The society of our “out of Africa” ancestors (I)
The migrant warriors that colonized the world

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The “out of Africa” hypothesis proposes that a small group of Homo sapiens left Africa 80,000 years ago, spreading the mitochondrial haplotype L3 throughout the Earth.1,2 Little effort has been made to try to reconstruct the society and culture of the tribe that left Africa to populate the rest of the world.3 Here, I find that hunter-gatherers that belong to mitochondrial haplotypes L0, L1 and L2 do not have a culture of ritualized fights. In contrast to this, almost all L3 derived hunter-gatherers have a more belligerent culture that includes ritualized fights such as wrestling, stick fights or headhunting expeditions. This appears to be independent of their environment because ritualized fights occur in all climates, from the tropics to the arctic. There is also a correlation between mitochondrial haplotypes and warfare propensity or the use of murder and suicide to resolve conflicts. The data implicate that the original human population outside Africa is descended from only two closely related sub-branches that practiced ritual fighting and had a higher propensity towards warfare and the use of murder for conflict resolution. This warfare culture may have given the out of Africa migrants a competitive advantage to colonize the world. But it could also have crucially influenced the subsequent history of The Earth. In the future, it would be interesting to see how we could further reconstruct the society and culture of the “Out of Africa Tribe.”

Introduction

More than ninety percent of the surface of inhabitable land on Earth is occupied by the descendants of a small group of extremely successful humans. How was this inequality achieved? The recent “out of Africa” hypothesis explains this by proposing that a small group of Homo sapiens left Africa 80,000 years ago, and that the descendants of that group colonized the rest of the Earth outside Africa.1-10

One consequence of this proposal is that the culture of the tribe(s) that left Africa to populate the rest of the world is likely to have dramatically shaped the subsequent cultures of history, because all non-Africans would have inherited those traditions as a primordial cultural background. What did that ancestral tribe that migrated out of Africa look like? What of their culture and religion? Were they peaceful or belligerent? Those are questions of utmost importance because the cultural biases of such tiny clans are likely to have influenced all non-African cultures. Despite the interest of those questions, little effort has been made to try to reconstruct the outlook of such tribe(s) that left Africa 80,000 years ago.

In order to explore what culture may have had the “Out of Africa Tribe(s)”, I have used genetic data like the mitochondrial haplogroups of different tribes of hunter-gatherers, and have correlated them with cultural behaviors. Hunter-gatherers were chosen because they are, in general, more isolated than other human groups. One possible caveat of this approach is that present day behavior may not represent the ancestral state of hunter gatherers several thousand years ago, and, therefore, it may not be possible to construct a “cultural phylogeny.”6 Counteracting this criticism, several recent studies have indicated that there is a general correlation between genetic relatedness and linguistic or cultural similarity, suggesting that cultural inheritance is almost as stable as genetic inheritance. For example, a recent genome-wide study of a set of diverse Africans revealed the presence of 14 genetically distinct ancestral population clusters in Africa.7 Interestingly, each cluster consisted of populations that shared genetic similarity, as well as cultural and/or linguistic properties (for example Khoesan-speaking hunter-gatherers, Bantu-speakers, Cushitic-speakers, etc.). This supports the view that although some exceptions occur,8 genetics and culture correlate to a great extent.9 And, moreover, those ancestral populations were culturally and geographically structured before modern humans migrated out of Africa.6

Using the genetic mitochondrial haplotypes as an evolutionary framework, I have studied the pattern of ritualized fights, archeological and ethnographical evidence for warfare, or the use of murder and suicide as a mean for conflict resolution among several tribes of modern hunter-gatherers throughout the world. This allowed the reconstruction of cultural evolution superimposed on current genetic and migratory data.1-10

The evidence presented suggests that a tribe of belligerent people, possibly warriors, populated the earth out of Africa.
African hunter-gatherers. Among the African foragers, the Ju/'hoansi or 'Kung of the Kalahari desert in South Africa, Botswana, and Namibia have been shown to carry the most basal mitochondrial DNA haplogroup, \(^{20}\) L0 (Fig. 1 and Table 1), and are therefore the best choice as being considered an ancestral state with regards to human behavior. 'Kung do not gather for ritual fights (Fig. 2) and prefer dance and storytelling as pastimes. Among the 'Kung, murder and suicide are also uncommon (Fig. 3) and conflicts are normally eased with humor or avoiding contact. However, some physical fights do occur. Finally, although the 'Kung are generally a peaceful society, they can resort to war in order to defend their territory (Fig. 4) and there is evidence that this has also been happening in the past because there are rock paintings depicting 'Kung bushmen fighting. In general, 'Kung men prided themselves on being good hunters.\(^{16-19}\)

Before the migration out of Africa, three main lines of Homo sapiens diverged from the 'Kung line: \(^{20}\) bearers of mitochondrial haplogroup L1 (mtDNA)/A (Y-DNA), bearers of haplogroup L2 (mtDNA)/B (Y-DNA), and carriers of haplogroup L3 (mtDNA).

