LETTER

The phylogenetic roots of human lethal violence

José María Gómez[1,2], Miguel Verdú[3], Adela González–Megías[4] & Marcos Méndez[5]

The psychological, sociological and evolutionary roots of conspecific violence in humans are still debated, despite attracting the attention of intellectuals for over two millennia[1–11]. Here we propose a conceptual approach towards understanding these roots based on the assumption that aggression in mammals, including humans, has a significant phylogenetic component. By compiling sources of mortality from a comprehensive sample of mammals, we assessed the percentage of deaths due to conspecifics and, using phylogenetic comparative tools, predicted this value for humans. The proportion of human deaths phylogenetically predicted to be caused by interpersonal violence stood at 2%. This value was similar to the one phylogenetically inferred for the evolutionary ancestor of primates and apes, indicating that a certain level of lethal violence arises owing to our position within the phylogeny of mammals. It was also similar to the percentage seen in prehistoric bands and tribes, indicating that we were as lethally violent then as common mammalian evolutionary history would predict. However, the level of lethal violence has changed through human history and can be associated with changes in the socio-political organization of human populations. Our study provides a detailed phylogenetic and historical context against which to compare levels of lethal violence observed throughout our history.

Debate on the nature of human violence has been ongoing since before the publication of *Leviathan* by Thomas Hobbes in 1651. Lethal violence is considered by some to be mostly a cultural trait[5,6,12]; however, aggression in mammals, including humans[13,14], also has a genetic component with high heritability. Consequently, it is widely acknowledged that evolution has also shaped human violence[2–4]. From this perspective, violence can be seen as an adaptive strategy, favouring the perpetrator's reproductive success in terms of mates, status or resources[15,16]. Yet this does not mean that violence is invariant or even adaptive in all situations[15]. In fact, given that the conditions under which violence benefits evolutionary fitness depend on the ecological and cultural context, levels of violence tend to vary among human populations[12,13,15,16]. Disentangling the relative importance of cultural and non-cultural components of human violence is challenging[3,5] owing to the complex interactions between ecological, social, behavioural and genetic factors.

Conspecific violence is not exclusive to humans. Many primates exhibit high levels of intergroup aggression and infanticide[4,10]. Social carnivores sometimes kill members of other groups and commit infanticide when supplanting older members of the same group[17,18]. Even seemingly peaceful mammals such as hamsters and horses sometimes kill individuals of their own species[19,20]. The prevalence of aggression throughout Mammalia raises the question of the extent to which levels of lethal violence observed in humans are as expected, given our position in the phylogenetic tree of mammals. In this study, we quantified the level of lethal violence in 1,024 mammalian species from 137 families (Supplementary Information section 9a) and in over

600 human populations, ranging from the Palaeolithic era to the present (Supplementary Information section 9c). The level of lethal violence was defined as the probability of dying from intraspecific violence compared to all other causes. More specifically, we calculated the level of lethal violence as the percentage, with respect to all documented sources of mortality, of total deaths due to conspecifics (these were infanticide, cannibalism, inter-group aggression and any other type of intraspecific killings in non-human mammals; war, homicide, infanticide, execution, and any other kind of intentional conspecific killing in humans).

Lethal violence is reported for almost 40% of the studied mammal species (Supplementary Information section 9a). This is probably an underestimation, because information is not available for many species. Overall, including species with and without lethal violence, we found that the percentage of deaths due to conspecifics was $0.30 \pm 0.19\%$ of all deaths (phylogenetically corrected mean $\pm$ s.e.m). This level was not affected by the number of individuals sampled per species (Supplementary Information section 1). These findings suggest that lethal violence, although infrequent, is widespread among mammals[19–21].

We determined whether related species tended to have similar levels of lethal violence by calculating the phylogenetic signal. We used the most recently updated mammalian phylogenies, including 5,020 extant mammals[22] and 5,747 extant and recently extinct mammals[23]. We found a significant phylogenetic signal for lethal violence, even after combining disparate causes of intraspecific killings ($\lambda > 0.60$, $P < 0.0001$; Supplementary Information section 2). While lethal violence was uncommon in certain clades such as bats, whales and lagomorphs, it was frequent in others, such as primates (Fig. 1). The phylogenetic signal was also significantly lower than one ($P < 0.0001$), indicating that lethal violence exhibits certain evolutionary flexibility (Fig. 1). For example, the level of lethal violence strongly differs between chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*)[10,17,20]. This outcome suggests that additional factors may subsequently modify the level of lethal violence in related species. Territoriality and social behaviour mediate conspecific aggression in mammals[20,24]. We scored these two traits for every mammal in our study and statistically related them to the level of lethal violence using phylogenetic generalized linear models. Using this method, we found that the level of lethal violence was higher in social and territorial species than in solitary and non-territorial species (Fig. 2; Extended Data Table 1).

The occurrence of a phylogenetic signal for lethal violence in mammals enables the phylogenetic inference of lethal violence in humans. We used ancestral-state estimation methods that infer the value of a trait in any extant species according to its position in the phylogenetic tree[25]. The level of human lethal violence was estimated both with and without considering the territoriality and sociability of mammals. Because phylogenetic inferences are much more accurate and reliable when including information from close relatives[26]

