Article:

Spikins, Penny orcid.org/0000-0002-9174-5168, Needham, Andrew, Wright, Barry John Debenham orcid.org/0000-0002-8692-6001 et al. (3 more authors) (2019) Living to fight another day:The ecological and evolutionary significance of Neanderthal healthcare. Quaternary Science Reviews. pp. 98-118. ISSN 0277-3791

https://doi.org/10.1016/j.quascirev.2018.08.011

***Living to fight another day*:**

The ecological and evolutionary significance of Neanderthal healthcare

Submission to *Quaternary Science Reviews Special Issue: Neanderthal Ecology and Evolution* (Callname: CarrionNEANDER)

*Penny Spikins[1], Andrew Needham[1], Barry Wright[2], Calvin Dytham[3], Maurizio Gatta[1], Gail Hitchens[1]

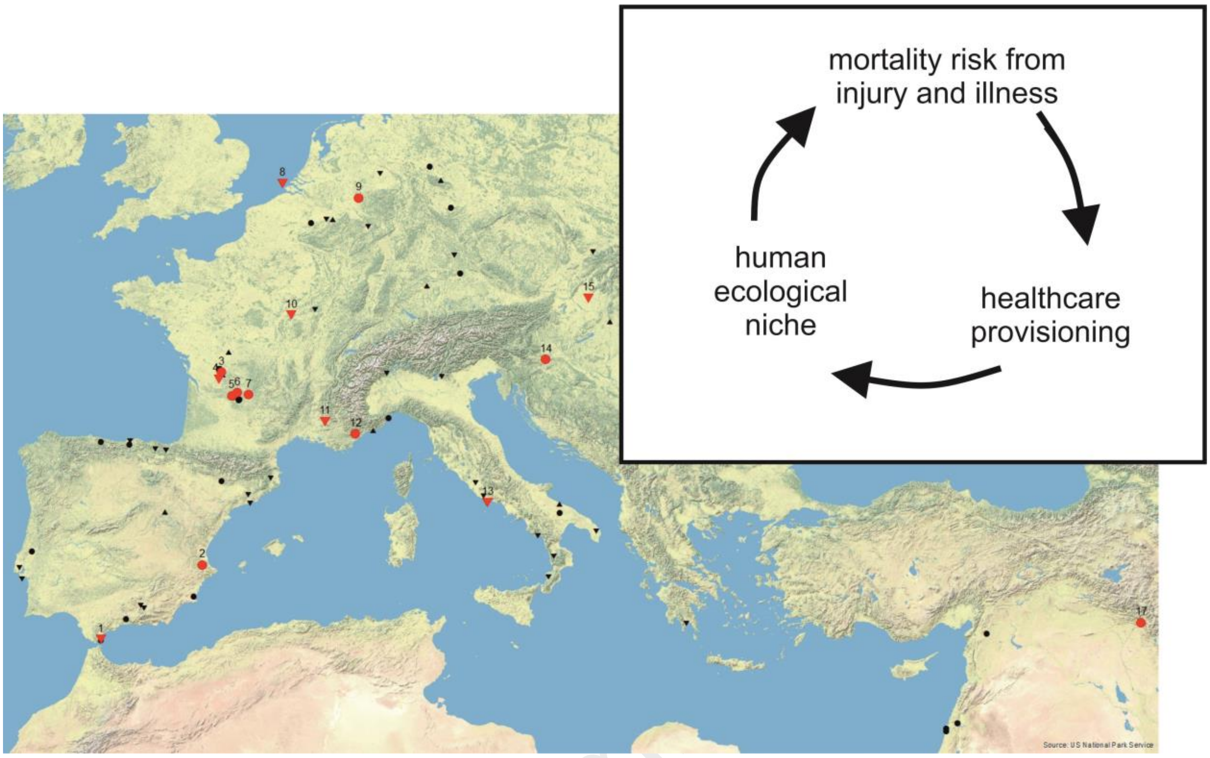
[1] PALAEO Research Centre in Human Evolution and Palaeoecology and Department of Archaeology, University of YORK, UK
[2] Hull York Medical School and Department of Health Sciences, University of York, YORK, UK
[3] Department of Biology, University of York, YORK, UK