African hunter-gatherers that correspond to the mitochondrial haplogroup L1 are several groups of pygmies like the Aka and Efè from Congo, the Baka from Cameroon and the Hadza from Tanzania\(^{6,20,21}\) (Fig. 2). Consistent with their genetic relatedness, they also share many cultural similarities. For example, their ritual gatherings revolve around storytelling, music, hunting and dancing, and there are no ritual fights involved. Also, little murder and violence is involved in their relationship with their neighbors (Fig. 3) and in all cases they rather have peaceful commercial relationships with neighboring pastoralist tribes such as the Bantu. Moreover, unlike the 'Kung there is no archeological nor ethnographical evidence of war (Fig. 4). It seems that in case of conflict all L1 mtDNA bearers choose to move apart rather than to fight.\(^{16,20,21}\)

African hunter-gatherers that correspond to the mitochondrial haplogroup L2 are the Mbuti from Congo\(^{6,20,21}\) (Fig. 1). They also form a pacific society with no archeological or ethnographical evidence of war and where conflicts are ridiculed and jokes used to alleviate tensions. Again, their ritual gatherings involve music, storytelling and dancing, without ritual fights (Figs. 2–4). And their wives value their men as long as they consider them good hunters.

Finally, descendants of the mitochondrial haplogroup L3 constitute the vast majority of hunter gatherers all over the world\(^{22}\) (Fig. 1 and Table 1). The reason for this is that anatomically modern humans that evolved in Africa, migrated to Eurasia and Oceania within the last 80,000 years\(^{22-25}\) and then migrated to the Americas within the last 30,000 years.\(^{26}\) The geographic expansion of a small number of anatomically modern humans out of Africa resulted in a population bottleneck. For example, based on mtDNA studies it has been proposed that all non-Africans belong to one tiny African branch, bearers of haplotypes M and N, which are closely related in an L3 sub-branch,\(^{6,20,22}\) meaning that the entire human population outside of Africa is descended from only two closely related sub-branches of L3.\(^{6,22}\)

Furthermore, the data implicate that the original human population outside Africa is descended from only two closely related sub-branches of L3 that practiced ritual fighting and probably had a higher propensity towards warfare and the use of murder for conflict resolution. This may have crucially influenced the subsequent history of the world.

Results

Current paleontological data suggest that modern humans appeared in sub-Saharan Africa 200,000 years ago.\(^{10,11}\) Moreover, mtDNA, X and Y-chromosome studies and Genome-wide data have indicated higher levels of genetic diversity in Africans compared to non-Africans, as expected if the first humans appeared in Africa.\(^{5,9,12-15}\) Therefore, African hunter-gatherers seem a reasonable starting point to study the evolution of human culture. I will focus here on the archeological and ethnographical evidence for warfare, the use of murder and suicide as a mean for conflict resolution or the practice of ritualized fights. However, a similar approach could be taken for other aspects of culture such as social structure, religion, art, music or technology.
Table 1. Tribes of hunter-gatherers analyzed in this study