[1]Estación Experimental de Zonas Áridas (EEZA-CSIC), E-04120 Almería, Spain. [2]Dpto de Ecología, Universidad de Granada, E-18071 Granada, Spain. [3]Centro de Investigaciones sobre Desertificación (CSIC-UV-GV), E-46113 Valencia, Spain. [4]Dpto de Zoología, Universidad de Granada, E-18071 Granada, Spain. [5]Área de Biodiversidad y Conservación, Universidad Rey Juan Carlos, E-28933 Madrid, Spain.
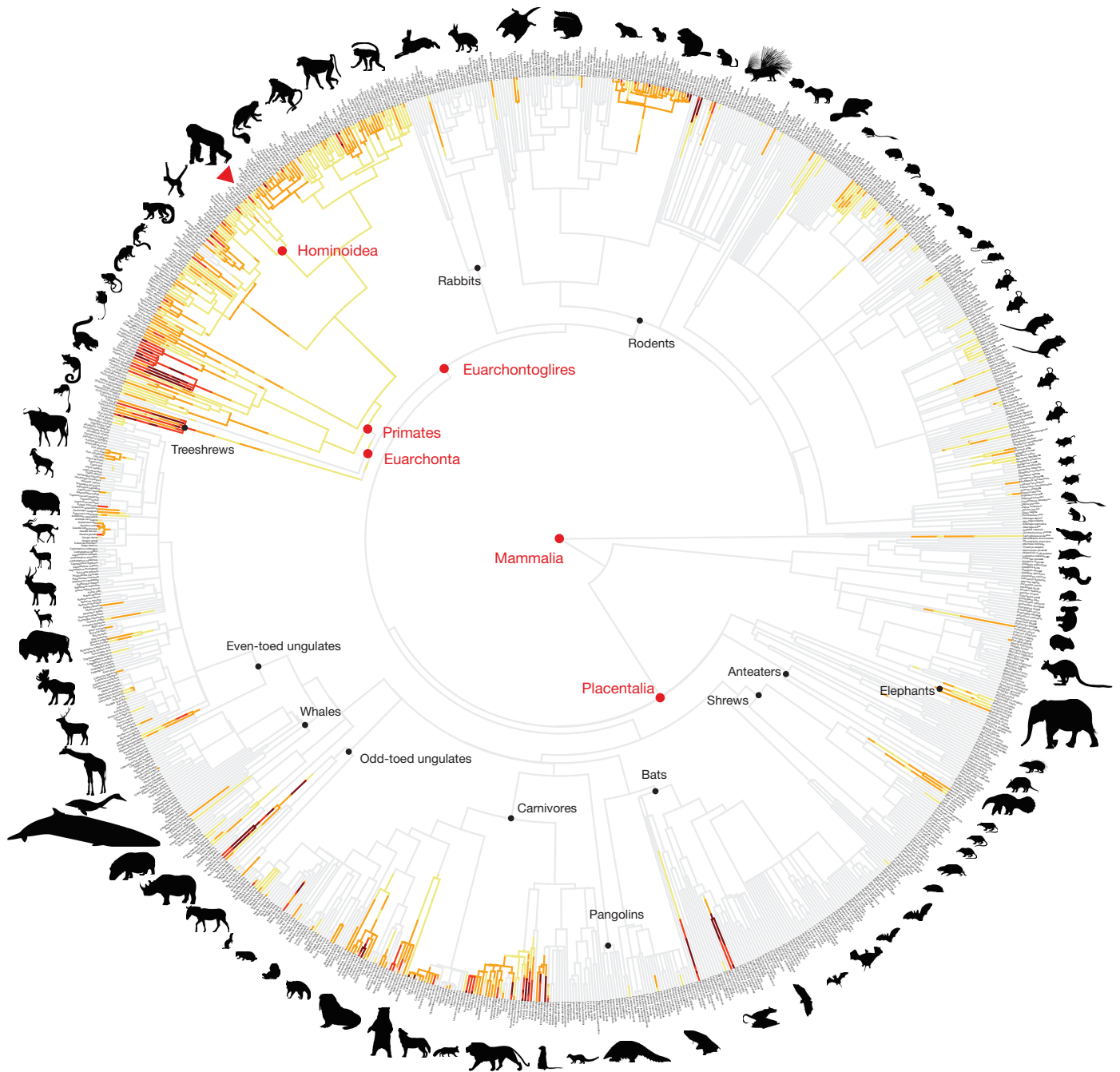
Figure 1 | Evolution of lethal aggression in non-human mammals. Tree showing the phylogenetic estimation of the level of lethal aggression in mammals ($n = 1,024$ species) using stochastic mapping. Lethal aggression increases with the intensity of the colour, from yellow to dark red. Light grey indicates the absence of lethal aggression. Mammalian ancestral nodes compared with human lethal violence are shown in red, whereas main placental lineages are marked with black nodes. The red triangle indicates the phylogenetic position of humans. The silhouettes of representative mammals (downloaded from http://www.phylopic.org) illustrate the main mammalian clades. They are licenced for use in the Public Domain without copyright, except for the silhouettes of Murinae (D. Liao), *Jaculus* (M. Karaka), *Philander* (S. Werning), *Rattus* (R. Groom), *Molossus* (Zimices), *Balaenoptera* (C. Hoh), *Rousettus* (O. Peles), *Connochaetes*, *Redunca*, and *Kobus* (J. A. Venter, H. H. T. Prins, D. A. Balfour and R. Slotow), that are licenced under a Creative Commons 3.0 license (http://creativecommons.org/licenses/by/3.0).

and fossils[23], information on *Homo neanderthalensis* was included when estimating the level of human lethal violence (Supplementary Information section 9b). In addition, because the level of violence varies among populations of the same species[10,20,21], all models include intraspecific variation in the level of mammalian lethal violence. The phylogenetically inferred level of lethal violence, averaging

across all models, was $2.0 \pm 0.02\%$ of all deaths (Fig. 3a). These estimates seem to be robust to many potential biases, such as phylogenetic uncertainty, phylogenetic depth, sampling effort, and phylogeny size (Supplementary Information sections 3–6). Territoriality and sociability affect the phylogenetic inference of the level of lethal violence, as it was $1.9 \pm 0.01\%$ in the models without these two variables but $2.1 \pm 0.02\%$
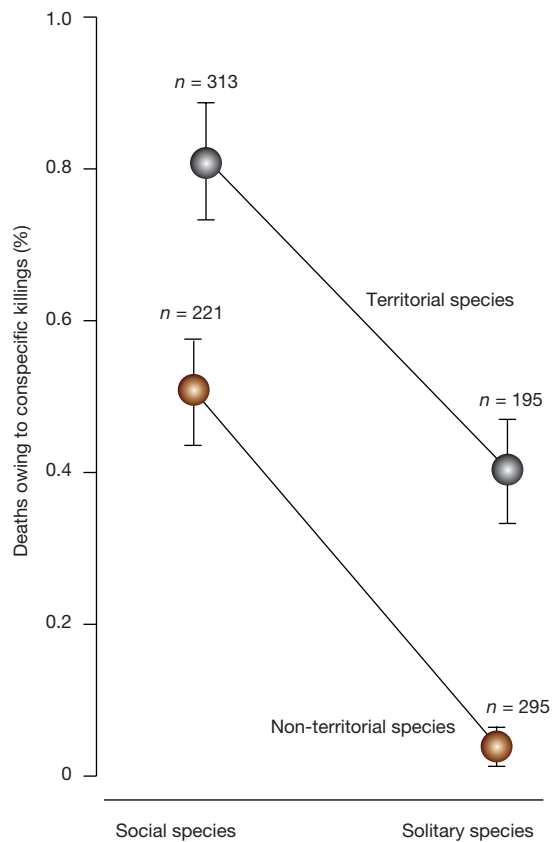
Figure 2 | Social behaviour and territoriality influence lethal aggression in mammals. The figure shows the phylogenetically corrected level of lethal aggression per group (mean ± s.e.m) and the number of mammalian species included in each group. We used a phylogenetic generalized linear model (PGLS) to test the effect of territoriality (yes or no) and social behaviour (social or solitary) on lethal aggression. The level of lethal aggression was more intense in social and territorial species (PGLS, $P < 0.05$ in all cases and mammal phylogenies; Extended Data Table 1), with no interaction between these two terms (Extended Data Table 1).

in the models including them (Fig. 3a). This is a consequence of *H. sapiens* being both social and territorial, two characteristics associated with a stronger tendency towards lethal violence in mammals (Fig. 2).