**Corresponding author*

Abstract

Evidence of care for the ill and injured amongst Neanderthals, inferred through skeletal evidence for survival from severe illness and injury, is widely accepted. However, healthcare practices have been viewed primarily as an example of complex cultural behaviour, often discussed alongside symbolism or mortuary practices. Here we argue that care for the ill and injured is likely to have a long evolutionary history and to have been highly effective in improving health and reducing mortality risks. Healthcare provisioning can thus be understood alongside other collaborative 'risk pooling' strategies such as collaborative hunting, food sharing and collaborative parenting. For Neanderthals in particular the selective advantages of healthcare provisioning would have been elevated by a variety of ecological conditions which increased the risk of injury as well their particular behavioural adaptations which affected the benefits of promoting survival from injury and illness. We argue that healthcare provisioning was not only a more significant evolutionary adaptation than has previously been acknowledged, but moreover may also have been essential to Neanderthal occupation at the limits of the North Temperate Zone.

Graphical abstract



Keywords

Neanderthal; Injury; Mortality risk; Hunting practices; Healthcare; Palaeopathology; Medicine

1. Introduction

1.1 Neanderthal healthcare

Evidence for care of individuals who were ill or injured, from the provisioning of food, water and protection to active treatment for injuries, is widely accepted in Neanderthals (Hublin 2009; Thorpe 2016; Trinkaus and Villotte 2017). Injuries appears to have been common in these archaic hominins, and most Neanderthals appear to have suffered from some traumatic injury and recovery, often several cases of such (Berger and Trinkaus 1995; Trinkaus 2012). Even the limited remains of one of the earliest Neanderthals discovered, the Feldhofer Neanderthal or 'Neanderthal 1' individual, discovered in 1856, demonstrated recovery with likely care from several injuries and illnesses for example. These included a severe fracture of the left arm and a healed injury to the frontal bone as well as continued survival with extensive inflammation of the paranasal sinuses and metastatic disease (Schultz 2006). Care over his lifetime may have included short term intensive care when injured, accomodation for a lack of movement in the arm in foraging for food, as well as probable care for systemic disease prior to death. He was not alone with many other Neanderthals displaying a range of severe injuries and pathologies before death.

Though there have been debates over the precise levels of care implied by recovery in particular cases (for discussion see Spikins et al. 2018), provisioning and care appear to have been common practices. Despite a limited skeletal sample, evidence for remarkable recovery attributable to care from others is evident in several individuals. Fractures to the main weight bearing bones of La Ferrassie 1, and La Ferrassie 2 are likely to have entailed care from others to ensure recovery, whilst a break or sprain of the left foot of Shanidar 3 is also likely to have entailed support as would the recovery from serious cranial injuries seen in St Cesaire 1 and Krapina 37. In several cases healthcare or support is likely to have been long term, and potentially costly, with severe periodontal inflammation likely to have restricted the capacity of Aubesier 11 and Guattari 1 to forage for themselves, and serious arm injuries likely to also make foraging (and certainly hunting activities) difficult for the Feldhofer Neanderthal (Neanderthal 1), Krapina 180 and La Quina 5 (for further details of these cases see (Trinkaus and Zimmerman 1982; Fennell and Trinkaus 1997; Zollikofer et al. 2002; Erik Trinkaus, Maley, and Buzhilova 2008b; Hublin 2009; Estabrook 2009; Thorpe 2016; Tilley 2015a; Cunha 2016; Trinkaus and Villotte 2017).

Cases where care needs must have been extensive, requiring high levels of daily input over long time scales, have attracted the most attention. Such cases are 'costly' in evolutionary terms as great efforts are made to help someone survive who apparently could give little back in return, and are seen as good evidence that the motivations for care from others were 'uncalculating' (Spikins et al. 2018). Perhaps the most famous individual benefitting from such care, Shanidar I, survived for at least a decade despite a withered arm, damaged leg, probable blindness in one eye and probable hearing loss through what is likely to have been daily care and provisioning from others (Crubézy and Trinkaus 1992; Trinkaus and Zimmerman 1982; Trinkaus 2014; Trinkaus and Villotte 2017). Trinkaus and Shipman comment that '*A one-armed, partially blind, crippled man could have made no pretense of hunting or gathering his own food. That he survived for years after his trauma was a testament to Neandertal compassion and humanity' (Erik Trinkaus and Shipman 1993, 341)*. Extended periods of interpersonal care, despite a lack of any overall economic benefit to such care, is also clearly evident in other cases such as that of La Chapelle aux Saints I who suffered from several debilitating conditions, including severe osteoarthritis and systemic disease (Tilley 2015a). Tilley comments *'it seems unquestionable that during the last months of LC1's life, at least, the effects of these pathologies, both individually and in combination, would have constituted loss of independence – and therefore significant disability – when assessed within the Neanderthal lifeways context. The extent and impact of his pathologies suggest that LC1 needed and received health-related care provision to achieve survival to age at death*' (Tilley 2015a, 235). Most older Neanderthals have healed pathologies prompting Trinkaus and Zimmerman to comment *'that the Neanderthals had achieved a level of societal development in which disabled individuals were well cared for by others of the social group. … Several of them, particularly Shanidar 1 and 3, lived for many years with severely disabling conditions, which would have prevented them from actively contributing to the subsistence of the local group'* (Trinkaus and Zimmerman 1982, 75).