| Hunter-gatherer tribe | Prevalent haplotype (mtDNA/Y-DNA) | Geographical location | Fighting rituals | Murder or suicide during conflict resolution | Ethnographical or archeological evidence of war |
|-----------------------|-----------------------------------|-----------------------|------------------|---------------------------------------------|---------------------------------------------|
| Aché                  | B (mtDNA) Q(Y-DNA)                | Paraguay              | Yes. Club fight once a year. Some participants die. | Yes. Raided their neighbors for food.       | Yes.                                        |
| Aeta                  | M (mtDNA) M(Y-DNA)                | Philippines           | Yes. They practice a form of ritual fight called Buno or Dumog. | No.                                         | No.                                         |
| Ainu                  | Y (mtDNA) D2 (Y-DNA)              | Japan                 | Conflicting. Sumo may be partially derived from Ainu folk wrestling. | Yes. Murder was not common and ritual suicide may have existed. | Yes. Inter-ainu wars and wars with Japanese. |
| Aka                   | L1 (mtDNA) B(Y-DNA)               | Congo                 | No. Ritual hunting is practiced instead. | No. They have established stable trading relationships with neighboring tribes (The Ngandu). | No.                                         |
| Aleut                 | A/D (mtDNA) Q(Y-DNA)              | Alaska, Kamchatka, Aleut Islands. | Yes. Aleut wrestling and stick fights. | Yes. Murder was not common and ritual suicide existed. | Yes. Aleut exterminated the Nicolerło Indians. |
| Andamanese (Jarawa, Onge, Sentinelese) | M (mtDNA) D(Y-DNA) | Andaman Sea Islands | Yes. Ritual wrestling is a popular pastime. | Yes. Frequent conflict between neighboring groups over access to resources and hostility against foreign visitors. | Yes. Endemic fighting among the Andaman Sea tribes. |
| Asmat                 | MQ (mtDNA) M(Y-DNA)               | New Guinea            | Yes. Shield and bisj ceremonies. Headhunting rituals. | Yes. Headhunters and cannibalism as a revenge act. Attacks on trespassers of their territory. | Yes. Endemic warfare and veneration of accomplished warriors |
| Australian Aborigines | N (mtDNA) M(Y-DNA)                | Australia             | Yes. Ritual fights were practiced by most tribes called turdererin, partambelin, goombooboodoo, ami or donaman... | Unclear.                                    | Yes. Endemic warfare and cave paintings of ancient war. |
| Baka                  | L1 (mtDNA) B (Y-DNA)              | Gabon, Cameroon       | No. Ritual gatherings revolve around storytelling, music and dancing. | No. They have established stable trading relationships with neighboring Bantu tribes. | No.                                         |
| Batek                 | MB (mtDNA) M(Y-DNA)               | Malaysia              | Yes. Their ritual dance ends in a wrestling match. | No. Totally opposed to any interpersonal violence. | No.                                         |
| Cheyenne              | A (mtDNA) Q(Y-DNA)                | Dakota                | Yes. Warriors training to fight was a major activity. | Yes. Murder during endemic war and ritual sacrifices promoted by the chiefs. | Yes. Endemic war with neighboring tribes. |
| Efé                   | L1 (mtDNA) B (Y-DNA)              | Congo                 | No. Singing, dancing and storytelling is practiced. | No. Engage in trading partner relationship with neighbors (Lese) | No.                                         |
| Haida                 | A (mtDNA) Q(Y-DNA)                | British Columbia     | Yes. Formal training for warriors. | Yes. Warfare with neighbors for revenge and slaves. | Yes. Endemic war.                            |
| Hadza                 | L1 (mtDNA) B(Y-DNA)               | Tanzania              | No. Groups move apart to alleviate conflicts. | No.                                         | No.                                         |
| Hiwi                  | C (mtDNA) Q(Y-DNA)                | Venezuela, Colombia   | Yes. As an integral part of the training of warriors. | Yes. Murder is common as retaliation.       | Yes.                                        |
| Inuit                 | A (mtDNA) Q(Y-DNA)                | Canada                | Yes. Inuit wrestling is a favorite activity. | Yes. There are well-documented cases of ambush and murder. | Yes. The Inuit and their Athabaskan neighbors engaged in endemic wars. |
| Ju/’hoansi !Kung      | L0 (mtDNA) A(Y-DNA)               | Namibia               | No. Conflicts are eased with humor or avoiding contact but some reports of physical fights being common. | No.                                         | Yes. Some wars to defend their territory. Rock paintings depicting bushmen fighting. |
The “out of Africa” migration. Two main migratory routes out of Africa have been hypothesized for anatomically modern humans. One model involves a northern route of migration via North Africa and the Nile valley into the Levant with subsequent dispersal into both Europe and Asia.27 Alternatively, a later southern coastal route has been proposed in which modern humans left Africa by crossing the Bab-el-Mandeb strait at the mouth of the Red Sea and then rapidly migrated along the South Asia coastline to Australia/Melanesia where evidence of human settlement dated to around 60,000 years ago can be found.28,29 Strong support for an East African origin of migration of modern humans has been provided by a recent genetic study that correlated levels of microsatellite diversity and the geographic position of sampled populations inferred a waypoint of dispersal of anatomically modern humans out of Africa centered on the Red Sea.9 Although this study was not able to rule out the possibility of multiple migrations out of Africa, prior analysis of autosomal haplotype variability suggests that migration events originating from multiple genetically distinct source populations in Africa are unlikely.30 Therefore strong support exists for a single successful migration out of Africa that occurred across the Red Sea and along the east coast of Arabia ca 80,000 years ago. The size of the ancestral population(s) that left Africa is estimated to be around 1,000 effective founding males and females based on autosomal microsatellite loci,31 or around 1,500 effective founding males and females based on combined mtDNA, Y-chromosome and X-chromosome re-sequencing data.32

Unfortunately, no M or N bearers live as foragers in East Africa (Fig. 1), so there is no hunter-gatherer population remnant of the tribe that originally crossed the Red Sea. Therefore, we will now try to follow the remnant hunter-gatherers of that migration outside Africa.

