin of human society and civilization

Before building a model of the origin of human society, there is one aspect mentioned earlier as being characteristic to the Homo genus and which needs to be discussed further. This is the increased sociability arising from (or perhaps leading to) encephalisation which led to an increasing order of compassion and cooperation among tribe members. We can already note that the oldest record of compassion and care for tribe members is assigned to H. erectus as corroborated by the 'old man' fossil of Dmanisi, Republic of Georgia, which dates around 1.8 m.y.a. The skull of this old individual who lost all but one of its teeth while living (and not after death) showed that he lived for a significant period after this disability and this feat can only be assigned to conspecific compassion and care from other tribe members (Lordkipanidze et al., 2005. See also Lordkipanidze, in this volume) and I shall add protection of tribe members against predators too.

So, I shall again refer to the model of cooperative breeding and defence against predators, briefly mentioned earlier for langurs (Semnopithecus entellus), whose hypothesis can be tested by observations in other animal species (including species of birds and fish which form cooperative breeding groups, just like S. entellus) when group members join forces to mob a predator which threatens the community (for a list of those species, see Krams et al., 2010) and use it to form a model of evolution of the human society based on selection from predator pressure.

To start with, we have seen how specific characters of the Homo genus carved its evolution from the primitive hominin society, of the late Pliocene and early Pleistocene and who were still part-time tree dwellers at night, to the more socially evolved tribes of pre-humans (or archaic human) species, such as H. heidelbergensis and H. erectus, where members were either sheltered in a cave or, at a later stage of their evolution, gathered around fire at night. In such a type/ model of society, where everyone cares for the safety of the group, as inferred from the example of H. erectus of Dmanisi, it could be inferred that tribe members would attempt to rescue instead of fleeing for dear life while a predator is busy mauling any unfortunate tribe companion (not necessarily a close relative. See Jordania in this volume).

I am therefore asserting that this character is almost exclusive to Homo species (quite ascertainable from H. erectus, as mentioned) and this separates us, if not differentiate us, from most, if not all, non-human primates. This set the base for later human societies which would evolve according to this model.

This latter society, enlarged tribes (or assembly of tribes), would be the one to develop as a pre-modern one, into building huts centered around a common night gathering place, caring for the sick and injured members, sharing the day's hunting bag among tribe fellows and their dogs, the latter watching over the whole camp and their penned livestock.

So how did we arrive to such a stage of evolution of a society which forms the building block of civilisation?

To answer this question some specific aspects need to be considered such as how defence against predator threat come to influence the size of the group and how can a number of males with almost equal breeding rights (except the chief, or king or the strongest warrior, whatever…) can accommodate themselves within such a society.

Lesser degree of sexual dimorphism in humans

We can note that the formation of this type of society depends on how many males can coexist in a tribe without conflict. Humans have evolved towards displaying a lesser degree of sexual dimorphism as compared to other hominoids, as "…the relatively small sex difference in stature (~7%) and its decrease during human evolution have been widely presumed to indicate decreased male contest competition for mates…" (Lassek & Gaulin, 2022), hence towards a monogamous society.

Fossil records suggest a gradual decrease in sexual dimorphism from Plio-Pleistocene hominins such as species of the genera Australopithecus and Paranthropus (which exhibit a similar degree of dimorphism compared to extant hominoids e.g. gorillas) to the early Homo species (e.g. H. erectus) up to anatomically modern humans which have the least degree of dimorphism (McHenry, 1991a; 1991b; Harmon, 2006; Villmoare et al., 2019). Humans, therefore exhibit a clear divergence from the extant apes (Lassek & Gaulin, 2022) and I cannot but remark that there is a correlation between encephalisation (with its implications towards complex sociality) and degree of sexual dimorphism.

I shall therefore suggest that non-human primates, in general, could have evolved towards a higher degree of sexual dimorphism as resulting from a completely different response to predator pressure as opposed to hominin species and later humans, who in parallel, had the degree of complexity of their society increase through increasing compassion and cooperation and where there is a number of males who can share the task of foraging and defending the colony more efficiently against predators.

Size of group and predator pressure

In most prey species, for example ungulates, the herd or group size correlates with the degree of threat of predation (predator pressure) (Creel et al., 2014). The group size is large so that nearly all of them can flee to safety when a predator or predators manage to bring one of them down and the degree of threat of predation seems unrelated to the number of males in the group, quite logical if we consider that while males contribute less to group vigilance, they are not there to defend the group as they would also flee at the first alarm (Childress & Lung, 2003). This strategy of flight in wholesale number guarantees the survival of the species in the long term as regards to predation. There are other checks to optimise the size of their population such as natural disasters (drought, for instance) but they are not relevant to the discussion here.

As for primates, it has been observed that species living on the ground and in smaller groups suffer higher predation rates than those in large groups (Shultz et al., 2004). This observation already led to an earlier-mentioned discussion on increased sociality in primates as a consequence of predation. But unlike in ungulates where predation pressure was unrelated to the number of males, there is an observed correlation between predation pressure and the number of males in a S. entellus group (Schaik & Hörstermann 1994), and of course with the size of the group also as explained above.

During a predator threat, langur males actually form the first line of defence and display aggressivity and other aposematic tactics to allow the female and young to flee to safety (Ibid). Expanding this hypothesis to humans, where native tribes in some countries, I point that this behaviour has been observed and documented, amongst others, in Amerindian tribes during the great Indian wars of the 19th century (Brown, 1972) where the predator threat was in the form of an offensive human enemy army. This latter hypothesis test result fits the model I am trying to develop here.

Predation pressure and construction of shelter

Observed in some fish species which "…neither suffer from habitat saturation, nor are their groups composed primarily of relatives...", it was found that "…enhanced safety from predators by cooperative defence and shelter construction are the primary benefits of sociality…" (Groenewoud et al., 2016). In human tribes, who had developed a form of social (or collective) intelligence, such benefits are obvious from an evolutionary point of view. They had several males cooperating for defence of the community, who were skilled craftsmen through development of the culture for tool industry (both for foraging and non-foraging), which included language and other forms of communication. So, it follows from the previous cited conclusion that they were apt to build shelters as the ultimate benefit of their sociality. And if we go back to see where this whole process started, we observe that it was because of predators.

So, in this paper I would ultimately suggest that the evolution of the human society and ultimately civilisation is a consequence from the defence against predators.

Conclusion

Anatomically modern humans do not need to defend against predators anymore. Such could be a condensed tagline of this paper.

However, this had not been the case at the start of our evolutionary period. The evolution from its roots, from the most basal hominins, more arboreal than terrestrial, at the near bottom of the food chain with very limited self-ability for defence, to the undisputed top predator place has taken only a few million years.

During this period of evolution, specific characters had been either acquired or improved, all of which makes us human and each of them played their part to reverse the hierarchy between us and the top predators. These are:

1. encephalisation: for increased sociability and compassion, creative skills and cooperation for foraging and non-foraging.
2. diet: entering in direct competition with predators.
3. post-cranium morphology: for power and precision grip to handle tools and become skilled craftsmen.
4. tool technology: arising from spread of culture, and which kept on improving and upgrading.

It is also pointed out that the domestication of fire and the arrival of the dog in the human tribe contributed further towards keeping predators away from the settlement. As a result of those evolutions the balance of power between humans and predators started shifting from being the hunted to being the hunter.

Since all those aspects of human evolution were in parallel with the evolution of the means of defence against predators, a correlation had been observed. So, in short, it is predator pressure that shaped the evolution of humans and its society.

As such, a model of human evolution was constructed with defence against predators being the driving force for the enhanced cooperation between more male members of a group of humans to form a settlement with the building of shelters to provide more protection for the group.

To put it simplest possible: Evolution of defence from predators in humans, has set the base for civilisation, not by the survival of the fittest but by the *survival of the smartest*.

Analysing the models proposed for the conference

Referring to the "Call for abstracts" listed in Appendix 1

I note that there are several models which fit partially with the model that I developed. But some models do not fit in at all.

So, I shall make a brief recap of these models and see where they fit, if partially or not at all.

Model 1: "No defense strategies were required for early humans, as they lived in an environment lacking dangerous predators."

This model is eliminated as humans evolved in Africa, the renowned land of predators and fossil of early hominins display clear evidence of predation.

Model 2: "No defense strategies were required as early humans were the top predators and ruthless killers of their ecosystem."

This model is true only now, after civilisation has been established and most large predators exterminated. But this was not true in earlier periods, even some centuries ago as shown.

Model 3: "Early humans were not big game hunters, but scavengers."

Unfortunately, I have not been able to ascertain at 100% if the earliest archaic human, *Homo habilis* was a scavenger (passive or aggressive) or if it was already a hunter. But this model cannot be discounted as there is a good probability that early archaic humans were scavengers. So potentially this model contains some elements of truth.