1.2 Healthcare as part of an adaptive system

Healthcare is now widely accepted as part of Neanderthal social behaviour (Trinkaus and Villotte 2017). However care for the ill or injured has been seen as a purely cultural trait, demonstrating complex cognitive and social capacities but without necessarily contributing to survival in any direct way. This perspective on healthcare is likely to be influenced by the nature of the archaeological evidence for pathology and probable care.

The most archaeologically visible cases of healthcare tend to be 'costly' (in terms of efforts invested from others with little apparent return) which is likely to have skewed our understanding of the adaptive role of caring for the ill and injured. What is visible in the anatomical record poorly represents likely typical healthcare practices. A well known 'osteological paradox' affects how we make interpretations of health, disease and care from skeletal material (Bishop 2011). The skeletal record is biased as to which individuals are preserved, only certain elements may be present, and many diseases leave no evidence in bone. However these biases also specifically act to reduce the apparent adaptive value of healthcare practices in several ways. Only the most severe cases of pathology (such as bone trauma and severe degenerative diseases) are identified in skeletal material for example, and of these only the most severe cases can be attributed to probable care from others with any confidence. Equally many injuries or illnesses which are life threatening without moderate care leave no palaeopathological signature in skeletal material. These could include healthcare that allows rest by provisions of food, water or warmth or by prevention of deteriorations (e.g. wound cleaning). Effectively costly cases of care are highly visible archaeologically whilst more common and highly effective care for moderate injuries and illness are largely invisible. The visible archaeological evidence for care is best understood as the 'tip of the iceberg' of practices of healthcare which would have been predominantly low cost, highly effective and adaptive in improving health and reducing mortality.

A predominance of minor injuries and illnesses and an overall adaptive value of even modest healthcare practices in modern contexts illustrate that typical healthcare is likely to have taken the form of a low cost and highly effective response to minor injury and illness. The profile care needs in modern wilderness activities is one in which severe trauma is very rare, and medical attention is typically focused on sprains and strains, particularly of the lower body, followed by moderate illnesses such as gastrointestinal complaints for example (McIntosh et al. 2007) (*figure 1*). Minor injuries, such as sprains, strains and lacerations which nonetheless require rest and treatment are by far the vast majority of injuries and illnesses which require some form of healthcare in active outdoor occupations across a range of modern contexts ranging from general athletics injuries (DeHaven and Lintner 1986), to those sustained by paramedics (Maguire et al. 2005) to injuries seen in big game hunters (Lambrecht and Hargarten 1993; Reishus 2007), expeditions in extreme environments (Heggie and Küpper 2018) or extreme sports such as rodeo riding (Griffin et al. 1987; Stoneback, Trizno, and Albright 2018). 96% of the the injuries requiring medical attention in wilderness activities, mostly through hiking with a heavy pack, were moderate (such as sprains and minor lacerations) and only 4% severe, such as fractures (of 633 cases) (Leemon and Schimelpfenig 2003). In the anatomical record of injuries recorded in palaeolithic material in contrast (Wu et al. 2011) almost all would be classed as 'severe', taking the form of fractures and head injuries, whilst far more common and much less serious pathologies are largely invisible yet would have far greater payoffs.