The colonization of Asia, Australia and Europe. Once in West Asia, the people who took the southern route spread generation by generation around the coast of Arabia and Persia until they reached India.22,33 From Arabia to India the proportion of haplogroup M increases eastwards.22,23,33 The indigenous people of the Andaman Islands also belong to the M lineage.24 The Andamanese are thought to be offshoots of some of the earliest inhabitants in Asia because of their long isolation from mainland Asia.24 They are evidence of the coastal route of early settlers that extends from India along the coasts of Thailand and Indonesia all the way to Papua New Guinea.22-24 Since M is found in high frequencies in highlanders from New Guinea as well, and both the Andamanese and New Guineans have dark skin and Afro-textured hair, it is believed that they are all part of the same wave of migrants who departed across the Red Sea ~80,000 years ago in the Great Coastal Migration.22-24 Here is where we find the first modern hunter gatherers of the L3 lineage21,22,24 (Fig. 1). The Andamanese (Jarawa, Onge, Sentinelese) of the Andaman Islands, the Aeta of the Philippines, the Batek from Malaysia, and finally several tribes of foragers from Papua/New Guinea such as the Asmat. Interestingly, they share a cultural aspect that differs from that of the non-L3 African foragers: they all practice ritual fighting (Fig. 2). The Aeta from Philippines practice a form of ritual fight called Buno or Dumog.21 The Batek of Malaysia practice a ritual dance that ends in a wrestling match.21 Also among the Andamanese ritual wrestling is a popular pastime.21 Finally, tribes of Papua/New Guinea also practice ritual fights and wars. For example, the Asmat celebrate shield and bisj ceremonies, collaboration of accomplished warriors and bloody headhunting rituals.5,21 Interestingly, although all those tribes share the practice of fighting or warrior rituals, they differ markedly in their belligerent behaviors (Fig. 3) and their tendencies towards warfare (Fig. 4). For example, Asmat are headhunters, practice murder and cannibalism as a revenge act, attack trespassers of their territory and live in an endemic state of warfare.5,21 Likewise, Andamanese are also an aggressive culture, suffering from frequent conflict between neighboring groups over access to resources that translates into endemic fighting among the Andaman Sea tribes and display armed hostility against foreign visitors.21 In contrast, the Aeta of the Philippines and the Batek of Malaysia are totally opposed to any interpersonal violence and have no evidence of warfare.1,2,21 This suggests that the original tribe that left Africa had a tradition of ritual fighting and were probably a clan of warriors, although it is unclear what their propensity towards war was.

Within around 5,000 years, some of these early human pioneers had managed to spread along the edge of the Indian Ocean and down through South East Asia, arriving in Australia around 60,000 years ago.22,24 Unlike New Guinean tribes where the M haplogroup is predominant, among Australian Aborigines the N mtDNA haplogroup is prevalent.24,33 Despite this genetic difference, ritual fights were also practiced by most tribes of hunter gatherers in Australia21 (Fig. 2). Those ritual fights were variedly

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Table 1. Tribes of hunter-gatherers analyzed in this study (continued)

| Tribe       | A/D(mtDNA) Q(Y-DNA) | Pacific coast of North America | Yes. Mock fights are performed at weddings. | Yes. It is possible to acquire privileges through murder. Scalps are taken and used in ceremonial dances. | Yes. Warriors are trained for war. War expeditions are common. |
|-------------|----------------------|--------------------------------|--------------------------------------------|-------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------|
| Kwakiutl    | A/D(mtDNA) Q(Y-DNA) | Pacific coast of North America | Yes. As an integral part of the training of warriors. War dances. | Yes. Murder of an enemy, as well as suicide in the battle, brought prestige. | Yes. Important to the extent that social positions were earned in warfare |
| Mbti        | L2 (mtDNA) B (Y-DNA) | Congo                         | No                                         | No. Conflict is ridiculed and jokes are used to alleviate tensions. | No                                                                                  |
| Shoshone    | D(mtDNA) Q(Y-DNA)    | Wyoming                       | Yes. As an integral part of the training of warriors. War dances. | Yes. Murder of an enemy, as well as suicide in the battle, brought prestige. | Yes. Important to the extent that social positions were earned in warfare |

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(continued)
called turdererin, partambelin, goombooboodoo, ami or donaman by different tribes. Additionally, among Australian aboriginals, endemic warfare was present (Fig. 4) and cave paintings of ancient war suggest that those wars had been present since thousands of years. For example, cave paintings in northern Australia, some dated to 10,000 years ago, show scenes painted by aboriginal peoples depicting of large battles, small skirmishes and people attacking one another with spears and boomerangs, documenting an ancient tradition of warfare by aboriginal hunter-gatherers.