Model 4: "Early human ancestors were not powerful predators, but a weak prey species, with their best survival option still to climb trees."

The earliest human ancestors (*H. habilis* again) were most probably not powerful predators but only ambush hunters as I argued in this paper. So, this model fits only if we consider the early human ancestors as from *H. erectus* and *H. Heidelbergensis*. But definitely early human ancestors were not fast climbers compared to non-hominid primates as I demonstrated. So it was not one of their survival options.

Model 5: “Early humans used various defenses, still not well-studied and understood.”

This model seems the most appropriate of all and it fits many aspects developed in my paper. However, I consider that I have explored almost all the defensive arsenal, from tools to cooperation to fire to dogs and finally construction of shelter.

Model 6: “Early humans used an aposematic strategy of defense.”

I accept that non-human primates certainly do use aposematic strategies of defence, even the powerful gorilla male shows teeth, beats things around and mocks charges in the presence of a threat. But in this paper I showed that early human ancestors (of the *Homo* genus) did not display aposematic tactics for defence. But it is well documented that even some modern human tribes use aposematic tactics to steal prey from predators but not so much for defence.

In my model proposed, humans evolved to assemble in communities composed of several males (an upgrade from the primitive tribe) as a result of cooperation in defence against predators. This cooperation widens to provide care and to be compassionate towards the members of the group, for foraging and building of shelter. At this stage of their evolution, humans were highly apt to spread their culture, particularly in tools industry and technology, and were skilled craftsmen. Therefore, they easily expanded in number and in range, until they colonised all the habitable continents. It can therefore be resumed that predator pressure is the driving force behind human evolution towards civilisation.

Analysing the key questions to be addressed at the conference

Referring to Appendix 2.

1. How do monkeys and apes deal with the problem of predation?

This question has been addressed in this paper. It was inferred that the preferred strategy of defence of monkeys against predation was flight in trees instead of fight. Some monkeys do display aposematic tactics but for generally flight in trees was the preferred tactic. Apes, on their part, are semi-arboreal or mostly terrestrial for some and depending on the predator or threat, they either flee in trees, display aposematic tactics, or even defend aggressively by throwing stones or using sticks.

2. How do predate or defense strategies differ among terrestrial and arboreal species?

This question was addressed in reference to monkeys that live in trees and the first hominins that became more terrestrial than arboreal. It was inferred that both species had recourse to flight in trees. When hominins became fully terrestrial, they used their hands to grab a stick or threw stones as a means of defence.

3. Why do most large predators in the wild avoid humans on foot?

In the paper, it was found that the height of humans due to their bipedalism (or upright walking) were not a deterrent for predators (Lions still attack 12 feet giraffes without giving a second thought.) But from what Corbett says, a predator will avoid humans except when defending their young or territory or kill and when in dire necessity of food as a result of either incapacity or old age and I would add, if there is no prey as well.

It was then inferred that humans have almost exterminated wild predators except in Africa where they are relatively higher in numbers than elsewhere. I shall therefore suggest that a predator will avoid a human as they know by instinct that humans are very dangerous.

4. How could our ancestors defend themselves while sleeping on the open ground?

For this question there was no answer given for early hominins as there was no evidence collected for that. But for more later archaic humans and modern humans, the use of caves, use of camp fire and thorns, and the dog were the means of defence as given in the paper.

5. Are the origins of human bipedalism connected to predation control?

This paper answers a formal NO to this question. It was found that bipedalism occurred much earlier than thought, even before our ancestors first became fully terrestrial.

6. Were early humans big game hunters or scavengers?

It was difficult to give an answer without some uncertainty in it. While the first signs of butchery on animals and a possibility of ambush hunting appears in the in the first *Homo* species, we cannot say for sure if the butchered remains found were that of a scavenged corpse or a kill from a hunt.

7. How effective was early human use of projectiles and other tools available to them?

It has been found in this paper that H. heidelbergensis and H. erectus were the first archaic human species to use projectiles to hunt. Wooden spears, or stone-tipped spears were found and some animals fossils found in association with those hunting tools ascertain the effectiveness of such primitive projectile weapons

8. What can we learn from contemporary African hunter-gatherers?

First it is suggested in this paper that these contemporary tribes use perhaps the same means of defence against predators as more primitive tribes of the past (fire, dog, thorn enclosures). The method of hunting too should be characteristic of archaic or early humans. Humans are not adapted for fast sprints but for marathon-type of running, the morphology of their feet shows this. So, the method of hunting of wearing down preys over long distances by hit and chase would the same employed by our ancestors.

9. What can we learn from contemporary human-animal conflicts?

A lot has been said in this paper as answer for this question. It will be too long to re-enumerate them here.

10. Could some well-known human art forms (like choral singing, synchronous dancing, body painting) evolve as defense strategies against predation and competitors?

In this paper, the case of the Tsavo man-eaters showed that the lions attacked at night despite the aposematic tactics of group singing or battle trance. The lions did not attack the group (who would have done so?) but the forms of aposematism did not cause them to leave the camp area at all and waited until they could find a leak to get through for their next victim.

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Appendix 1 - Call for abstracts: Models for investigation

Scholarly Background of the Conference: The purpose for such a scholarly meeting is to address the glaring gap in the existing literature on defense strategies in early human evolution. Although defense strategies in the animal kingdom have been an important topic for decades, the defense strategies of early humans are still surprisingly neglected. There are several reasons for this disregard for such an important topic. We can probably distinguish six historically formulated models on human defense against predators:

Model 1: “No defense strategies were required for early humans, as they lived in an environment lacking dangerous predators.” This model was proposed by Charles Darwin in his book on human evolution (1871). Darwin mused, that humans probably evolved on a big warm island (either in Australia, Borneo, or New Guinea) with no major predators. Today scholars are sure that humans evolved in Africa, which abounds in large predator species (including fierce competition among them), but Darwin’s model of human evolution, based predominantly on the forces of sexual selection, still remains very popular among many contemporary scholars.

Model 2: “No defense strategies were required as early humans were the top predators and ruthless killers of their ecosystem.” This model, known as the “Killer Ape hypothesis,” was proposed by the “Father of Australopithecine” Raymond Dart (1949), and popularized by Robert Ardrey (1961). This model had a powerful grip on the human psyche, and the image of our ancestors as powerful big-game hunters still has an influential place in scholarship, although the progress of an alternative hypothesis that our ancestors were more scavengers than apex predators (see the next model) has somewhat eroded the popularity of the “killer ape” hypothesis.

Model 3: “Early humans were not big game hunters, but scavengers.” This model developed as an alternative of the “Killer Ape hypothesis” during the 1980s “new archaeology” revolution (e.g., Binford, 1985). Two modes of scavenging were proposed: (1) confrontational (aggressive, power) scavenging, in which the original killer is chased from the carcass, and (2) passive scavenging, in which the carcass is accessed only after the original killer has left. Current consensus favors the confrontational scavenging in early human evolution.

Model 4: “Early human ancestors were not powerful predators, but a weak prey species, with their best survival option still to climb trees.” This model, known as the “man the hunted” hypothesis, was based on the diligent study of taphological early human remains by Charles Brain (1981, 2004) and further developed by Donna Hart and Robert Sussman (2008). This model acknowledges the immense pressure of predators on early humans, but finds it difficult to explain how such a weak primate prey species without any serious means of defense managed to live on open savannah and to travel outside of Africa, gradually becoming the widest distributed species on the planet.

Model 5: “Early humans used various defenses, still not well-studied and understood.” This model, potentially uniting many possible strategies, can be attributed to Adriaan Kortlandt, Dutch ethnologist, a rare exception among scholars, who was deeply interested in early human defense strategies. In the 1960s and 1980s he proposed that early humans probably used sticks and rocks as contemporary apes do, and possibly also thorny branches to secure themselves from powerful African predators of the time.

Model 6: “Early humans used an aposematic strategy of defense.” The origins of this model can be traced to Lewis Leakey, who tried to explain the fact that wild lions rarely attack humans, proposing that lions are deterred by human unpalatability (1967). The idea was further developed by Paul Weldon, who proposed that humans were chemically aposematic (2018), and also by Joseph Jordania (2014, 2017), who proposed that during early stages of evolution humans used a wide arsenal of audio, visual, olfactory and behavioral intimidation displays to defend themselves against African predators, gradually becoming the apex aggressive scavengers (links to model 3) in the African savannah and the widest distributed species on earth.

Appendix 2 - The Themes of the Conference

There were not any strict thematic restrictions on the participating scholars, so all the presentations that deal in any way with defense strategies from predators were valuable for the conference. It should be remembered that the conference was planned as a multi- and inter-disciplinary forum to address this important topic. Here are several suggested themes, formed as questions, that was hoped to be addressed during the conference:

1. How do monkeys and apes deal with the problem of predation? The discussion of various predator defense strategies used by animal species (and particularly by monkeys and apes) is very useful in order to have a perspective of the evolutionary options available to our distant ancestors while they lived in the trees and when they moved to the ground.