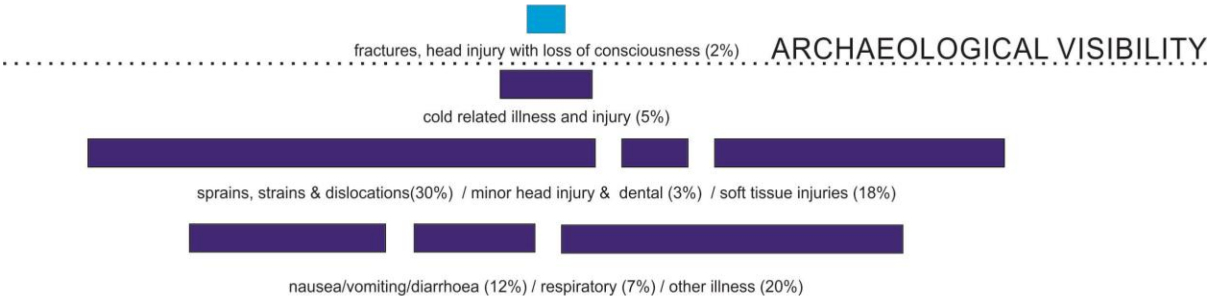


Figure 1. Medical treatment in wilderness locations. National Outdoor Leadership school's incidents requiring medical attention in wilderness activities in Wyoming, Alaska, Arizona, Washington, Idaho, Mexico, Chile and the Yukon Territory 1051 individuals (average age 22 years) 1998-2003 (data from McIntosh et al. 2007).

A profile of frequent injury and ill health, and predominantly small scale but effective care for the ill and injured is also typical of modern hunter-gatherer contexts. Amongst the modern Ache of Paraguay for example adult males were typically too sick or injured to hunt on 21% of 470 man days reported, being provisioned or cared for due to what are mostly moderate illnesses or injuries (Gurven et al. 2000; Hill and Hurtado 2009). Pre contact populations experienced similar rates of ill health (Hill and Hurtado 2009). Likewise records illustrate that between 1981 and 1982 men amongst the Efe of the Ituri forest were also ill or injured 21% of the time (Bailey 1991). Vulnerable and ill members of modern hunter-gatherers groups are thus routinely provisioned when in need, much in the same way as with vulnerable young. Sometimes runs of ill health requiring provisioning and care to aid recovery can be lengthy. For the Ache during the same period runs of being debilitated through ill health lasted at least 30 days in 40% of cases (Hill and Hurtado 2009, 3865). 75% of Tsimane adults had been incapacitated by illness or injury in the past three months (Hill and Hurtado 2009, 3865), and 42 of the 49 men in the Arroya Bandera Ache experienced at least one 90 day period with no meat acquisition in a seven year period, largely due to ill health (Hill and Hurtado 2009). Amongst the Shiwiar forager-horticulturalists around 50% of adults had been incapacitated and unable to forage for at least a month due to illness or injury, and would not have survived without care from others (Sugiyama 2001, 2004). Small investments in care, such as wound cleaning and provisioning significantly reduce the risk of more severe conditions developing which might further affect health, whilst moderate investments in healthcare can play an important role in radically reducing mortality.

Our understandable sensitivity to recognising the emotional motivations which are likely to underlie the most visible cases of costly healthcare in the distant past may have made us blind to the selective benefits of providing care for the ill and injured to human evolution in general, and moreover to the role healthcare may have played in Neanderthal survival in particular.

2. Healthcare provisioning in long term evolutionary context

A re-appraisal of existing material as well as recent evidence argues for a long evolutionary history to healthcare provisioning in hominins. Both the behavioural ecology of care for the ill and injured in other species, and archaeological evidence for healthcare prior to archaic humans argue for a long term adaptive function to such practices. Unsurprisingly Neanderthal healthcare provisioning demonstrates not only investments in others' wellbeing but knowledge and expertise accumulated over a long time period.

2.1 Care for the ill and injured in non human primates and social mammals

Care for the ill and injured is often portrayed as uniquely human, however such care is also evident in non-human primates and in social mammals in general. Examples of short term care for ill or injured peers are often recorded in non human primates, particularly apes, and range from tending wounds (Fabrega 1997; Hart 2011; Fashing and Nguyen 2011) to more complex practices such as birth assistance (Demuru, Ferrari, and Palagi 2018). These behaviours fit within primate and ape tendencies to respond to distress through consolation as well as capacities to help in a targeted way (Romero, Castellanos, and de Waal 2010; Clay and de Waal 2013; Pérez-Manrique and Gomila 2017). Other mammals also demonstrate care practices. Dolphins will support an injured group member at the surface to allow them to breathe for example, and elephants will also protect and lift injured members of the group (Pérez-Manrique and Gomila 2017). It is in highly social mammals outside of the primate order, and particularly in social carnivores where we see the most widespread evidence of *long term care* for illness and injury however. Wolves can provision ill group members by regurgitating food for example (Barber-Meyer et al. 2016), and in one instance a lioness was provisioned for eleven months while severely injured (Schaller 2009; Hart 2011). Provisioning of the ill and injured and their survival from what might otherwise have been injuries bringing a high probability of mortality is recorded in highly social mammals as diverse as lions, wolve and mongooses (Rasa 1983).