The fact that foragers of both N and M mitochondrial haplogroups share the activity of ritual fighting, a propensity towards warfare, and the use of murder for conflict resolution suggests that these cultural traditions migrated out of Africa together with the tribe that presumably crossed the Red Sea 80,000 years ago.

While some settlers crossed into Australia, others may have continued eastwards along the coast of Sunda, eventually turning northeast to China and finally reaching Japan. This coastal migration leaves its trail in the mitochondrial haplogroups descended from haplogroup M, and in Y-chromosome haplogroup C. The next tribe of hunter-gatherers that we find along the coast of Canada is the Ainu of Japan (Fig. 1). The Ainu are also considered to be a remnant population from the initial peopling of Japan. Among them, murder was not uncommon as a mean to solve conflicts and ritual suicide also was common, possibly the precursor of modern hara-kiri. They were equally a tribe of warriors and there is evidence of inter-ainu wars and, later on, wars with the Japanese. Evidence is therefore inconclusive at this time.

Thereafter, it may have become necessary to venture inland possibly bringing modern humans into contact with archaic humans such as Homo erectus. Others made their way north through the Middle East and Pakistan to reach central Asia. Around 50,000 years ago they also began spreading into Europe via the Bosporus at the Istanbul Strait. The expansion is thought to have begun 45,000 years ago and may have taken up to 15,000 years for Europe to be fully colonized. Unfortunately no modern hunter-gatherers persist in Europe and central Asia (Fig. 1).

The colonization of America. By 30,000 years ago, humans had spread into northern Europe and Siberia and then walked across the Bering land bridge into Alaska. Several tribes of hunter-gatherers persist in the northern most part of America (Fig. 1), for example the Aleut living in Alaska, Kamchatka and the Aleut Islands, the Haida from British Columbia, the Kwakiutl on the Pacific coast of North America or the Inuit on the Atlantic coast of Canada. Interestingly, all those cultures practice ritual fighting (Fig. 2). The Aleut have wrestling and stick fights, the Kwakiutl perform mock fights at weddings and scalps are taken and used in ceremonial dances. Haida warriors are trained in ritual fighting and wrestling is a favorite activity among the Inuit. Moreover, except perhaps the Inuit, all tribes have a war-culture of endemic fights for revenge or booty and slaves, where war expeditions are common (Fig. 4) and it is possible to acquire privileges through murder (Fig. 3).

The peak of the last ice age, which was reached around 19,000 years ago, saw human populations pushed south by the extreme cold. Among the tribes remaining from such south-bound migration, one finds the hunter and gatherer tribe of the Shoshone Indians from the Great Plains, in what is currently Wyoming (Fig. 1). Shoshones also performed ritual fights as an integral part of the training of warriors and murder of an enemy, as well as suicide in the battle, which brought prestige to the extent that social positions were earned in warfare (Figs. 2–4). Other tribes of hunter-gatherers like the Cheyenne may have acquired their lifestyle after a period of farming and herding. Nevertheless, as foragers, they retained their war-culture. For example, warriors training to fight was a major activity among the Cheyenne (Fig. 2) and they were involved in endemic wars with neighboring tribes (Fig. 4). Murder was again a normal way to resolve conflicts with the neighbors and ritual sacrifices were promoted by the chiefs to ease internal conflicts (Fig. 3).
Finally, it was about 15,000 years ago that South America became the last major region on the planet to be colonized. In South America the best studied tribes of hunter-gatherers are probably the Aché from Paraguay and the Hiwi from Venezuela and Colombia (Figs. 1 and Table 1). Again, both groups of hunter-gatherers practice ritual fighting (Fig. 2). The Aché, for example, fight with clubs once a year in a ritual where some participants die, and the Hiwi perform ritualized fights as an integral part of the training of warriors. Both the Aché and the Hiwi have a propensity towards warfare (Fig. 4), raiding their neighbors for food and practicing murder as a common mean for retaliation (Fig. 3).

**Correlation between mtDNA haplogroups and behaviors.** Analyzing all the above data together, the correlation coefficient between the mtDNA haplogroup (0, 1, 2, 3) and the practice of ritual fights showed the highest value with 0.9184 (Fig. 2). The correlation coefficient oscillates between 0, when there is no correlation between two sets of data (i.e., they are random) and 1, when there is perfect correlation. Therefore the correlation between the mtDNA haplogroup of a particular tribe and the practice of ritual fights is very high. The correlation coefficient between the mtDNA haplogroup and the use of murder or suicide to solve conflicts was also high, 0.80 (Fig. 3). The correlation coefficient between the mtDNA haplogroup and the ethnographical or archeological evidence of war was the weakest with 0.58, mostly due to the rather weak evidence of warfare among !Kung (Fig. 4).