2. How do predator defense strategies differ among terrestrial and arboreal species? During the early stages of evolution our ancestors underwent a crucial change from an arboreal to an arguably more dangerous terrestrial ecosystem. We want to discuss the kind of challenges they had to overcome, for example, why virtually all the primates that became terrestrial, increased the size of their canines, whereas human ancestors' canines gradually decreased.

3. Why do most large predators in the wild avoid humans on foot? Avoidance of humans on foot by all major animal species is well documented in scholarly literature, and we would like to discuss the possible reasons for this phenomenon, as it might not be connected to their fear of armed humans instilled during the last few decades or centuries.

4. How could our ancestors defend themselves while sleeping on the open ground? This is possibly one of the hardest questions to answer about our ancestors who managed to survive living in the open savannah. Adriaan Kortlandt proposed that the same way as chimpanzees often organize noisy evening displays in order to scare away possible predators before they go to sleep, some contemporary African tribes also organize evening (or night) loud "concerts," arguably with the same goal of securing the safety of their night's sleep. Human body smell as a deterrent at night was also considered by Leakey, Weldon, and Jordania.

5. Are the origins of human bipedalism connected to predation control? Bipedal posture as a "threat display" in many animal species is widely known. This mode of locomotion was proposed to be a strategy for predator defense in early humans for at least two reasons: (1) watching out for predators, and (2) intimidating predators with an in-creased height. Even today, big predators more readily attack crouching humans than fully erect ones, and the advice given to those who suddenly find themselves facing dangerous predators is to stay tall and even raise hands.

6. Were early humans big game hunters or scavengers? The question whether our distant ancestors were big game hunters or scavengers (more likely aggressive scavengers) had been in active discussion since the 1980s. We are happy to review the contemporary evidence on this important topic and discuss the various viewpoints on this issue.

7. How effective was early human use of projectiles and other tools available to them? Use of projectiles has been long known as one of our ancestors' potent means of defense and attack, although the technical details of the efficient use of projectiles by early humans is still unknown. The male shoulder shows a remarkable adaptation for this kind of physical activity. We also would like to discuss the use of projectiles both for attack (within the viewpoint of model 2, the killer ape model), and for defense (within the viewpoint of model 3, the scavenging model) in early human evolutionary history.

8. What can we learn from contemporary African hunter-gatherers? The perspective from some of the contemporary African tribes that until recently employed the elements of hunter-gatherer lifestyle (like the Hadza, Pygmies, or San people), and particularly the existing records about their habits in dealing with predators before wide contact with Europeans, can allow us to illuminate new possibilities in discussing the possible defense strategies of our distant ancestors.

9. What can we learn from contemporary human-animal conflicts? The problem of man-eating animals is still active in many regions of the world, some more (such as India or Africa, mostly with tigers, lions, and leopards) and some less (such as North America with mountain lions and grizzly bears).

Doing a comparative study between ancient and contemporary human populations, we can learn in both ways: understanding the evolutionary strategies of our ancestors from knowledge of the current state of this problem in contemporary populations, as well by implementing our knowledge and insight of evolutionary strategies for the better defense of contemporary populations in vulnerable regions.

10. Could some well-known human art forms (like choral singing, synchronous dancing, body painting) evolve as defense strategies against predation and competitors? At least the above-mentioned aposematic model of defense in human evolution (model 6) proposes that some forms of human arts (rhythmically united group singing and dancing, as well as the universal human tradition of body painting) primarily had the function of defense from predators by using them as elements of multi-modal aposematic displays, and at the same time, profoundly transforming the mental state of the participating members of the group.

Possible Role of the Tree-to-Ground Sleep Transition in the Imagination of Defense Strategies by Means of Music, Song, Dance, and Pantomime in Early Hominins

Alejandra Wah (Netherlands)

Abstract. Music, song, dance, and pantomime may have evolved as defense strategies in early hominins. In this chapter I examine what we so far know about the emergence of these behaviors by focusing on the human cognitive capacity to imagine. Based upon archaeological records, I first explore fossil evidence on the emergence of these behaviors. Drawing on cognitive archaeology, I subsequently focus on the possible emergence of the cognitive capacities underlying the experience of music, song, dance, and pantomime in hominin evolution. To fully understand these human abilities, I propose to consider the cognitive processes of interoceptive perception; an imaginative triadic system consisting of mental space travel, mental time travel, and mental mind travel; metacognition; and episodic memory – together constituting a cognitive capacity that I call *reflective imagination* – a capacity which seems to have begun to emerge in early hominins. Based on sleep science, I conclude that tree-to-ground sleep transition facilitated the evolution of reflective imagination in early hominins, allowing them to imagine defense strategies by means of music, song, dance and pantomime.

Introduction

The study of the emergence of music, its relation to song, dance, and pantomime is central to the evolutionary study of human behavior. Music, song, dance, and pantomime may have evolved as defense strategies in early hominins. For instance, rhythmically united group singing and dancing have been argued to function as defense from predators by using them as elements of multi-modal aposematic displays (Jordania 2014; 2017; in the same Volume). *What can be explored that can constitute "music," "song," "dance," and "pantomime" that is evident in human behavior cross-culturally?*

Humans have the universal capacity not only to move rhythmically but to entrain, that is, to synchronize their movements in a rhythmic fashion to an external timekeeper, such as a conspecific or a beating drum. This human ability to keep time should be distinguished from the ability of most nonhuman animals to move in a metric, alternating fashion (Brown et al. 2000). It is because of this capacity for rhythmic motor entrainment, that music, song, and dance can be treated as intrinsically related or as different manifestations of the same phenomenon. Nonetheless, music is mostly dependent on sound made on external objects; song on voice; and dance on bodily movement and gesture (Wah 2022). Behaviors that can be termed *musical* across cultures have been described as foundationally interactive, participatory, and social. This is evident from caregiver-infant interaction to rituals, particularly at times of significant life transitions (Cross 2016). The universality of *singing* in humans, and their singing faculties, strongly opposes the idea that singing behavior originated late in hominins. Singing among human ancestors must have started at the time when they still lived in the trees. Unlike other apes, who became silent in order to survive on the ground, human ancestors must not only have continued to sing, but in order to make their sound louder, must have developed the phenomenon of rhythmically united choral singing (Jordania 2011).

Archaeological, developmental, cross-cultural, and comparative evidence also illustrates the centrality of *dance* in human life and experience. Cross-cultural universals in dance styles and usages abound, indexed by universal preferences for particular movements. This suggests that the degrees of freedom of all possible movements of the human body depend on how many articulatory joints are involved and their rotational properties, and that a common human cognitive structure underlies the creation of dance (Christensen et al. 2017). Several researchers agree that in the evolution of hominin communication a mimetic or pantomimic stage was present, and consider this to be the basis of human linguistic narrative abilities (e.g., Donald 1991; Boyd 2009; Zlatev 2014; Corballis 2015; Ferretti et al. 2017). Taking into account the inherently narrative character of verbal language, *pantomime* must have been the nonverbal, mimetic means to communicate mental patterns to others using a narrative format (sequence of events) (Ferretti et al. 2017).

Based upon archaeological records, in this chapter I first explore fossil evidence on the emergence of music, song, dance, and pantomime in early hominins. Drawing on cognitive archaeology, I subsequently focus on the possible emergence of the cognitive capacities underlying the experience of these behaviors in hominin evolution. To fully understand these human abilities, I propose to consider the cognitive processes of interoceptive perception, an imaginative triadic system consisting of mental space travel, mental time travel, and mental mind travel; metacognition, and episodic memory – together constituting a cognitive capacity that I call *reflective imagination* – a capacity which seems to have begun to emerge in early hominins. Based on sleep science, I conclude that tree-to-ground sleep transition facilitated the evolution of reflective imagination in early hominins allowing them to imagine defense strategies by means of music, song, dance and pantomime.

1. Archaeological Evidence on the Emergence of Music, Song, Dance, and Pantomime in Early Hominins

Drawing on archaeological records, what do we so far know about the emergence of music, song, dance, and pantomime in early hominins?

Australopithecines and early Homo

About 5–7 million years ago (mya) hominins last shared a common ancestor with chimpanzees. Over this time they went through a series of evolutionary changes in anatomy, cognitive function, and social structure (Donald 2013). Evidence pointing to the emergence of *musical behaviors* can be found in the human fossil record. This record suggests that musicality does not emerge as a full-blown capacity but rather that subcomponents of that capacity emerge at different times, and probably in response to different selection pressures. The capacity to entrain or synchronize with others to an external perceived rhythm, pulse, or beat, characteristic of music, song, and dance must have arisen at some point in the hominin lineage over 5–7 mya (Cross 2016).