We subsequently explored how the level of lethal violence has changed during our evolutionary history by comparing it with the phylogenetically inferred level of lethal violence in relevant ancestral nodes that describe the course of human evolution (Fig. 1). The level of lethal violence was low in the most basal nodes, increasing to $2.3 \pm 0.1\%$ of all deaths in the two nodes closely related with the origin of primates and slightly decreasing to $1.8 \pm 0.1\%$ of all deaths in the ancestral ape (Fig. 3b). These results suggest that lethal violence is deeply rooted in the primate lineage.

We then compared whether the phylogenetically inferred level of lethal violence differed from the level empirically observed in human populations. The samples were categorized according to their age, using the standard periods from the New and Old World chronologies[27]. These data must be interpreted cautiously, because there was extensive intra-period variation in lethal violence. Nevertheless, a clear temporal pattern emerged (Fig. 3c). The level of lethal violence during human prehistory did not differ from the phylogenetic predictions (Fig. 3c). This result contrasts with some previous observations[9,11], probably

because we have included more populations in our study and weighted all the analyses by the number of individuals per sample. The level of lethal violence during most historic periods was higher than the phylogenetic predictions for both humans (Fig. 3c and Supplementary Information section 7) and the ancestral Hominoidea (Fig. 3b). However, on entering the Modern and Contemporary ages (defined in Methods), the level of lethal violence decreased markedly, as previously reported[11] (Fig. 3c). Several potential biases may affect these results. The level of lethal violence inferred from skeletal remains could be underestimated because many deadly injuries do not damage the bones[8]. Nevertheless, no underestimation was detected for the periods in which both skeletal remains and statistical yearbooks are available (Supplementary Information section 7). Similarly, the presence of battlefields may artificially overestimate the level of lethal violence. However, the periods with highest level of lethal violence were not those with more organized intergroup conflicts (Supplementary Information section 8). Thus, the temporal pattern in the level of lethal violence seems to hold even after considering these potential biases. Concomitant changes in the cultural and ecological human environment may have caused this pattern. Notably, population density, a common ecological driver of lethal aggression in mammals[18,21], was lower in periods with high levels of lethal violence than in the less violent Modern and Contemporary ages. High population density is therefore probably a consequence of successful pacification, rather than a cause of strife[7].

Socio-political organization is a factor widely invoked to explain changes in violence[5,7,11]. To assess this effect, we classified human populations into four types[28]: bands, tribes, chiefdoms and states. Levels of lethal violence in prehistoric bands and tribes did not differ from the phylogenetic inferences (Fig. 3d). However, lethal violence is common in present-day bands and tribes (Fig. 3d), possibly because there are more detailed data on mortality from living people than from archaeological records. Nevertheless, some authors suggest that the level of lethal violence has increased in hunter–gatherers because they now live in denser populations in which intergroup conflicts are more likely[3], or because they have contacted colonial societies where warfare or interpersonal violence is frequent[29]. The level of lethal violence in chiefdoms was also higher than the phylogenetic inferences (Fig. 3d). Severe violence has been frequently reported in chiefdoms[30], mostly caused by territorial disputes, population and resource pressures, and competition for political status[30]. Finally, the level of lethal violence in state societies was lower than the phylogenetic inferences (Fig. 3d). It is widely acknowledged that monopolization of the legitimate use of violence by the state significantly decreases violence in state societies[11,30].