Next, I decided to consider mortality data (Table 2). A culture with a propensity to murder and warfare would be expected to have higher mortality rates due to violence than a pacific society. Unfortunately, life tables for hunter gatherers are published for only five societies, Aché, Aeta, Hadza, !Kung and Hiwi. Disease is an important cause of death among African hunter gatherers representing 85% of the deaths of L0 foragers like the !Kung and L1 bearers like the Hadza. It is also an important cause of death among L3 descend hunter-gatherers, but in less proportion, accounting for 75% of the deaths among the Aeta from the Philippines, but representing only 20% of deaths in the Aché, and 45% among the Hiwi. On the contrary, violence is the major cause of death among the Aché accounting for 55% of deaths and very important among the Hiwi, with 30% of deaths. In the Aeta, violence produces 7% of total deaths and the lower percentages of violent death occur among the !Kung and the Hadza, with 3% of the deaths. Therefore, despite the few data points (Table 2), they again support the more aggressive nature of L3 groups when compared with L1 or L0 hunter-gatherers.

**Discussion**

Here I provide evidence that the “Out of Africa group” was probably a tribe(s) with a higher propensity towards violent resolution of conflicts than previous hunter-gatherers, that had an incipient war-culture and, above all, practiced ritual fighting. If one allocates the different hunter-gatherers to their proposed genetic evolution, the war-prone tribes seem to cluster together (Figs. 2–4). Interestingly, non-L3 hunter-gatherers like the !Kung bushmen and the Hadza seem to consider themselves hunters and do not practice war willingly. This is in contrast with the hunter-gatherers outside Africa, most of which prided themselves to be warriors and base their social status in their actions at war. When did such a transition occur? The most parsimonious interpretation will be that some predisposition to war must have been present in the common ancestor of all modern L3 hunter-gatherers (Fig. 5). This predisposition is likely to have been cultural although some genetic predisposition (such as increased strength and body size) cannot be ruled out at this stage.

The clearest correlation of all is probably the one shown when comparing mitochondrial haplotypes with the practice of ritual fighting (or not). This shows a very high correlation coefficient of 0.9184. Fighting rituals can vary in degree of belligerence and violence, ranging from ritualistic wrestling, through mock battles and serious war training to death combats. Intriguingly, ritual fighting also takes place among some tribes of East African origin such as the stick fights of the Suri and the ritual wrestling of the Nuba. However, those tribes are pastoralists and not foragers as the ancestral migrants are believed to have been 80,000 years ago when they left Africa. Despite that those tribes are no longer...
tribe proposed here, another option could be that they would be escaping from enemies after losing a particular war. A third option is that it was a deliberate effort to conquer new territory, an organized journey of exploration and conquer prepared by an aggressive tribe to occupy unknown land.

If the hypothesis proposed is correct, is there any reason why a tribe of more aggressive hunter-gatherers that considered themselves warriors in addition to hunters was the one that made it out of Africa? One possibility is that it may have been impossible for a more peaceful tribe to populate the world, displacing well-established tribes. For example, they may have encountered \textit{Homo erectus} or previous migrations of modern humans in Asia. And once in western Asia and in Europe they will have encountered Neanderthals, who had been living there for nearly a quarter of a million years. Because it took 15,000 years for Europe to be overrun, it indeed appears that humans and Neanderthals may have been constantly competing for territory. The Neanderthals were larger and had a more robust or heavy built frame, which may suggest that they were physically stronger than modern \textit{Homo sapiens}. Having lived in Europe for 200,000 years they would have been better adapted to the cold weather. The anatomically modern humans known as the Cro-Magnons, however, with superior technology and language and possibly with a more aggressive war-culture,\cite{42,43} would eventually completely displace the Neanderthals.

In addition, they may have had to survive subsequent expansions of other tribes of modern humans, and their aggressive war-culture may have put an effective stop to secondary migrations out of Africa. The warrior culture would therefore serve as a permanent competitive advantage against neighboring tribes, making the out of Africa migrants a clan with an increased capacity to displace, exterminate or replace neighboring groups (i.e., a lineage of “supercompetitors”\cite{44}).

### Table 2. Mortality rates

| Forager tribe (mtDNA) | Disease caused deaths | Violent deaths | Other deaths/unknown |
|-----------------------|-----------------------|----------------|---------------------|
| Ache (L3*)            | 20%                   | 55%            | 25%                 |
| Aeta (L3*)            | 75%                   | 7%             | 18%                 |
| Hadza (L1)            | 85%                   | 3%             | 12%                 |
| Hiiwi (L3*)           | 45%                   | 30%            | 25%                 |
| Ikung (L0)            | 85%                   | 3%             | 12%                 |

Figure 4. Ethnographical/archeological evidence of war and mtDNA haplogroups. (A) Ethnographical/archeological evidence of warfare. (B) mtDNA haplogroups and the ethnographical or archeological evidence of war.