Early hominin ancestors, the *Australopithecines* (4.2 mya) share several anatomical features with other great apes such as a narrow scapula and long, curved phalanges; which are clear indicators of arboreal adaptation (Samson & Nunn 2015). The strong curvatures displayed in their finger bones thus suggest that *australopithecines* were tree climbers. They seem to have sought the shelter of trees to escape predators, especially at night (Gurche 2013). However, terrestrial habits evolved in *australopithecines* (Jerison 2000). The shift from quadrupedal to bipedal locomotion demanded substantial changes in the body's anatomical structure. The fossil record, in particular their angled knee, also suggests that although *australopithecines* retained some anatomical features of tree dwellers, they were biped (Corballis 2011; Gurche 2013). The possible connections between bipedalism and entrainment remain to be established. At this stage their inner ear bony labyrinth could not yet have provided full balance for walking, but as Steven Mithen states, the better our ancestors walked, the more rhythmic they became; and the more rhythmic they became, the better they walked (Mithen 2005). It was about 3 mya that the primate foot with an opposable digit suitable for grasping and climbing evolved, specialized for walking and running (McKee, Tobias, & Clarke 1996).

Musical behaviors might have driven brain expansion. Paleoneurology provides direct evidence regarding brain history by relating changes in its external appearance (as mirrored in casts molded by the cranial cavity) to the evolution of behavior and cognition. Because brain size and complexity are intimately related, the evolution of musicality must be correlated with the evolution of cognitive capacities and associated encephalization (Jerison 2000). *Australopithecines* had brain sizes similar of those of extant chimpanzees (around 400 cc). The external cranial base in *australopithecines* is within the chimpanzee range, and generally flatter than that of later hominins. This is true of all but an *australopithecine* specimen from east Turkana, (ER 406), dated to about 1.6 mya (Wolpoff 1996). No significant increase in relative brain size occurred until about 2.5 mya, with the advent of hominins assigned to the genus *Homo*. *Homo habilis* had a brain size around 650 cc (DeLouize, Coolidge, & Wynn 2016; Coolidge and Wynn 2016).

Fossil records contribute to an understanding of the evolution of *singing.* In other apes and *australopithecines*, the nasal bones are flat (Franciscus and Trinkaus 1988). This lack of an external nose and their long, narrow palates may explain why other apes lack the ability to produce consonants (Savage-Rumbaugh and Lewin 1994). With regard to the rib cage, *australopithecines* had funnel-shaped chests, which do not permit sufficiently fine control over phonation to make the subtly differentiated vocal sounds required for singing (Cross 2016). However, the reconstructed thorax of late *australopithecines* (Lucy), dated at around 3.2 mya, has been described as somewhere between the funnel-shaped chest, like that of chimpanzees, and the barrel-shaped chest, like that of humans (Gurche 2013). Among some of the possible *proto-musical and proto-singing behaviors* present in late *aus-*

tralopithecines are a rich repertoire of calls (entailing pitch changes) used to express affection and emotions (Falk 2000; Jerison 2000), hand clapping, foot stamping, whistling, chorusing, and drumming on the chest or on external objects (Wescott 1973; Jordania 2011).

Findings in the reconstruction of vocal anatomy also contribute to an understanding of the evolution of *singing.* Limited fossil records, data, and inferences from bony regions surrounding critical areas for the production of human speech sounds, indicate that the ability to produce the sounds of song and language appeared in early *Homo*, dated to around 1.5 mya (Frayer and Nicolay 2000). In early *Homo* populations, the lungs (as measured by the rib cage) attained an extant human shape (Frayer and Nicolay 2000). Around 2 mya bipedalism became obligate rather than facultative, freeing the hands and arms for manipulative purposes, including manual gestures (Corballis 2011). Again, before verbal language evolved, human ancestors probably developed nonverbal skills for reading each other's minds through vocal modulation and whole-body gesticulation preceding *dance* and *pantomime*.

Homo ergaster or African Homo erectus

In the artification hypothesis Ellen Dissanayake argues for the origin of behavioral entrainment, *proto-musical*, *proto-singing*, and *dance-like behaviors* in the adaptive ancestral mother-infant interaction. This interaction seems to have evolved around 1.7 mya, but perhaps earlier. It must have been present in *Homo ergaster* or *African Homo erectus*, and have helped to address the skeletal alterations in the birth canal required by upright posture in bipedalism in the Pleistocene. These skeletal alterations conflicted with continuing encephalization or brain enlargement, resulting in a gradual reduced gestation length and a greater physical helplessness of the human infant at birth (Leakey 1994; Dissanayake 1992, 2000a, 2000b; Morgan 1995; Falk 2004). The modifier "proto" indicates that these behaviors were spontaneous, nonconscious, and unintentional (Dissanayake 2009).

By about 2 mya, *Homo erectus* seem to have evolved new behaviors and adaptations. They were fully bipedal, almost 2 meters tall, weighed about 60 kilograms, had an active lifestyle, and made the complete transition to terrestrial life (Coolidge 2020). Brain size in early *Homo* had somewhat increased compared with the brains of *australopithecines*, but was little more than half the size of the average human brain. The endocast of the left frontal lobe of a *Homo rudolfensis* specimen (KNM-ER 1470) revealed sulci that delimit Broca's speech area in humans and are not seen in brains of *australopithecines* (Tobias 1981; Falk 1983). At that time, the brain shape also changed due to apparent expansion in the prefrontal cortex (Falk 1983). *Homo erectus* had an increase in relative brain size, about 950 cc. The size of extant human brains is 1,350 cc. When *Homo erectus* first appeared about 1.9 mya their brain thus was about sixty-five percent the size of extant brains. After the appearance of *Homo erectus'* handaxe, about 1.5 mya, their brains approached eighty percent of extant human brain size (Coolidge 2020).

With *Homo ergaster* or *Homo erectus*, the barrel-shaped chest is fully present, and the capacity to control fine-grained sounds, such as *sing-song vocalizations*, can be fully postulated (Frayer and Nicolay 2000; Morley 2013; Cross 2016). The earliest appearance of an extant human rib cage occurs at about 1.5 mya in the Nariokotome boy (WT 15000) from west Turkana, Kenya (Jellema, Latimer, and Walker 1993). A distinctly humanlike external nose also makes its appearance in fossils by about 1.5 mya, identified as *Homo ergaster* or *African Homo erectus* (ER 3733). *Singing* requires a much greater control of airflow than does speaking, in terms of duration, amplitude, and pitch range of sound. Paleontological evidence also suggests that by 1.5 mya, both the respiratory and nasal systems of hominins assumed the same form as that of extant humans. It seems likely that by this date a singing capacity was present in hominins (Frayer and Nicolay 2000). Thus, drawing on fossil records, it is reasonable to suggest that *proto-musical*, *proto-singing*, and *dance-like behaviors* emerged in early hominin ancestors at least around 2.0-1.5 mya, if not earlier – and that musical, singing, dancing, and pantomiming behaviors must have been in place with *Homo ergaster* or *African Homo erectus.*

2. Cognitive Archaeology on the Emergence of Reflective Imagination (the Cognitive Process Underlying the Experience of Music, Song, Dance, and Pantomime)

Drawing on cognitive archaeology, I now focus on the possible emergence of the cognitive capacities underlying the experience of music, song, dance, and pantomime in hominin evolution. To fully understand these human abilities, I propose to consider the cognitive processes of interoceptive perception, an imaginative triadic system consisting of mental space travel, mental time travel, and mental mind travel; metacognition, and episodic memory – together constituting a cognitive capacity that I call *reflective imagination* (Wah 2019, 2020, 2022). The degree of these processes present in humans seems to underlie the ability to experience preverbal and nonverbal narratives by means of music, song, dance, and pantomime – a capacity which seems to have begun to emerge in early hominins (Wah 2019; 2022).

The recursive modes of thought underlying the human narrative capacity seem to have been gradually shaped during the Pleistocene (Corballis 2011). All human cultural manifestations, including the arts, philosophical inquiry, and the sciences seem to have emerged from feeling, that is, from *interoceptive perception*, because all these make use of a broad range of feelings and in turn contribute to their homeostatic effects. For instance, the emergence of music seems linked to the resolution of problems posed by feelings, and musical behaviors are both a product of feeling and powerful inducers of feeling. The emotive responses and the ensuing feelings caused by the sound in music, the voice in song, and the body in dance and pantomime would have been welcomed by early hominins. As movements, sounds, and gestures were added together, they could produce layers of effect, mimic objects and events in a sequence, and begin to tell a story or narrative (Damasio 2018).

