However, neither Mallick *et al.* nor Malaspinas *et al.* exclude the possibility of multiple out-of-Africa dispersals. Indeed, their models are consistent with earlier dispersals, as long as these early voyagers made little or no contribution to the gene pool of contemporary non-African populations (which is essentially what Pagani *et al.* find). Studies of ancient DNA clearly show that large-scale population turnovers have happened throughout human history: populations that once lived in Eurasia, for example, vanished without a trace, except for their bones[11,12]. Thus, although some differences between the proposed models are yet to be reconciled, they are not as disparate as they might seem to be.

The three studies also provide resources to better define models of genetic mixing between modern humans and their archaic hominin relatives, such as Neanderthals and Denisovans. Malaspinas and colleagues propose that the genomes of present-day Aboriginal Australians might harbour traces of an ancient liaison with an unknown hominin group. Although evidence for gene flow from an unknown hominin group is tentative, it highlights the potentially surprising things that can be learnt from a comprehensive sampling of human genomic variation.

These studies fill in some missing pieces in the puzzle of human history, but many fascinating questions remain. The continued sampling of human genomic diversity and the development of increasingly sophisticated statistical tools promise to reveal more secrets about our past. Nonetheless, it is crucial to recognize the limits of genetics. As previously pioneered[13], the integration of data across traditionally distinct disciplines, such as linguistics, archaeology, anthropology and genetics, will be necessary to fully retrace the steps taken by early humans as they explored and colonized the world. ■

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This article was published online on 21 September 2016.

ANIMAL BEHAVIOUR

Lethal violence deep in the human lineage

Researchers estimate that the incidence of human lethal violence at the time of the origin of our species was about six times higher than for the average mammal, but about as violent as expected, given our great-ape ancestry. SEE LETTER P.233

MARK PAGEL

Are humans naturally violent, as the seventeenth-century philosopher Thomas Hobbes thought[1], with the prevailing condition of humans being one of "continuall feare, and danger of violent death", or as Jean-Jacques Rousseau imagined[2] a century later, neither good nor bad but moulded by their environments? Social scientists have long confronted this question by estimating rates of human violence after controlling for factors such as age, sex, race and income in large cohorts of individuals drawn from a variety of circumstances. On page 233, Gómez *et al.*[3] adopt a different approach: they use comparative methods from evolutionary biology[4] to reconstruct probable ancestral rates of lethal violence at the time of the origin of our species roughly 160,000 to 200,000 years ago.

One of Charles Darwin's great insights was that all living things evolve by a process of descent with modification, such that species give rise to daughter species that inherit many of their ancestors' traits. Comparative biologists can use the family trees (phylogenies) that arise from this process to infer the history of biological evolution, to date past events, and to reconstruct probable ancestral features of species that lived hundreds of thousands to hundreds of millions of years ago.

Gómez and colleagues applied comparative statistical techniques to a phylogeny of mammals, which includes primates — the grouping of mammals that comprises monkeys, great apes and the lineage that leads to modern humans. The authors compiled information on more than 4 million deaths from 1,024 mammal species drawn from 137 mammalian families (80% of the total number of mammalian families), including mice, horses, bats, rabbits and monkeys. Information for humans came from 600 studies, and was derived from palaeolithic samples (defined by the authors as 50,000 to 12,000 years ago), New World and Old World Mesolithic (12,000 to 10,200 years ago) and Neolithic (10,200 to 5,000 years ago) sites, Bronze Age (5,300 to 3,200 years ago) and Iron Age (3,200 to 1,300 years ago) samples, and anthropological sources from the past few centuries.

The authors then calculated the proportion of deaths attributable to violence from a

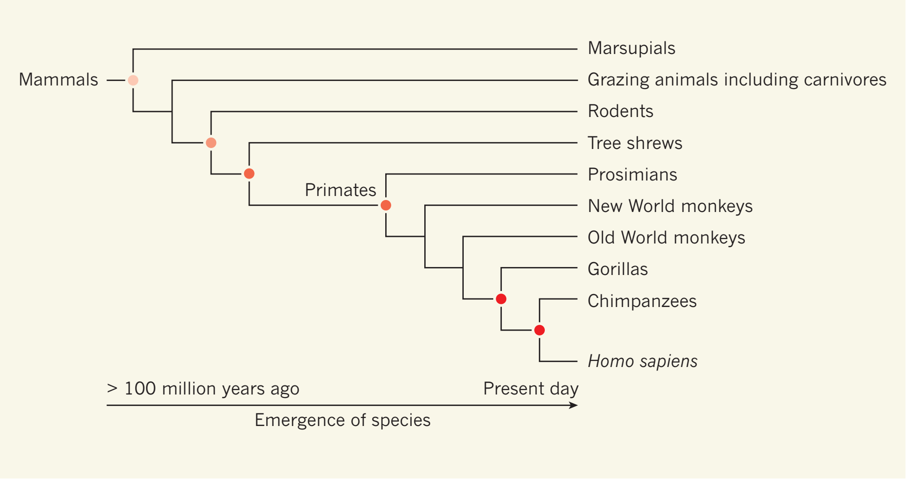

Figure 1 | Rates of lethal violence in a mammalian family tree. Gómez *et al.*[3] used data about causes of death in more than 1,000 mammalian species to determine for each species the proportion of deaths caused by members of the same species. These data were grouped into a phylogenetic family tree for mammals, of which a simplified representation is shown here. The rates of lethal violence against members of the same species are indicated by a colour scale that ranges from low rates in light red to higher rates in darker red.