Figure 5. A war-prone tribe migrated out of Africa to populate the world. The hypothesis proposed that the tribe that migrated out of Africa ca. 80,000 years ago was a tribe that practiced ritual fighting and possibly was a clan(s) of warriors that used murder and war to solve conflicts.
In the future it would be interesting to see how we could further reconstruct the society and the culture of the tribe that left Africa to colonize the rest of the world. Cultural characteristics that also seem to correlate with the migrational event out of Africa include body painting associated with fighting, tattooing, religious association of the sun and the serpent and belief in a "tribe specific God" (unpublished observations). Interestingly, all the above characteristics may have formed a possible war-culture. For example, wars to defend a tribe-specific God are amongst the most common, the use of body painting or tattooing is linked to preparation for war among many cultures and may constitute part of a rite of passage linked to achieving a warrior status.

In summary, the evidence presented here suggests that a tribe of belligerent people, possibly a tribe(s) of warriors, populated the earth out of Africa (Fig. 5). I propose that this “warfare culture” has dramatically influenced the behavior of non-African communities, and possibly the fate of the world we live in. If the hypothesis of the migrant warriors is correct, one can only wonder what might have been the fate of the earth if a more peaceful tribe would have left Africa to populate the rest of the world.

References
1. Moreno E. A war-prone tribe migrated out of Africa to populate the world. Nature 2010. Available at https://hdl.handle.net/10101/npre.2010.4303.1.
2. Kelly RC. The Evolution of Lethal Intergroup Violence. Proc Natl Acad Sci USA 2005; 102:15924-8.
3. Guthrie RD. The nature of Paleolithic art. Chicago: University of Chicago Press, 2005.
4. Taçon P. Chippindale C. Australia’s Ancient Warriors. Camb Archaeol J 1994; 4:229-31.
5. Keeley LH. War Before Civilization: the Myth of the Peaceful Savage. Oxford University Press, 1996.
6. Campbell MC, Tushoff SA. African genetic diversity: implications for human demographic history, modern human origins and complex disease mapping. Annu. Rev. Genomics Hum. Genet 2008; 9:403-33.
7. Stringer C. Human evolution: Out of Ethiopia. Nature 2003; 423:652-3.
8. Ovchinnikov B, Weiss G, von Haselner A, Paskojaan S, Sertheeram-Ishida W, et al. Recent origin and cultural reversion of a hunter-gatherer group. PLoS Biol 2005; 3:71.
9. Tushoff SA, Reed FA, Friedlaender FR, Ebert C, Ranciato A, Froment A, et al. The genetic structure and history of Africans and African Americans. Science 2009; 32:1035-44.
10. McDougall IBF, Feagle JG. Stratigraphic placement and age of modern humans from Kibish, Ethiopia. Nature 2005; 435:753-6.
11. White T, Asho B, DeGuaza D, Gilbert H, Richards G, Suwa G, et al. Pleistocene Homo sapiens from Middle Awash, Ethiopia. Nature 2003; 423:742-7.
12. Keinan A, Mullikin JC, Patterson N, Reich D. Accelerated genetic drift on chromosome X during the human dispersal out of Africa. Nat Genet 2009; 41:66-70.
13. Conrad DF, Jakobsson M, Coop G, Wen X, Wall JD, Rosenberg NA, et al. A worldwide survey of haplotype variation and linkage disequilibrium in the human genome. Nat Genet 2006; 38:1251-60.
14. Jakobsson M, Scholz SW, Scheet P, Gibbs JR, VanLiere JM, Fung HC, et al. Genotype, haplotype and copy-number variation in worldwide human populations. Nature 2008; 451:998-1003.
15. Ramachandran S, Deshpande O, Roseman CC, Rosenberg NA, Feldman MW, Cavalli-Sforza LL. Support from the relationship of genetic and geographic distance in human populations for a serial founder effect originating in Africa. Proc Natl Acad Sci USA 2005; 102:15942-7.
16. Ehret C. The Civilizations of Africa: A History to 1800. Charlottesville: University of Virginia Press 2002.
17. Lee Richard B. The Dobe Ju/hoansi, 3rd Ed., Thomson Learning/Wadsworth 2003.
18. Shottak M. Njia The Life and Words of a !Kung Woman, Boston: Harvard University Press 2006.
19. Thomas EM. The Old Way, A Story of the First People. New York: Farrar Strauss Giroux 2006.
20. Vigilant L, Stoneking M, Harpending H, Hawkes K, Wilson AC. African populations and the evolution of human mitochondrial DNA. Science 1991; 253:1503-7.