The *imaginative* cognitive processes underlying the characteristically human narrative ability, including nonverbal and verbal narratives, seem to be global coherence (the capacity to relate events causally), and particular degrees of *mental space travel* (the capacity to imagine spatial locations decoupled from the immediate external environment), *mental time travel* (the capacity to imagine oneself or others at different times, distinguishing between past, present, and future), and *mental mind travel* (the capacity to attribute mental states to oneself or others, also referred to as mindreading or theory of mind) (Ferretti et al. 2017; Wah 2019). In humans, these imaginative processes seem to be closely related to interoceptive perception, metacognition, and episodic memory. For instance, mental time travel involves the use of episodic memory and episodic future thinking (Schacter et al. 2018; Suddendorf and Corballis 2007).

Metacognition is self-awareness or self-reflective consciousness, making it possible for humans to escape from the immediacy of exteroceptive perception and emotion, that is, to escape from being stimulus bound (mental space travel); to pre-experience in the imagination, foresee and evaluate events beforehand (mental time travel); to take another's viewpoint (mental mind travel); and to reflect upon, and change, own behaviors and actions and their outcomes (Metcalfe 2008). To explain the characteristic degree of metacognition present in humans, Endel Tulving (1972) proposed the term autonoesis. *Autonoetic consciousness* refers to the unique human ability to become aware of the subjective nature of time allowing mental time travel and involving the use of episodic memory. The function of *episodic memory* seems thus to remember and reconstruct relevant personal episodes and to simulate alternative future scenarios and outcomes. Greater working memory capacity would allow to actively choose or create an action based on one's past successes and failures to solve novel problems by actively comparing multiple simulated scenarios and combining them into novel actions (Schacter et al. 2011; Baddeley 2012; Coolidge 2020).

Nonhuman animals seem to evolve their own different levels of conscious awareness, including degrees of imagination, metacognition, and episodic memory (Romanes 1885; Clayton et al. 2001; Reiss and Marino 2001; Nelson 2005; Plotnik et al. 2010; Corballis 2013). The fact that these capacities exist to some extent in nonhuman animals suggests that they precede verbal language (Ferretti et al. 2017). Nonetheless, no evidence of narrative consciousness or of understanding anything like a story has been reported in nonhuman animals (Nelson 2005; Wah 2020). *Drawing on cognitive archaeology, when might the particular degrees of these cognitive capacities have emerged in early hominins?*

Australopithecines and early Homo

Cognitive archaeologist Merlin Donald argues that the evolutionary source of the human capacity to imagine is in what he calls mimesis. He explains that this mimetic capacity emerged around 3.4 mya, had its origins in late *australopithecines*, and can be fully found in *Homo ergaster*. This cognitive capacity depended upon changes in the nervous system, and meant a radical change in hominin evolution. Previously, the action systems in every known mammalian species were focused on the environment rather than internally on the action itself. Inward-directed attention allowed humans to focus in detail on their own actions, to evaluate them, and to change them on the basis of an imagined idea, which may have originated in the event structure of the environment or in the acts of themselves or others. A mimetic act is thus a performance that reflects, reenacts, or recreates an event. Its cognitive core is kinematic imagination, the ability to envision one's own body in motion (Donald 1991, 2001, 2006, 2013).

Mimesis has three behavioral manifestations: *mime*, in which one reproduces patterns of action, usually of others; *rehearsal of skill*, in which the actor imagines and reproduces recalled actions with a view to improving them; and *nonlinguistic gesture*, in which an action communicates an intention through resemblance. Metacognition (self-awareness) and sophisticated event representation (imagination) seem to be the neurocognitive mechanisms underlying mimesis. The emergence of mimetic skills was accompanied by some pedagogical capacity. This involves imagining and planning a motor act, executing it under conscious metacognitive supervision, predicting and analyzing the outcome, practicing and refining the final form of the action-pattern, and copying and profiting from the skill of others. Intentionally created stone tools evidencing the emergence of mimetic capacities thus date as early as 3.4 mya. Irrefutable evidence of intentionally created stone tools is found in the Oldowan industrial complex in South Africa, dated 2.3 mya (Donald 2013). Thus, although *Homo habilis* were thought to be the first to make stone tools, the almost 3.4 million-year-old stone tools discovered in Lomekwi, west Turkana, Kenya evidence that *australopithecines* also made and used sharp flakes. Based on these recent findings, cognitive archaeologist Frederick Coolidge argues that either the genus *Australopithecus* should now be changed to *Homo* or *Homo habilis* should be changed to *Australopithecus habilis* (Coolidge 2020).

The stone tools of *australopithecines* and *habilines* were relatively simple: mostly sharp stone flakes struck from a pebble core. These tools were used to butcher animal carcasses obtained through scavenging, and this access to higher quality nutrition arguably powered the increase in cognitive capacities (DeLouize, Coolidge, and Wynn 2016; Coolidge and Wynn 2016). Archaeological evidence thus suggests that late *australopithecines* and early *Homo* made and used stone tools; activities which are intrinsically rhythmic and require some initial capacity to imagine space from different perspectives, or mental space travel (Wah 2022). Mental time travel has been suggested to have been present in *Homo rudolfensis* (Corballis 2011). The evolutionary source of the human capacity to imagine seems thus to have begun to emerge around 3.4 mya having its origins in late *australopithecines* and can be fully found in *Homo ergaster* or *African Homo erectus* (Donald 2013).

Homo ergaster or African Homo erectus

An important transition in hominin cognitive evolution appears with *Homo erectus* about 2 mya (Donald 1991; 2013). *Homo erectus* must have had episodic memories. Evidence of episodic memory is found in the stone materials they used for knapping. These materials often came from long distances evidencing conscious decision-making and novel problem solving. It is still unclear whether this ability was autobiographical in the autonoetic sense. Increase in brain size and brain shape influence cognitive change. Paleoneurologists have shown that the shape of *Homo erectus'* brain was changing compared to that of *australopithecines* and *habilines* (see Bruner and Holloway 2010). *Homo erectus* had slightly wider frontal lobes; which are involved in decision-making and theory of mind. Although *Homo erectus* may not have possessed higher levels of theory of mind, this shift in brain shape does seem to evidence the presence of elements of theory of mind or mental mind travel. *Homo erectus* also had the vocal and breathing apparati to produce language-like sounds (see Walker and Leakey 1993). They communicated with one another and must have had some form of protolanguage with many different sounds that probably included exclamatives, imperatives, declaratives, and interrogatives (Coolidge 2020).

The Acheulian industrial complex appears in the Lower Paleolithic at about 1.8–1.6 mya with teardrop-shaped bifacial symmetrical hand axes (Asfaw et al. 1992; Chazan et al. 2008). These hand axes demand considerable exertion of time and effort (Stout 2002). They suggest constant monitoring and correcting of achieved results, and evidence not only imitation but also signs of a mind predisposed to innovate (Nielsen 2012). *Homo erectus* made these hand axes by trimming around the margins of a large flake to produce a sinuous cutting edge. In doing so, they gave the tool a bilateral symmetry. This process clearly required spatial cognitive abilities and hierarchical organization of action, relying on mechanisms of cognitive control whose use was not evident in the stone tools of earlier hominins (Hecht et al. 2014; Wynn 2002). About 1.75 mya, their handaxes show greater working memory capacity. There seems to be a strong correlation between working-memory capacity and the ability to solve novel problems (Shelton et al. 2009; Coolidge and Wynn 2016; Coolidge 2020). 500,000-year-old Acheulian handaxes, so-called S-twist handaxes, evidence greater spatial cognition (Wynn and Coolidge 2016; Coolidge 2020). Further archaeological evidence includes 500,000-year-old engraved shells found in Java, Indonesia (Joordens et al. 2015). These geometric and symmetric zigzag engravings show that *Homo erectus* were producing drawings with a meticulous attention to detail.

Within just a few hundred thousand years of their first appearance, *Homo erectus* groups began to expand to other parts of Africa, the Middle East, and Europe. About 1.7 mya, *Homo erectus* populated Southern Asia, India, and Southeast Asia and Indonesia (Coolidge 2020). The fact that *Homo erectus* quickly spread from Africa into Asia and to the border of Europe evidences spatial mapping skills (Gurche 2013). The fact that they also controlled fire (Gowlett 2016), and took their tools with them to different locations also suggests their foresight, or mental time travel capacity (Gurche 2013). Frederick Coolidge and Thomas Wynn hypothesize that the mental space travel capacity in *Homo erectus* may have been facilitated by physiological changes in sleep patterns related to the tree-to-ground sleep transition. A single integral sleeping period on the ground would allow for better sleep and for extended periods of SWS and REM sleep, this would allow for the consolidation and enhancement of procedural and declarative memories, having a possible correlation with creativity and the ability to solve novel problems (Coolidge and Wynn 2006, 2009, 2016; Samson and Nunn 2015; Shelton et al. 2009); and thus with the capacity to imagine defense strategies by means of music, song, dance, and pantomime – as I will explain in the third section.