In this study, we have explored the origin and evolution of human lethal violence by integrating a phylogenetic approach with an empirical analysis of lethal violence in human populations. The phylogenetic analysis suggests that a certain level of lethal violence in humans arises from the occupation of a position within a particularly violent mammalian clade, in which violence seems to have been ancestrally present. This means that humans have phylogenetically inherited their propensity for violence. We believe that this phylogenetic effect entails more than a mere genetic inclination to violence. In fact, social behaviour and territoriality, two behavioural traits shared with relatives of *H. sapiens*, seem to have also contributed to the level of lethal violence phylogenetically inherited in humans. Our analysis of human lethal violence shows that lethal violence in prehistoric humans matches the level inferred by our phylogenetic analyses, suggesting that we were, at the dawn of humankind, as violent as expected considering the common mammalian evolutionary history. This prehistoric level of lethal violence has not remained invariant but has changed as our history has progressed, mostly associated with changes in the socio-political organization of human populations. This suggests that culture can modulate the phylogenetically inherited lethal violence in humans.
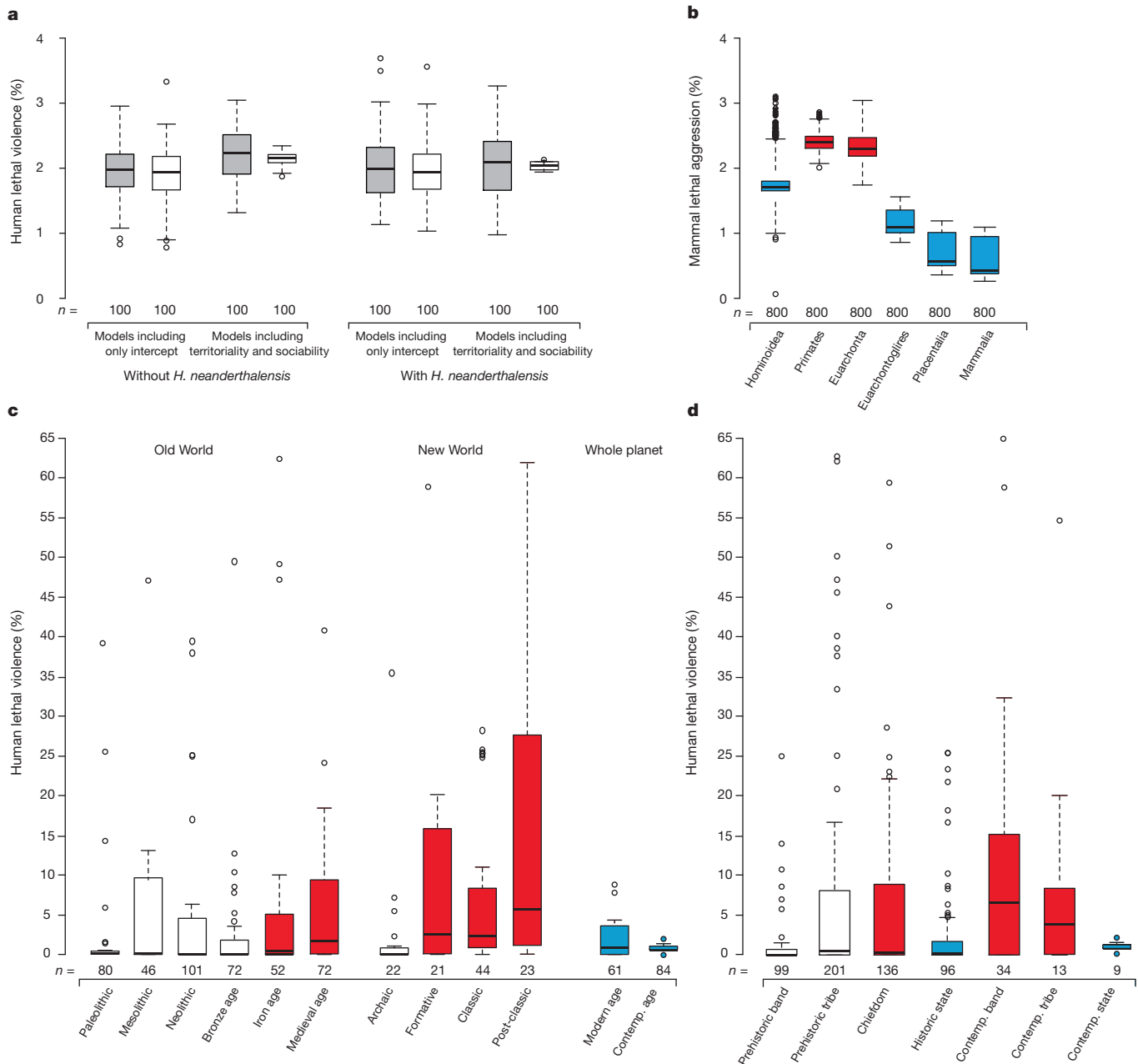
Figure 3 | Lethal violence in humans. a–d, Box plots showing **a,** the phylogenetic inferences of human lethal violence assessed as the percentage of human deaths caused by conspecifics. These estimates were achieved through phylogenetic generalized linear models and correspond to the ancestral node of the tree rooted at the node separating *H. sapiens* from the rest of the mammals. All models were performed after logit-transforming the dependent variable and considering the intraspecific variation in mammal lethal aggression. Phylogenetic uncertainty was incorporated by using the tree provided by Fritz *et al.*[22] (grey colour) and a set of 100 randomly sampled trees from Faurby and Svenning[23] (white colour). **b,** The lethal aggression inferred for six important ancestral nodes of human evolution (apes, primates, Euarchonta, Euarchontoglires, placental mammals, and all mammals). **c,** Human lethal violence during different temporal periods of human history, according to the Old World and New World chronologies[27]. **d,** Human lethal violence in different socio-political organizations[28]. In all cases the boxplots show median values, 50th percentile values (box outline), 95th percentile values (whiskers), and outlier values (circles). We tested whether the level of lethal violence observed in each ancestral node, human period and human socio-political organization differed significantly from the phylogenetic inferences in **a.** Colour indicates whether the observed lethal violence was statistically similar (white), higher (red), or lower (blue) than the phylogenetic inferences (Extended Data Tables 2, 3). In **a** and **b,** *n* indicates the number of iterations and in **c** and **d** it indicates the number of human populations (see Supplementary Information sections 7, 9c for the number of deaths).

Online Content Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

1. Kelly, R. C. The evolution of lethal intergroup violence. *Proc. Natl Acad. Sci. USA* **102,** 15294–15298 (2005).

2. Archer, J. The nature of human aggression. *Int. J. Law Psychiatry.* **32,** 202–208 (2009).

3. Bowles, S. Did warfare among ancestral hunter-gatherers affect the evolution of human social behaviors? *Science* **324,** 1293–1298 (2009).

4. Wrangham, R. W. & Glowacki, L. Intergroup aggression in chimpanzees and war in nomadic hunter-gatherers: evaluating the chimpanzee model. *Hum. Nat.* **23,** 5–29 (2012).

5. Fry, D. P. & Söderberg, P. Lethal aggression in mobile forager bands and implications for the origins of war. *Science* **341,** 270–273 (2013).