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member of the same species out of all deaths counted for each species. Including only acts of within-species violence is a key point. Lions and tigers routinely kill members of other species, but they are less often lethally violent towards each other. Within-species violence therefore gets at what Hobbes and Rousseau disagreed about, and is interesting because members of the same species typically have all the same weapons, making violence between them risky.

Using the values from contemporary species, the authors reconstructed the rate of lethal violence (caused by members of the same species) at the phylogenetic origin of mammals at about 0.30%, which is approximately 1 in 300 deaths. Rates of lethal violence then rose steadily over time throughout the mammalian phylogeny (Fig. 1) as the reconstructed ancestors drew closer to primates: the rate is about 1.1% for the ancestor of primates, rodents and hares; 2.3% for the common ancestor of primates and tree shrews; then drops slightly to 1.8% for the ancestor of the great apes. The increases in lethal violence coincide with species having increasing amounts of group living and territoriality. Group living places individuals routinely in close contact, and territoriality means that groups might potentially compete over resources. Gómez and colleagues reconstructed the incidence of human lethal violence at the origin of our species at 2%, about six times higher than the reconstructed mammalian value.

Gómez and colleagues' study risks being misunderstood, so it is necessary to be clear about its interpretation. Humans emerged from an evolutionary lineage with a long history of higher-than-average levels of lethal violence towards members of the same species. Even so, followers of Rousseau might step in to say that our species' figure of 2% tells us nothing about our innate tendencies; it might merely reflect a calculated or environmentally induced response to the environments in which early humans lived.

Perhaps, but this objection falters when we appreciate that species that live in particular kinds of environments over long periods of time tend to adapt to those environments genetically, and this makes some kinds of outcomes more likely than others: a wolf raised as a sheep will probably one day turn on its fellow sheep. For this reason, the authors' finding of a steady increase in violence throughout the 100 million or so years of the mammalian tree is important — there was plenty of time for our ancestors to acquire and bequeath us genetic adaptations towards lethal violence. Our nearest living relatives, the chimpanzees, with whom we share around 98% identity of our gene sequences[5], form packs to hunt down and kill stray males from other chimpanzee tribes[6], and their hunting parties bear resemblances to human hunter–gatherer warfare[7]. Even the usually peaceful bonobo *Pan paniscus* can sometimes display violent behaviour (Fig. 2).

Figure 2 | Primate violence. Aggressive behaviour can occur even in the normally peaceful bonobo, *Pan paniscus*.

Some will object that it is difficult to derive reliable estimates of lethal violence. Anticipating this, the authors test for several biases, including variation in sample sizes and sampling effort, and uncertainty about the phylogeny of mammals itself, showing that none of these qualitatively alters their results. They also find that species we expect to be violent, such as the predatory carnivores, are violent, and species that we do not expect to be violent because they are mainly vegetarian, tend not to be. Finally, the authors show that rates of violence are heritable in the mammalian phylogeny, by demonstrating that closely related species tend to have similar levels of lethal violence.

Still, the Rousseau camp might have a corner to fight. The authors' estimates of rates of lethal violence in humans vary widely over time, in most cases too quickly to be attributable to genetic changes. Their palaeolithic samples have rates very close to the 2% predicted at the origin of our species, but then rates rise to as high as 15–30% (with high statistical uncertainty) in samples from between 3,000 and 500 years ago, before declining in contemporary populations (approximately 100 years ago to the present day). The rise tends to correlate with moving from an early pre-societal 'state of nature' to tribal groupings and then to organized political societies that have a warrior class.

Where does this leave us? Social scientists take note: the work by Gómez and colleagues opens up a new approach to uncovering the origins of human violence, giving good grounds for believing that we are intrinsically more violent than the average mammal, and their findings fit well with anthropological accounts that describe hunter–gatherer societies as being engaged in 'constant battles'[8,9]. But societies can also modify our innate tendencies. Rates of homicide in modern societies[10] that have police forces, legal systems, prisons and strong cultural attitudes that reject violence are, at less than 1 in 10,000 deaths (or 0.01%), about 200 times lower than the authors' predictions for our state of nature. Hobbes has landed a serious blow on Rousseau, but not quite knocked him out. ■

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This article was published online on 28 September 2016.