3. Possible Role of the Tree-to-Ground Sleep Transition in the Imagination of Defense Strategies by Means of Music, Song, Dance, and Pantomime in Early Hominins

All animals exhibit a form of sleep. Sleeping is a period of immobility during which one responds to internal stimuli but disconnects from the external environment. Sleep states are constrained by the light–dark cycle and by seasons. Some organisms reverse these patterns in order to improve or to avoid predation (Coolidge 2020). Changes in sleep are central to human evolution. Although along the human lineage we still know little about the specifics of sleep, sleep science is already beginning to shed light on the emergence of cognitive processes and behaviors in the evolution of early hominins (Samson and Nunn 2015).

Sleep science points out four sleep stages in humans. Wakefulness is characterized by exteroceptive perception, sustained attention, learning, and recalling of memories to solve novel problems. Wakefulness is accompanied by rapid cortical brain waves, while periods of resting or daydreaming are accompanied by alpha waves. Of the four human sleep stages, (1) *Stage 1* is a transition stage from wakefulness to sleep; it is the lightest stage from which to awaken, and consists of waves of low amplitude, irregular, and desynchronized. (2) *Stage 2* is also a light stage of sleep, consisting of waves similar to stage 1, with two additional waves: sleep spindles and K-complexes. (3) *Slow-wave sleep* (SWS) is the deepest stage of sleep; it consists of delta waves, which are the slowest but have the highest amplitude. During this stage the parasympathetic system dominates and the gastrointestinal system becomes more active. Degrees of SWS sleep have been observed in all mammals, birds, and some fishes and reptiles. (4) *Rapid eye movement sleep* (REM) is associated with dreaming, accompanied by fast cortical brain waves, and characterized by muscle atonia (voluntary muscle paralysis). Degrees of REM sleep have been observed in mammals, birds, and some lizards. In human infancy and early childhood, REM sleep accounts for most of a total sleep period. By adolescence the percentage drops to about one fourth of a total sleep period, and this declines slightly after sixty years of age. Associated with human REM sleep are highly detailed images and stories (Coolidge 2020).

An important reason for the evolution of sleep in humans seems to be the processing of newly learned information, its storage, and its integration with previous memories (Coolidge 2020). While humans are awake, synapses are strengthened by learning and the formation of memories, placing extra demands on neurons and their supporting glia. During sleep, synaptic strengths seem to renormalize, restoring the ability to learn (Tononi and Cirelli 2014). SWS and REM sleep seem to play an important role in processing relevant daily information into long-term memory, consolidating procedural memories, and processing emotionally valent declarative memories, that is, episodic memories (Samson and Nunn 2015). Moreover, SWS sleep appears to reinforce memories in an “uncoordinated” fashion, suppressing coherent thoughts, whereas REM sleep binds and reinforces memories in a “coordinated” fashion. Cycles of uncoordinated reinforcement of memories during SWS, followed by coordinated reinforcement of memories during REM sleep, seem to have cognitive benefits (Kavanau 2002). Apparently one of the major biological functions of dreaming is to simulate threatening events. This is demonstrated in nightmares and dreams after trauma (Revonsuo 2000). By means of dreaming, REM primes sleepers, rehearsing threatening events or social scenarios that may occur in their waking environments (Samson and Nunn 2015). *When might these sleep stages and the tree-to-ground sleep transition have emerged in early hominins?*

Australopithecines and early Homo

Among primates, sleeping terrestrially is unusual. The ancestral primate was probably arboreal. Small-bodied primates often use tree-holes to care for their young, to stay within optimal temperatures, and to avoid predators and mosquito vectors that spread parasites. As primate body mass expanded, a transition occurred from fixed-point nest sleep to tree-branch sleep. The “sleep-quality hypothesis” suggests that, in great apes, more stable sleeping sites allowed deep and sustained sleep and thus enhanced cognitive function. By contrast, the “engineering hypothesis” argues that greater cognitive performance enabled them to build nests. It could be that increased complexity in construction of sleeping platforms improved cognition, which in turn enhanced nest-building potential (Samson and Nunn 2015). Interesting to note here is a phenomenon during the onset of sleep in most primates: the hypnic jerk. This is a sudden reflexive muscle movement that commonly awakens the sleeper. It seems to be an archaic response to misinterpretation of the muscle relaxation characteristic of the onset of sleep as a signal that the sleeping primate is “falling out of a tree” (Coolidge 2006; Coolidge 2020).

Their smallish bodies compared to their longer limbs indicate that *australopithecines* travelled on the ground while foraging, but probably slept in nests in trees. They had diets that included meat, but they seem to have resembled other apes in terms of brain size, brain shape, and behaviors (Coolidge and Wynn 2016). The body proportions of *Homo habilis* remained similar to those of *australopithecines* (longer limbs, shorter and lighter bodies), suggesting that they also probably still slept in trees (DeLouize, Coolidge, and Wynn 2016; Coolidge and Wynn 2016). *Homo habilis*, like *australopithecines,* thus appear to have maintained their largely arboreal lifestyle and restricted range. Although they spent time on the ground, foraging and scavenging for meat, *australopithecines* and *habilines* probably slept in trees for protection from predators. Both *australopithecus afarensis* (Lucy) and *Homo habilis* must have had SWS and REM sleep (Coolidge 2020).

Homo ergaster or African Homo erectus

About 1.9 mya, *Homo erectus* made a full transition to terrestrial life, including sleeping on the ground instead of in nests in trees (Coolidge 2020). *Homo erectus* seems to have been the first obligate biped with limb proportions that would make it difficult to facilitate arboreal sleep. Due to dramatic morphological changes and increasing body volume, they appear to have been the first full-time terrestrial ground-sleeping hominin (Samson and Nunn 2015). *Homo erectus* also seem to have been the first hominins to have relatively uninterrupted sleep, which preserves the integrity and benefits of SWS and REM cycles on learning and memory, including the replay of episodic memories during these periods. They may have been the first hominins to have derived cognitive benefits from qualitatively better sleep and a single, integrated sleeping period. All the benefits of sleep would have been enhanced because they slept on the ground, in shelters, and in much larger social groups (Coolidge 2020).

Drawing on findings in evolutionary anthropology and sleep biology, David R. Samson and Charles L. Nunn (2015) propose the “sleep intensity hypothesis”. According to this hypothesis, early hominins sleeping in novel terrestrial environments must have experienced selective pressures, such as increased predation risk and threats from intergroup conflict, to fulfill sleep needs in the shortest time possible. Shorter and deeper sleep would also enable more net hours of activity and increased social interaction in which to acquire and transmit new skills and knowledge. Samson and Nunn argue that deeper sleep led to both cognitive and behavioral benefits in early hominins. Of the cognitive benefits, increased sleep intensity conferred at least three: threat priming, memory consolidation, and increased innovation, all of which would probably improve survival in challenging novel terrestrial environments. Human sleep patterns are the shortest recorded among primates, and seem more efficient because the sleep is shorter and deeper, and exhibits a higher proportion of REM than the sleep in nonhuman primates. By means of dreaming, a higher proportion of REM sleep may have resulted in greater creativity, insight, and innovation (Samson and Nunn 2015).

For hominins, the transition from tree to ground life posed a challenge, as living on the ground entailed a greater risk of predation. To make the terrestrial sleep transition, early hominins seem to have evolved behavioral adaptations to counteract the risks and the loss of benefits of arboreal platforms. These new behaviors include defense strategies against predation such as the management of fire (Coolidge 2020). *Homo erectus* seems to have been the first hominin ancestor to use fire (Samson and Nunn 2015). Fire tending has been proposed as essential to make sleep possible in terrestrial environments. Fire at night would have helped to scare off predators, keep individuals warm during cold nights, and fumigate sleep sites with smoke to avoid biting insects (Coolidge 2020). For *Homo erectus*, fire management would also have allowed for increased group cohesion.

Musical, singing, dancing, and pantomiming behaviors also seem to have been crucial for group cohesion in early hominins. Robin Dunbar argues that behaviours, including singing and dancing, act functionally in humans. These emerged as forms of social grooming, as they are capable of triggering the endorphin system, functioning as group-bonding mechanisms, reducing aggression and enhancing social cohesion (Dunbar 2020). According to Joseph Jordania, rhythmically united, synchronous singing together with dancing, trigger a mental state characterized by analgesia (painlessness) and aphobia (fearlessness). Jordania describes this collective experience as an effective survival strategy, as well as a defense or attack system for critical moments such as wars. This experience creates a collective identity and a strong bond between group members, and sends a strong message to the predator about the unity and determination of the group (Jordania 2011). Loud evening group musical behaviors may have been organized in order to scare potential predators and secure nocturnal sleep (Kortlandt 1973). Human choral singing may have been used to defend territory (Hagen and Bryant 2003; Geissmann 2000; Rice 2014; Jordania 2014, Nettl 2022; Jordania in this Volume). Audio signals seem also to have been augmented by visual displays of threatening body movements, such as coordinated dance movements and pantomimic gestures (Jordania in this Volume).