6. Sussman, R. W. in *War, Peace, and Human Nature: the Convergence of Evolutionary and Cultural Views* (ed. Fry, D. P.) 97–111 (Oxford Univ. Press, 2013).
7. Morris, I. *War! What is it Good For? Conflict and the Progress of Civilization from Primates to Robots* (Farrar, Straus & Giroux, 2014).
8. Martin, D. L. & Harrod, R. P. Bioarchaeological contributions to the study of violence. *Am. J. Phys. Anthropol.* **156,** (Suppl. 59), 116–145 (2015).
9. Keeley, L. H. *War Before Civilization* (Oxford Univ. Press, 1996).
10. Wrangham, R. & Peterson, D. *Demonic Males: Apes and the Origin of Human Violence* (Mariner Books, 1996).
11. Pinker, S. *The Better Angels of our Nature* (Viking Press, 2011).
12. Ferguson, R. B. in *War, Peace, and Human Nature: the Convergence of Evolutionary and Cultural Views* (ed. Fry, D. P.) 191–240 (Oxford Univ. Press, 2013).
13. Anholt, R. R. H. & Mackay, T. F. C. Genetics of aggression. *Annu. Rev. Genet.* **46,** 145–164 (2012).
14. Huber, R. & Brennan, P. A. Aggression. *Adv. Genet.* **75,** 1–6 (2011).
15. Daly, M. & Wilson, M. *Homicide* (Aldine de Gruyter, 1988).
16. Low, B. S. *Why Sex Matters: a Darwinian Look at Human Behavior* (Princeton Univ. Press, 2010).
17. Packer, C. & Pusey, A. E. in *Infanticide, Comparative and Evolutionary Perspectives* (eds Hausfater, G. & Hrdy, S. B.) 31–42 (Aldine Transactions, 1984).
18. Cubaynes, S. *et al.* Density-dependent intraspecific aggression regulates survival in northern Yellowstone wolves (*Canis lupus*). *J. Anim. Ecol.* **83,** 1344–1356 (2014).
19. Polis, G. A., Myers, C. A. & Hess, W. R. A survey of intraspecific predation within the class Mammalia. *Mammal Rev.* **14,** 187–198 (1984).
20. Lukas, D. & Huchard, E. Sexual conflict. The evolution of infanticide by males in mammalian societies. *Science* **346,** 841–844 (2014).
21. Archer, J. *The Behavioural Biology of Aggression* (Cambridge Univ. Press, 1984).
22. Fritz, S. A., Bininda-Emonds, O. R. & Purvis, A. Geographical variation in predictors of mammalian extinction risk: big is bad, but only in the tropics. *Ecol. Lett.* **12,** 538–549 (2009).
23. Faurby, S. & Svenning, J. C. A species-level phylogeny of all extant and late Quaternary extinct mammals using a novel heuristic-hierarchical Bayesian approach. *Mol. Phylogenet. Evol.* **84,** 14–26 (2015).
24. Opie, C., Atkinson, Q. D., Dunbar, R. I. & Shultz, S. Male infanticide leads to social monogamy in primates. *Proc. Natl Acad. Sci. USA* **110,** 13328–13332 (2013).
25. Garland, T. Jr & Ives, A. R. Using the past to predict the present: confidence intervals for regression equations in phylogenetic comparative methods. *Am. Nat.* **155,** 346–364 (2000).
26. Goberna, M. & Verdú, M. Predicting microbial traits with phylogenies. *ISME J.* **10,** 959–967 (2016).
27. Shaw, I. & Jameson, R. *A Dictionary of Archaeology* (Blackwell, 1999).
28. Johnson, A. W. & Earle, T. K. *The Evolution of Human Societies: From Foraging Group to Agrarian State* (Stanford Univ. Press, 2000).
29. Allen, M. W. & Jones, T. L. *Violence and Warfare Among Hunter–Gatherers* (Left Coast Press, 2014).
30. Abrutyn, S. & Lawrence, K. From chiefdom to state: toward an integrative theory of the evolution of polity. *Sociol. Perspect.* **53,** 419–442 (2010).

METHODS

No statistical methods were used to predetermine sample size. The investigators were not blinded to allocation during experiments and outcome assessment.

Lethal aggression in mammals. To estimate lethal aggression in mammals (defined as the percentage of deaths caused by conspecifics) we compiled a database including the amount of conspecific killing observed in many species of mammals. We conducted computer searches including the words (alone or in combination): 'mammal', 'mortality factors', 'causes of mortality', 'infanticide', 'death', 'conspecific mortality', 'conspecific fighting', 'intraspecific aggression' and 'conspecific aggression', as well as some other words related to relevant mortality factors in some mammal species, such as 'bushmeat', 'road killing' and 'overhunting'. We pooled all sources of conspecific mortality (active and passive infanticide, intergroup aggression, cannibalism and intraspecific predation, male–male fighting during mating period, territorial defensive behaviour, maternal abandonment, accidental injury). We considered only lethal conspecific interactions, ignoring non-lethal aggression, because the recording of aggressive interactions ending in the death of any of the interacting organisms, both in humans and non-human mammals, is more precise[8]. We found information about more than four million deaths in the 1,024 mammal species (~20% of the total species) from 137 families (~80% of total families) and the three main extant mammalian clades (Prototheria, Metatheria and Eutheria) (Supplementary Information section 9a). We obtained information from several studies in order to incorporate the intraspecific variability in lethal aggression for each mammal species. For each mammal included in our database, we recorded its territoriality (yes or no) and social behaviour (social or solitary) using information compiled in the Animal Diversity Web (http://www.animaldiversity.org).

Mammal phylogeny. The phylogenetic relationship between the mammals included in the database was built using Fritz et al.[22] and Faurby and Svenning[23] phylogenies, which are updated phylogenies of the supertree of Bininda-Emonds et al.[31], to account for the more recent mammalian taxonomy of Wilson and Reeder[32]. First, we used the phylogeny provided by Fritz et al.[22] including 5,020 extant mammals. Afterwards, we used a set of 100 phylogenies provided by Faurby and Svenning[23] that contains 5,747 extant and extinct mammals (including species with dated records from the Late Pleistocene, defined as the last 130,000 years). Using this set of phylogenies, we were able to incorporate phylogenetic uncertainty in all our analyses. In each phylogeny we pruned all species not included in the database and, in the few cases in which a species was missing in the supertree, we selected the closest relative (usually, a congeneric species, see Supplementary Information section 9a). Mortality data about subspecies were pooled at the species level.

We performed additional analyses with the inclusion of *H. neanderthalensis* because: i) close relatives of modern humans can be very informative to estimate their phylogenetically shared traits, and ii) including fossils in the phylogeny results in more reliable ancestral state reconstructions[33]. The Faurby and Svenning[22] phylogeny includes *H. neanderthalensis*. However, the Fritz et al.[23] phylogeny only contains extant species. For this reason, we grafted *H. neanderthalensis* into this latter phylogeny, indicating an evolutionary divergence from *H. sapiens* 0.43 million years ago (Mya)[34] and extinction 0.028 Mya[35]. Although these dates are contested[36], variations of a few thousand years did not significantly alter the phylogenetic prediction of human lethal violence. For example, when time of divergence was changed to 0.23 Mya, the mean prediction remained the same but with a slightly smaller confidence interval. The level of lethal violence in *H. neanderthalensis* was obtained from multiple sources (see Supplementary Information section 9b).