21. Lee RB, Daly RH. The Cambridge Encyclopedia of Hunters and Gatherers. Cambridge University Press 1995.
22. Renfrew C. Archaeogenetics—towards a 'new synthesis'.Curr Biol 2010; 20:162-5.
23. Majumder PP. The human genetic history of South Asia. Curr Biol 2010; 20:184-7.
24. Kayser M. The human genetic history of Oceania: near and remote views of dispersal. Curr Biol 2010; 20:194-201.
25. Stoneking M, Defini F. The human genetic history of East Asia: weaving a complex tapestry. Curr Biol 2010; 20:188-93.
26. O’Rourke DH, Ruff JA. The human genetic history of the Americas: the final frontier. Curr Biol 2010; 20:202-7.
27. Mellars P. Why did modern human populations disperse from Africa ca. 60,000 years ago? A new model. Proc Natl Acad Sci USA 2006; 103:5931-6.
28. Stanyon R, Sutini M, Luinili D. Timing of the first human migration into eastern Asia. J Biol 2009; 8:18.
29. Quintana-Murci L, Semino O, Bandelt HJ, Passarino G, McElreavey K, Santarchi-Berenerecki AS. Genetic evidence of an early exit of Homo sapiens sapiens from Africa through eastern Africa. Nat Genet 1999; 23:437-41.
30. Tushoff SA, Dietzsch E, Speed W, Pakstas AJ, Kidd JR, Cheung K, et al. Global patterns of linkage disequilibrium at the CD4 locus and modern human origins. Science 1996; 271:1380-7.
31. Liu H, Prugnolle F, Manica A, Baloux F. A geographically explicit genetic model of worldwide human settlement history. Am J Hum Genet 2006; 79:230-7.
32. Garzaan D, Kinigan SB, Pillington MM, Wilder JA, Cox MP, Soodyall H, et al. Inferring human population sizes, divergence times and rates of gene flow from mitochondrial, X and Y chromosome ‘resequencing’ data. Genetics 2007; 177:2195-207.
33. Underhill PA, Kidvald T. Use of y chromosome and mitochondrial DNA population structure in tracing human migrations. Annu Rev Genet 2007; 41:539-64.
34. Habu J. Ancient Jomon of Japan. Cambridge: Cambridge University Press 2004.
35. Righerme GP. Out of Africa: modern human origins special feature: middle and later Pleistocene hominins in Africa and Southwest Asia. Proc Natl Acad Sci USA 2009; 106:16046-50.
36. Hill K, Hurtado AM, Walker RS. High adult mortality among Hwi hunter-gatherers: implications for human evolution. J Hum Evol 2007; 52:443-54.
37. Walker R, Curwen M, Hill K, Migliano H, Chagnon N, De Souza R, et al. Growth rates and life histories in twenty-two small-scale societies. Am J Hum Biol 2006; 18:295-311.
38. Albinki J. Ritual and political forms of violent practice among the Suri of Southern Ethiopia. Cahiers d’études africaines 1998; 38:271-95.
39. Carroll ST. Wrestling in Ancient Nubia. J Sport Hist 1988; 15:121-37.
40. Gonder MK, Mortensen HM, Reed FA, de Sousa A, Tushoff SA. Whole-mtDNA genome sequence analysis of ancient African lineages. Mol Biol Evol 2007; 24:757-68.
41. Verdu P, Austerlitz F, Estoup A, Vitalis R, Georges M, Thery S, et al. Origins and genetic diversity of pygmy hunter-gatherers from western Central Africa. Curr Biol 2009; 19:312-8.
42. Scholz CA, Johnson TC, Cohen AS, King JW, Pick JA, Overpeck JT, et al. East African megadroughts between 135 and 75 thousand years ago and bearing on early-modern human origins. Proc Natl Acad Sci USA 2007; 104:4616-21.
43. Walter RC, Buffler RT, Braugmann JH, Guillaume MM, Berhe SM, Negassi B, et al. Early human occupation of the Red Sea coast of Eritrea during the last interglacial. Nature 2000; 405:65-9.
44. Moreno E, Basler K, dMytnc transforms cells into supercompetitors. Cell 2004; 117:117-29.

Methods

To perform the statistical tests, values of -1, 0 or +1 were given to the different categories, depending on whether the answer was no (-1), unclear/conflicting (0) or yes (1). The correlation coefficient between the mtDNA haplogroup (0, 1, 2, 3) and the practice of ritual fights showed the strongest correlation with 0.9184. The correlation coefficient between the mtDNA haplogroup and the use of murder or suicide to solve conflicts was also quite high, 0.80. The correlation coefficient between the mtDNA haplogroup and the ethnographical or archeological evidence of war was the weakest with 0.58, mostly due to the evidence of warfare among !Kung.

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