Musical, singing, dancing, and pantomiming behaviors seem thus to have been crucial for group cohesion in early hominins. As discussed in the first and second section, these behaviors seem to have emerged in late *australopithecines* and early *Homo*, and appear to be fully found in *Homo ergaster* or *African Homo erectus*. The tree-to-ground sleep transition seems to have facilitated the evolution of reflective imagination in early hominins, which in turn would allow them to imagine defense strategies by means of music, song, dance and pantomime. Future research and new findings will continue to shed light on the emergence of these behaviors as defense strategies in early hominins.

Conclusions

In this chapter I have examined what we so far know about the emergence of music, song, dance, and pantomime in early hominins by focusing on the human cognitive capacity to imagine. Based upon archaeological records, I first explored fossil evidence on the emergence of these behaviors. Drawing on cognitive archaeology, I subsequently focused on the possible emergence of the cognitive capacities underlying the experience of music, song, dance, and pantomime in hominin evolution. To fully understand these human abilities, I proposed to consider the cognitive processes of interoceptive perception; an imaginative triadic system consisting of mental space travel, mental time travel, and mental mind travel; metacognition; and episodic memory – together constituting a cognitive capacity that I call *reflective imagination* – a capacity which seems to have begun to emerge in early hominins. Based on sleep science, I concluded that tree-to-ground sleep transition facilitated the evolution of reflective imagination in early hominins, allowing them to imagine defense strategies by means of music, song, dance and pantomime.

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The Lions and the San

Elizabeth Marshall Thomas (USA)

In the scientific world, an interesting question has arisen regarding our ancestors, formerly known as Bushmen, now known as San. For thousands of years the San lived in parts of Africa with a large number of lions and other important predators, and unlike our earlier ancestors, the apes who lived in the trees, the San lived on the ground where predators could find them.

How did they do this? What were their defense strategies? How were they able to sleep on the ground at night when such major predators as lions, lion-sized hyenas, and leopards were prowling around them?

It might seem strange but it is a fact that most scholars of human evolution haven't seemed interested in how our ancestors defended themselves from predators. Darwin (1871), for example, was sure that humans evolved in the safe environment of a large warm island with no predators, and that the biggest evolutionary force for human evolution was sexual selection. Raymond Dart and his follower Robert Ardrey (1961) believed that our human ancestors did not need a defense against predators because they themselves were apex predators, ruthless killers and cannibals. Taking a different point of view, Charles Brain (1981) and later Robert Sussman and Donna Hart (2005) suggested that our human ancestors were a humble species whose best defense was to climb a tree.

Studies trying to find the relevant strategies of defense from predators were almost non-existent. As a rare exception I should mention Adriaan Kortlandt (1965, 1980), a scholar who suggests that our ancestors defended themselves from predators by using sticks, stones, and thorny bushes. There are also recent suggestions that our ancestors were using the so called "aposematic" strategy of defense, which means they tried to scare away the predators by standing up, shouting and singing, clapping and stomping, and throwing sticks and stones.

Scholars are beginning to see that we need more research of this important topic, and an international conference was held in June 2023, thanks in large part to Dr. Joseph Jordania, who is and has been one of surprisingly few people who sees that the many thousand years survival of our ancestors the San has yet to be explained or understood. In the light of everything mentioned above, the experience of the San who managed to live among lions for tens of thousands of years can provide a window to the co-existence of humans and lions, and also to the cultural differences of lions. Lions in different areas have different cultures just like we do.

Make no mistake, lions were rightly seen as the most dangerous predators. The other large cats, the cheetahs and leopards, were not as dangerous – cheetahs were too small to successfully hunt people and leopards were easy to discourage – I knew a San woman who drove a leopard away with a stick, preventing him from attacking her sleeping husband.

Compared to the larger predators, the San were fairly small – a man might be about five feet tall and weigh a little over a hundred pounds, and although the San could run fast, “fast” for humans isn’t much more than twenty miles an hour. In contrast, a lion can weigh five hundred pounds and run at fifty miles an hour, as I discovered when I was young and strong and living in what then was South West Africa.

I was almost killed by a lioness who saw me from afar and started running toward me. I ran faster than I’d ever run before and jumped into the truck I’d arrived in right before she would have caught me. In just a few seconds she ran three times as far as I did, and perhaps sixty years later I remember the experience as if it had happened this morning.

The San lived mostly on vegetable foods but lions lived on the meat of large hoofed mammals such as antelopes, all of whom ran faster, some much faster, than the San. The San also ate large hoofed mammals maybe once every two or three weeks, so for hunting they had poison arrows. But defending yourself against a lion with anything less than a gun is pretty much doomed to failure, and more so if you’re counting on one of the San’s poison arrows, because the poison takes days to do its work.

This brings us to the question that now interests the scientists. How did the San survive as a species when living among large, successful predators while seeming like easy prey?

The answer is simple but hard to believe, and has to do with culture. Humans have cultures – quite various ones, as all of us know – but most of us are unaware that lions have various cultures too. I have seen lions of two different cultures starting with the culture of the lioness who chased me. This lioness was in Etosha Park, Namibia, and I later learned that the lions there were so dangerous to humans that while Namibia was fighting for independence, the lions prevented well-armed freedom fighters from entering Namibia from the north.

In contrast were the lions in a huge, “unexplored” area that existed until the 1960s and included much of the Kalahari Desert with parts of Namibia and Botswana, an area the San had inhabited for thousands of years and the white people hadn’t yet messed up. This area was the last part of unspoiled southern Africa and the lions who lived there did not harm people. To do so was against their culture.

The San and these lions were alike. Both were intelligent, both lived in groups, both lived near water, and both hunted the same large antelopes in the same way – they’d creep up on the victim for about the same distance, then a lion would charge or a San would shoot a poison arrow. Both attacks were fatal but the San’s took longer to get a result because the poison worked so slowly – the hunters had to follow the victim, often for several days, until the victim stopped walking or died. The big difference between the lions and the San was that the lion prides had chiefs or headmen but the groups of San did not. The San believed that everyone was equally important and they didn’t need special people to guide them.

Starting in 1950, it was my good fortune to visit the San and the lions in this vast, “unexplored” land. My parents, Laurence and Lorna Marshall, with my brother John, age eighteen, and me, age nineteen, went there to learn about the San, and because I learned I continue to put quote marks around “unexplored.” For thousands of years the San who lived there knew everything there was to know about every life-form big enough to see – every insect, reptile, bird, and mammal, every bush and tree. The area should have been called “The Perfectly Understood Area,” but since those who understood it had dark skins, wore animal hides for clothing, couldn’t read or write and didn’t speak Afrikaans or English, their knowledge didn’t seem like knowledge and didn’t count. Many years later, after multiple studies had been done, I heard a Harvard professor say that the San “know almost as much as we do” about their ecosystem. This stayed with me. Any teenaged San knew more about that ecosystem than all the Harvard professors together.

Most of the vast “unexplored” land had no surface water. During the dry season, the only water was in waterholes and most of these were hard to find – you could be standing near one and not know it was there. Some animals get what moisture they need from plants and morning dew, but lions and people need drinking water and during the dry season the area around each and every waterhole was home to a group of San and also a pride of lions. The San would make a camp somewhere near the waterhole, my family would make a camp next to them, and the lions would find a resting place out of sight of the San – we never saw the lions unless they came to see us. The San and the lions kept apart quite carefully, not wanting to involve each other. The San were active in the daytime and the lions were active at night.

Water may have influenced the peace the residents maintained. If the two groups harmed each other, one group might want to drive the other group out of the area, which meant away from a waterhole. If people were driven off, they could live with friends or relatives at other waterholes, but if lions were driven off, they’d have to fight the lions at some other waterhole. Whichever group was driven off would have to survive on morning dew while waiting for the rainy season. If the water situation made a difference, as I believe it did, the lions had better reasons than the people for keeping the peace.

The group of San we knew the best called themselves Ju/’hoansi. *Ju* means *person*, / is a click made by your tongue behind your front teeth as if you were saying *tsk tsk*, */’hoan* means *safe, harmless*, and *si* makes it plural. They had rightly named themselves “the Harmless People” – they saw the benefits of peace and of people being equal. Each person owned very little, so together they shared almost everything they had including a large tract of land.

The Ju/’hoansi saw the world as filled with interesting lifeforms whose skills and motives they had worked to understand. In short, they seemed not only open hearted but also open minded. To show the extent of this, I point to eighteen thousand kinds of beetles that live in southern Africa. The larvae of several of these beetles provide the poisons the San put on their arrows. The Ju/’hoansi called these beetles *kua* and also */oan (poison)*, the scientists called them *Diamphidia,* and their larvae were found about a foot down in sandy ground under Commiphora trees. Nothing seemed to grow under those trees. Why dig in bare sand where nothing is growing?