Lethal violence in humans. To estimate lethal violence in humans (defined as the percentage of people that died owing to interpersonal violence) we compiled information from almost 600 human populations and societies spanning from the Palaeolithic to the present (Supplementary Information section 9c). Because of the extremely wide temporal range, we obtained information derived from very disparate sources, namely bioarchaeological and palaeo-osteological reports, ethnographic records, statistical yearbooks and verbal autopsies (a method to determine probable causes of death when no medical record or formal medical attention is available; they are performed by non-medical field workers, recording written narratives from reliable informants in local languages that describe the events that preceded the death). Owing to this heterogeneity, and because our goal was to compare the level of lethal violence in humans with the level of lethal aggression in mammals, we did not differentiate the specific causes of intraspecific mortality. Rather, we pooled together the deaths caused by war, homicide, manslaughter, infanticide, sacrifice, cannibalism and so on, without differentiating whether lethal events involved only one perpetrator or were coalitional and collective killings. Although it is worth investigating how specific types of violence have evolved in humans, we could not explore this issue because some types of violence have been insufficiently studied, both in non-human mammals (for example, inter-group aggression in social mammals other than chimpanzees) and humans (for example, infanticide in historical

societies). Lethal violence was determined for each source using the criteria of the researchers. Ethnographic records, statistical yearbooks and verbal autopsies commonly included the casualties of the interpersonal violence. The death toll owing to interpersonal violence in bioarchaeological studies was found by following the most widely used criterion in this type of study; that is, the presence of perimortem and blade injuries as an indication of death caused by interpersonal violence[8,37]. This means that we did not include antemortem and healed injuries in our calculation of lethal interpersonal violence[37]. Nevertheless, skeletal trauma should be viewed as minimal estimates, since many injuries caused by conspecifics do not damage the bones[8,38].

The samples were categorized according to their age and socio-political organization. To assign the age to each sample, we considered the periods used to divide human history according to both the New World and Old World chronologies[27]. Old World human societies were grouped into Paleolithic (~50,000–12,000 BP), Mesolithic (~12,000–10,200 BP), Neolithic/Calcolithic (~10,200–5,000 BP), Bronze Age (~5,300–3,200 BP), Iron Age (~3,200–1,300 BP) and Medieval periods (~1,300–500 BP). New World human societies were grouped in Archaic (~12,000–3,000 BP), Formative (~3,000–1,500 BP), Classic (~1,500–800 BP) and Post-Classic periods (~800–500 BP). From then on, we considered two further periods affecting human societies throughout the entire world, the Modern Age (~500–100 BP) and the Contemporary Age (~100 BP–present day).

We followed the widely accepted socio-political classification[28,39], according to which human societies can be classified into four types: bands (small, nomadic, egalitarian groups of people, usually hunter–gatherers), tribes (small, mostly egalitarian, groups with limited social rank usually resident in permanent villages as hunter–horticulturalists), chiefdoms (stratified, hierarchical non-industrial societies usually based on kinship) and states (politically organized complex societies). To assign each sample to different socio-political and temporal categories, we relied on the information from each original source (Supplementary Information section 8c). The use of standard statistics to summarize information coming from disparate sources with extremely different sample sizes and time coverage is problematic, as has been reported[40]. To avoid such issues, we pooled all the samples (skeletal remains, dead individuals and so on) found during each period (see Supplementary Information section 8c for an exhaustive list of cases, samples and studies) and depicted them using box plots.

Phylogenetic signal of mammal lethal aggression. The phylogenetic signal for lethal aggression was calculated using Pagel's lambda[41] that compares the similarity of the covariances among species with the covariances expected under Brownian evolution. Significant phylogenetic signal occurs when $\lambda > 0$ and may take values of either $0 < \lambda < 1$ (indicating that close relatives resemble each other less than expected under Brownian evolution) or $\lambda = 1$ (indicating that close relatives are as similar as would be expected under Brownian motion). Values of $\lambda > 1$ (indicating that close relatives are more similar than expected by Brownian evolution) cannot be reached because the off-diagonal elements in the variance–covariance matrix cannot be larger than the diagonal elements[42]. To account for the possibility of a phylogenetic signal higher than expected under Brownian motion, we also calculated Blomberg's K (that is, the ratio between the observed phylogenetic signal and that expected under a Brownian evolution model)[43]. This phylogenetic signal metric is not restricted in its upper limit, and ranges from 0 (no phylogenetic signal) to infinity, with $K = 1$ indicating Brownian evolution. Statistical significance of Pagel's λ was calculated through a likelihood ratio test, comparing the likelihood of the model that was fitted to the data to that of a model in which λ was fixed to 0. Significance of Blomberg's K was calculated through a randomization test from a null model constructed with 1,000 random permutations of the data across the tips of the mammal tree. Both tests were performed using the R package 'phytools'[44]. The level of phylogenetic signal of lethal aggression in mammals measured as Blomberg's K ($K = 0.09$) was significantly higher than 0 ($P = 0.013$) and lower than 1 ($P \ll 0.001$). This indicates that close relatives tend to have similar values of lethal violence but at a level lower than would be expected under Brownian evolution. This evolutionary pattern is consistent with that shown by Pagel's lambda ($\lambda = 0.60$) and therefore only this metric is shown in the main text. The evolution of lethal aggression throughout the phylogeny of mammals was estimated using stochastic mapping as implemented in the R package 'phytools'[44]. Lethal aggression was logit-transformed before all analyses.

Effect of territoriality and sociability on mammal lethal aggression. To examine which factors explained the level of lethal aggression in mammals, we performed a phylogenetic generalized-least-squares (PGLS) model[45], with lethal aggression (logit-transformed) as the dependent variable and territoriality and sociability as independent variables. PGLS takes into account the phylogenetic signal in the residuals of the model fitted to the data[45]. To account for the intraspecific variability in lethal aggression, for each of the 1,024 mammal species, we generated a normal distribution of lethal aggression values with their empirically observed means and standard errors. To control for potential biases produced by between-study

differences in sample size, the means and standard errors that were used to generate the random distributions were first weighted by the number of individuals included in each study. We then ran the analysis 100 times, randomly sampling each time a value from each of the 1,024 normal distributions. When a species was represented by a single value, we used as its standard error the across-species average of standard errors. The analyses were run with the help of the PGLS command in the R package 'caper'[46].