But the San favored knowledge over assumption, and would have seen beetles climbing up and down those trees or burying themselves in the sand, and then would have dug them up to learn more about them. Perhaps this summarizes the tie between the San and their world. To explore the contents of their ecosystem was important to them for the same reason that smartphones are important to some of us. We want to know what's happening around us.

The lions were also harmless, not to large antelopes of course – -they were harmless to people. For instance, once in the "unexplored" land, we'd been traveling in our truck all day and were very tired, so when night came, instead of making a camp for ourselves we just put our bedding on the ground and fell asleep. In the morning we found lion tracks around us. They'd been standing beside us looking down at our faces, wondering what we were doing on their land. We didn't look like the San, but they must have decided we were some kind of human because after they'd examined us they all walked away. We were thankful, of course, but it's good we kept sleeping.

My brother and I had an interesting experience when taking a long walk over the veldt. We were about a mile from our camp when we walked around a bush and saw a big lion in front of us, not ten feet away. The San had said that if this happened, we should not run, we should seem uninterested and walk away at an oblique angle. But we were shocked. We couldn't think. We just stood there staring. Meanwhile, the lion was seeming uninterested. Then he walked away at an oblique angle.

Almost a life-time later I still remember him, needless to say. He was full grown but still young, his mane was light colored, not dark like that of an older lion, and he was alone, which could mean he'd been kicked out of his pride by its male owner who didn't want to share the pride with another full-grown male.

Later we had a strange experience with a very large lioness. One night when we and the Ju/'hoansi were sitting around our campfires, this lioness walked out of the woods. She had come to tell us something, and began to walk up and down a little path that ran between our campsites, roaring so loudly we couldn't hear ourselves think, and no wonder – a lion's roar is so loud it can be heard five miles away. About twenty of us were sitting beside our campfires, but there was nothing we could do about the deafening roars except not move, which we did for what seemed like eternity.

At last the lioness stopped roaring and stood still, looking down at us fear-stricken humans too terrified to move. She seemed satisfied. Perhaps she didn't know we didn't speak lion. She turned as if her mission was accomplished and walked off among the trees. We had no idea what had just happened to us so we looked at each other, not knowing what to say.

My favorite lion memory is of three lionesses who came to visit at us at night. We'd see them about twenty feet away, standing among the trees, quietly watching what we were doing. Soon enough someone would notice them and one of the Ju/'hoan men would shake a burning stick at them, telling them politely but firmly to leave. They'd look at him, then at the rest of us, then at one another, and then they'd walk away.

They came to visit us quite a few times, and I think my family was of interest to them. Our hair and skins were strange colors and we wore weird cotton clothes. Obviously we weren't Ju/'hoansi, but what were we?

To ourselves we seemed careful and normal. To the Ju/'hoansi at least we seemed careful, and to the lions we seemed like all other humans, a species they did not eat. My brother, John Marshall, made a study of causes of death among the San, involving about a hundred people over about a hundred years. He found one person killed by a lion – a paraplegic girl who dragged herself along the ground with her hands. Maybe she didn't seem human to the lion, or maybe she was so disabled, so very easy to catch at any moment, that he made an exception to the don't-eat-people rule. And he wasn't the first to do this. Scholars who study the human-animal conflict have noticed that both lions and tigers are more likely to attack a person if that person is not standing up (see Blake in this volume).

Here we can also note, that scholars who study the human-animal conflict, noticed that lions and tigers are much more inclined to attack humans when humans do not maintain their usual upright bipedal posture (see Waltl in this volume).

As for the San, those we knew lived up to being Harmless People. To maintain good will among themselves, important decisions were made by the group, and everyone's voice was heard. Each person owned very little so most of their objects were shared, and together each group owned the huge stretch of land where they lived.

We don't like to see uninvited strangers on our land, and the Ju/'hoansi didn't either, but one day three San men who were not Ju/'hoansi came onto their land while following an antelope they'd shot with a poison arrow.

The Ju/'hoansi we knew learned about this – I think someone saw the strangers – and a group quickly gathered to decide what to do. They knew the intruders were hunting and couldn't control where their victim would go, and after their victim died from the arrow poison they'd go back to their encampment with the body. The group of Ju/'hoansi decided to do nothing and the trespassers did what was expected of them – they found their victim and went home. I'm sure this sounds like nothing much and perhaps it isn't much, but it was the one and only time in more than two years that the Ju/'hoasi we were with had to deal with possible wrongdoing. This kind of behavior explains why San culture persisted for twenty thousand years.

But the world keeps changing – it has certainly changed for the San. The "unexplored" area has been thoroughly visited and now is no different from the rest of Namibia. Some of the San seem to be desperately poor but others have permanent living quarters, cloth clothing, computers, telephones, and automobiles. In some places they're forbidden from hunting, which I believe is an effort to protect certain animals from going extinct, and this seems ironic because while the San were living as they had lived for twenty thousand years, the species that people hunted were not over-killed and did not go extinct.

The good part is that some of the San have email. I'm in touch with a splendid person, the grandson of a man we knew well. His name is Leon Tsamk/ao and I think of how we met his people…we had to bring a truck with us so we crossed the Atlantic by boat, then we found an interpreter and with him spent weeks searching the "unexplored" area until one day in the woods we saw the young man who became Leon's grandfather. He walked up to meet us, our study began.

Leon Tsamkgao knows the lions. "Lions only become dangerous," he says, "when they have babies or when a lion gets wounded. They don't eat humans. The Ju/'hoansi do not have any bad history about lions and other predators."

In contrast, he points out, "the lions at Etosha are different from the wild ones that the Ju/'hoansi know. The Etosha lions are very aggressive because they are living among humans, which is what makes them like that. People come [to Etosha] because they want to see lions, and in the culture of the Ju/'hoansi there's no way a person just decides to go see lions. The Ju/'hoansi do not have any bad history about lions and other predators."

That's Leon's view. My view is that the Ju/'hoansi do not have any bad history about anything. They survived by maintaining a peaceful relationship with lions. The San became the ancestors of the rest of us, but not all of them felt the need to change. Those people kept their marvelous culture, or the important parts of it, anyway, and evidently, like some of the lions, they have it to this day.

And today, in 2023, almost 60 years after our first meeting, the study continues, and we are coming to the realization that we might learn important details and lessons about our evolutionary history by paying closer attention to the vast traditional knowledge and wisdom of the San people, accumulated during their tens thousands of the years of peaceful co-existence with African lions.

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Adriaan Kortlandt, The memory of whom the conference was dedicated

New building of Grigol Robakidze University in Tbilisi, where we initially planned to have the International Conference "Defense Strategies in Early Human Evolution"

Mamuka Tavkhelidze, Rector of the Grigol Robakidze University, who opened the conference.

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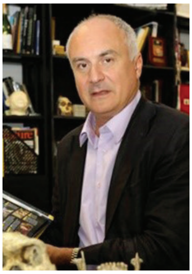

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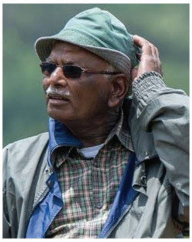

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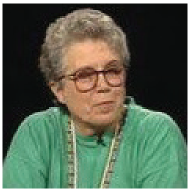

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How did our distant ancestors defend themselves from lethal African predators after they moved from the trees to the ground and started sleeping in the open?

Strangely, this important question of human evolutionary history has been largely ignored by scholars. For Charles Darwin, humans did not need to defend themselves from predators, as they evolved via sexual selection in a predator-free environment; For Raymond Dart human ancestors were ruthless killers and cannibals, the apex predators of their entire environment, so the need for a defense from predators seemed irrelevant; Charles Brain proposed that, on the contrary, our ancestors were weak prey species, vulnerable to a large number of predators in Africa. Contemporary scholars mostly argue over two paradigms: (1) our ancestors were big game hunter-gatherers (partly modified Dart's "Killer Ape" hypothesis), and (2) our ancestors were fearless aggressive scavengers (this idea was developed within the "new archaeology" paradigm of the 1980s, but the questions like how our ancestors managed to take kill away from powerful African predators and sleep on the ground at night, still remain open).

On June 23-26, 2023, an international multi-disciplinary conference "Defense Strategies in Early Human Evolution" took place at the Jim Corbett International Research Centre at the Grigol Robakidze University, Tbilisi, Georgia. The conference brought together behavioural ecologists, primatologists, biologists, cognitivists, philosophers, evolutionary musicologists, and conservationists, who were discussing various issues of this vast topic. The book that you hold in your hands is the result of this meeting.

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