Phylogenetic estimation of human lethal violence. Phylogenetic trait estimation techniques were used to obtain the lethal violence level for *H. sapiens* as a function of its position in the mammal phylogeny. These techniques take advantage of ancestral state estimation methods to predict traits of extant species[25,47]. The trait value of the focal species can be estimated as the ancestral node of the tree rerooted at the most recent common ancestor of the focal species and the rest of the tree[48,49]. The trait value estimated with this ancestral estimation method is the same as that provided by the intercept of a PGLS performed on the same tree. However, PGLS allows us to simultaneously include the level of the phylogenetic signal and other traits as covariates to improve the phylogenetic estimation of the study trait[25]. Following this approach, we also estimated human lethal violence with the help of a PGLS approach with territoriality and sociability as covariates and the phylogenetic information of the mammal tree rooted in the node where *H. sapiens* diverged from the rest of the mammals. The target species must be excluded from the analysis to estimate the PGLS parameters. Four PGLS models were fitted to our data: (i) without covariates and without *H. neanderthalensis*; (ii) with territoriality and sociability as factorial covariates but without *H. neanderthalensis*; (iii) without covariates and with *H. neanderthalensis*; and (iv) with territoriality and sociability as factorial covariates and with *H. neanderthalensis*. In all models, the dependent variable was logit-transformed and its variance was included using the approach explained in the previous section.

Lethal aggression in main ancestral nodes of the human lineage. We estimated levels of lethal aggression in the most recent common ancestor of six important clades defining the course of the evolutionary history of humans: the class Mammalia, the infraclass Placentalia (placental mammals), the superorder Euarchontoglires or Supraprimates (primates, tree-shrews, colugos, rodents and hares), the grandorder Euarchonta (primates, colugos and tree-shrews), the order Primates (primates) and the superfamily Hominoidea (apes). Lethal aggression in these ancestral nodes was inferred using the same analytical approach as that used to estimate lethal violence in humans.

Accuracy of the estimation of mammal lethal aggression from the PGLS. The accuracy of trait-estimation in a particular species increases with the level of phylogenetic signal of the study trait[25]. To test for the accuracy of our models under the observed phylogenetic signal, we used leave-one-out cross-validations with the whole mammalian data set in Supplementary Information section 9a. We inferred the level of lethal violence (logit-transformed) for each mammal species with the PGLS procedure and compared it with its actual value. We first examined the relationship between the estimated and observed lethal violence values[50] and subsequently calculated the proportion of species for which the actual value fell inside the 95% confidence interval of the estimated trait (Supplementary Information section 2).

Effect of sampling effort on the estimation of human lethal violence. To check whether the estimates of conspecific-mediated human mortality were influenced by inappropriate or insufficient sampling, we repeated all analyses considering the subset of mammalian species with more than 50 observations ($n = 645$ mammals). We performed PGLS analysis to test whether territorial and social behaviour still influence the level of lethal aggression (logit-transformed) for this subset of well-sampled species. Afterwards, we calculated the conspecific-mediated human mortality using this subset of well-sampled mammals (Supplementary Information section 4).

Effect of phylogenetic depth on the estimation of human lethal violence. To check whether the estimates of conspecific-mediated human mortality were influenced by the depth of the phylogeny, we repeated these analyses by progressively including deeper nodes to obtain the estimate and the 95% confidence intervals using the PGLS model without covariates. We considered the following hierarchically nested clades, from shallower to deeper: Homininae, Hominidae, Hominoidea, Catarrhini, Simiiformes, Haplorrhini, Primates, Primatomorpha, Euarchonta, Euarchontoglires, Boreoeutheria, Eutheria, Theriiformes and Mammalia[51]. We are aware that moving from shallower to deeper nodes means including an increasing number of species in the analyses (for example, we have only four Homininae but 1,022 Theriiformes in our phylogeny). To subsequently check whether the increasing number of species has any effect on the 95% confidence intervals, we repeated all analyses with random-pruned phylogenies equalling the number of species included in each of the clades described here (50 random phylogenies per clade) (Supplementary Information section 5).

Effect of phylogeny size on the estimation of human lethal violence. To check whether the estimates of conspecific-mediated human mortality were influenced

by the size of the phylogeny, we repeated these analyses with the progressive inclusion of more species in the phylogenies. Specifically, we estimated human lethal violence and its 95% confidence interval in 50 randomly generated phylogenies with 100, 200, 300, 400, 500, 800, 900 and 1,000 spp., using the PGLS model without covariates. Afterwards, we contrasted these values with the level of human lethal violence obtained using the empirical phylogeny, checking whether smaller phylogenies departed from empirical results more strongly than larger phylogenies (Supplementary Information section 6).

Statistical difference between phylogenetically estimated lethal violence in humans and ancestral nodes. We have checked whether the level of lethal violence phylogenetically inferred in humans is different from the lethal aggression inferred for the main ancestral nodes using *t*-tests. The phylogenetic estimates of both lethal violence in humans and lethal aggression in ancestral mammals were obtained by joining the 100 values obtained for each of the four PGLS models (with and without covariates and with and without *H. neanderthalensis*) and the two mammalian phylogenies used (Fritz *et al.*[22] and Faurby and Svenning[23] phylogenies). We subsequently tested, by means of *t*-tests, whether these two distributions differed. Because we repeated the same test six times (once per ancestral node), we corrected all *P* values by means of sequential Bonferroni corrections.

Statistical difference between observed and phylogenetically estimated lethal violence. For each temporal period and socio-political organization, we randomly sampled a given value of observed mortalities from a normal distribution with the same mean and standard error and compared it with a randomly sampled, phylogenetically estimated value. The phylogenetically estimated values were obtained by joining the 100 values obtained for each of the four PGLS models (with and without covariates and with and without *H. neanderthalensis*) and the two mammalian phylogenies (Fritz *et al.*[22] and Faurby and Svenning[23] phylogenies). We repeated these paired comparisons 800 times, and recorded the proportion of times where the observed values were higher or lower than the phylogenetically estimated values. We subsequently tested, by means of binomial tests, whether this proportion differed from the randomly expected deviation. We ran each binomial test 1,000 times and retained the average *P* values and deviance from the expected value. All *P* values shown underwent sequential Bonferroni correction.

31. Bininda-Emonds, O. R. P. *et al.* The delayed rise of present-day mammals. *Nature* **446,** 507–512 (2007); Corrigendum **456,** 274 (2008).
32. Wilson, D. E. & Reeder, D. M. *Mammal Species of the World: a Taxonomic and Geographic Reference,* 2nd–3rd edn. (Smithsonian Institution Press / John Hopkins Univ. Press, 1993–2005).
33. Finarelli, J. A. & Flynn, J. J. Ancestral state reconstruction of body size in the Caniformia (Carnivora, Mammalia): the effects of incorporating data from the fossil record. *Syst. Biol.* **55,** 301–313 (2006).
34. Finlayson, C. *et al.* Late survival of Neanderthals at the southernmost extreme of Europe. *Nature* **443,** 850–853 (2006).
35. Arsuaga, J. L. *et al.* Neandertal roots: Cranial and chronological evidence from Sima de los Huesos. *Science* **344,** 1358–1363 (2014).
36. Hublin, J. J. The origin of Neandertals. *Proc. Natl Acad. Sci. USA* **106,** 16022–16027 (2009).
37. Mays, S. *The Archaeology of Human Bones* (Routledge, 2010).
38. Milner, G. R. Nineteenth-century arrow wounds and perceptions of prehistoric warfare. *Am. Antiq.* **70,** 144–156 (2005).
39. Service, E. R. *Profiles in Ethnology* (Harpercollins College Div., 1963).
40. *War, peace, and human nature: the Convergence of Evolutionary and Cultural Views* (ed. Fry, D. P.) (Oxford Univ. Press, 2013).
41. Pagel, M. Inferring the historical patterns of biological evolution. *Nature* **401,** 877–884 (1999).
42. Münkemüller, T. *et al.* How to measure and test phylogenetic signal. *Methods Ecol. Evol.* **3,** 743–756 (2012).
43. Blomberg, S. P., Garland, T. Jr & Ives, A. R. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* **57,** 717–745 (2003).
44. Revell, L. J. phytools: an R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.* **3,** 217–223 (2012).
45. Freckleton, R. P., Harvey, P. H. & Pagel, M. Phylogenetic analysis and comparative data: a test and review of evidence. *Am. Nat.* **160,** 712–726 (2002).
46. Orme, A. D. *et al.* caper: Comparative analyses of phylogenetics and evolution in R (v.0.5.2). https://cran.r-project.org/web/packages/caper/index.html (2013).
47. Martins, E. P. & Hansen, T. F. Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. *Am. Nat.* **149,** 646–667 (1997).
48. Kembel, S. W., Wu, M., Eisen, J. A. & Green, J. L. Incorporating 16S gene copy number information improves estimates of microbial diversity and abundance. *PLOS Comput. Biol.* **8,** e1002743 (2012).
49. Nunn, C. & Zhu, L. in *Modern Phylogenetic Comparative Methods and their Application in Evolutionary Biology* (ed. Garamszegi, L. Z.) 481–514 (Springer, 2014).
50. Piñeiro, G., Perelman, S., Guerschman, J. P. & Paruelo, J. M. How to evaluate models: observed vs. predicted or predicted vs. observed? *Ecol. Modell.* **216,** 316–322 (2008).
51. Brand, S. J. *Systema Naturae 2000. The Taxonomicon* (Amsterdam, 2005).

Extended Data Table 1 | Outcome of the phylogenetic generalized linear model testing the effect of territoriality and social behaviour on the magnitude of lethal aggression in mammal species ($n = 1,024$ species)

	Estimate ± s.e.m	t-value	p-value
Fritz et al.'s phylogeny			
Territoriality	0.54 ± 0.50	3.80	0.001
Social behaviour	0.47 ± 0.51	2.71	0.014
Territoriality * Social behaviour	0.48 ± 0.55	1.33	0.244
lambda of the model	0.54		0.0001
Faurby & Svenning's phylogeny			
Territoriality	0.53 ± 0.51	3.01	0.001
Social behaviour	0.47 ± 0.51	2.70	0.009
Territoriality * Social behaviour	0.48 ± 0.51	0.43	0.341
lambda of the model	0.88		0.0001

We performed this analysis using the mammalian phylogeny provided by Fritz *et al.*[22] and 100 mammalian phylogenies provided by Faurby and Svenning[23]. In this latter case, we show the across-phylogeny mean of each statistical parameter. Lethal aggression was logit-transformed before all analyses.

Extended Data Table 2 | Outcome of the *t*-tests assessing difference between the inferred value of lethal violence at each of the chosen ancestral nodes in the mammalian phylogeny and the phylogenetic estimates of human lethal violence

Ancestral Nodes	t-test	p-value	Significance
Class Mammalia (mammals)	- 72.49	0.0001	YES
Infraclass Placentalia (placentals)	- 70.88	0.0001	YES
Superorder Euarchontoglires (primates, rodents, hares)	- 50.50	0.0001	YES
Grandorder Euarchonta (primates, tree-shrews, colugos)	15.66	0.0001	YES
Order Primates (primates)	20.78	0.0001	YES
Superfamily Hominoidea (apes)	- 16.31	0.0001	YES

We compared the lethal aggression of the ancestral nodes with the magnitudes of lethal violence obtained according to the four PGLS models (with and without covariates and with and without *H. neanderthalensis*) and the two mammalian phylogenies (Fritz *et al.*[22] and Faurby and Svenning[23] phylogenies) using a *t*-test. Significance after sequential Bonferroni correction at $\alpha = 0.05$.

Extended Data Table 3 | Outcome of the binomial tests assessing difference between the observed lethal violence in human societies and the inferred lethal violence according to the phylogenetic analysis

	Difference between the observed and the phylogenetically inferred lethal violence	p-value	Significance
Temporal periods			
Old World Chronology			
Paleolithic	+ 0.0 %	0.522	NO
Mesolithic	+ 4.6 %	0.064	NO
Neolithic	+ 5.4 %	0.029	NO
Bronze Age	+ 2.5 %	0.272	NO
Iron Age	+ 8.1 %	0.002	YES
Medieval Age	+ 7.7 %	0.002	YES
New World Chronology			
Archaic	+ 4.5 %	0.073	NO
Formative	+ 6.2 %	0.0001	YES
Classic	+ 16.5 %	0.0001	YES
Postclassic	+ 13.0 %	0.0001	YES
The Entire World			
Modern Age	- 37.1 %	0.0001	YES
Contemporary Age	- 23.7 %	0.0001	YES
Type of society			
Historic Band	+ 4.6 %	0.131	NO
Historic Tribe	+ 4.4 %	0.116	NO
Historic Chiefdom	+ 5.7 %	0.009	YES
Historic State	- 42.9 %	0.0001	YES
Contemporary Band	+ 18.5 %	0.00001	YES
Contemporary Tribe	+ 12.2 %	0.003	YES
Contemporary State	- 27.4 %	0.00001	YES

We compared the observed lethal violence of each type of human society with the magnitudes of lethal violence obtained according to the four PGLS models (with and without covariates and with and without *H. neanderthalensis*) and the two mammalian phylogenies (Fritz *et al.*[22] and Faurby and Svenning[23] phylogenies). Each binomial test was run 1000 times. Significance after sequential Bonferroni correction at $\alpha = 0.05$.