The most probable evolutionary explanation for apparently ‘selfless’ care of adult group members lies in both general pro-social responses to distress as well as the specific selective benefits of reducing the risk of mortality of other group members in situations in where groups are highly interdependent (Frank and Linsenmair 2017). The selective benefits of care for the ill and injured are clearest where groups consist of close relatives however where the survival of any one member is strongly linked to that of the others in the group caring for those who are injured is still selectively advantageous even without a high degree of genetic relatedness.

Care for the ill or injured in hominins, whilst seen as marking a distinctive human evolutionary threshold, is in fact not surprising when considered within this broad comparative evolutionary context. It has become increasingly clear that collaboration was essential to early human adaptation for example. From direct reciprocity common in primates human adaptation becomes increasingly dependant not only on indirect but also generalised reciprocity, with reputation likely to have played a key role in social dynamics (Manapat, Nowak, and Rand 2013; Jordan et al. 2016; Steinkopf 2017). As soon as collaboration became essential for survival, and individuals within any group highly interdependent selective pressures leading to care for ill and injured group members in highly social mammals are likely to have been increasingly significant, alongside distinctive social pressures emerging from trust and reputation (Spikins 2015, 2012; Steinkopf 2017). Care for the ill and injured would thus be expected to have emerged in hominins alongside other forms of collaboration such as collaborative parenting of increasingly vulnerable young, collaborative defence from predators, increased meat eating, food sharing, collaborative hunting and increased dependence on social learning (Fuentes, Wyczalkowski, and MacKinnon 2010; Burkart, van Schaik, and Griesser 2017). Rather than see these adaptations as separate responses, these different behavioural traits are perhaps best seen in terms of broader ‘health sharing’, in which risks to health or energetic costs are expended on behalf of others in the context of broader evolutionary advantages of proximate acts of altruism (Marsh 2016; Hare 2017).

2.2 Archaeological evidence for care for the ill and injured in early hominins

Unsurprisingly some of the earliest widely accepted evidence for care for illness and injury dates to precisely the time at which major changes in pro-social collaboration appear to be taking place in human evolution, ie around the emergence of Homo. Examples include the probable care for a 'toothless' hominin from Dmanisi with tooth loss and periodontal disease dated to 1.8 million years ago (Lordkipanidze et al. 2005; Trinkaus and Villotte 2017), for KNM-ER 1808, a *Homo ergaster* with hypervitaminosis (A. Walker, Zimmerman, and Leakey 1982; Skinner 1991; Doolan 2011) dated to around 1.6 million years ago, and for WT1500, a *Homo erectus* with juvenile disc herniation dated to 1.6 million years ago (Haeusler, Schiess, and Boeni 2013; Schiess et al. 2014). Earlier *potential* examples of care have however also been proposed in australopithecines such as a probable *Australopithecus africanus* from Sterkfontain in South Africa (Stw 363), dated to around 2-2.5 million years ago with severe damage to the foot (R. Pickering and Kramers 2010) (Fisk and Macho 1992) and an *Australopithecus sediba* juvenile from Malapa (MH1) dating to around 2 million years ago with a bony tumour of the spine which would have limited movement and caused chronic pain and muscle spasm (Randolph-Quinney et al. 2016).

Care for the ill and injured in early hominins may also have been under particular selection pressures unique to hominins themselves, quite apart from more general pressures on pro-social collaboration seen in other mammals. In comparison to other primates early hominins would have been unusually vulnerable to predation as they moved into more predator rich open environments, whilst lacking evolved defences to this type of predation. Moreover entering competition for scavenged and hunted food with other predators would also increase the risk of of injury (Brantingham 1998). Injuries are well attested in hominins from the australopithecines onwards, deriving from factors such as falls (L'Abbé et al. 2015), predator attacks (Berger and McGraw 2007; Pickering et al. 2004), encounters with prey (T. D. Berger and Trinkaus 1995), competition with other carnivores (Edgard Camarós, Cueto, et al. 2016) and even interpersonal violence (Underdown 2004; Trinkaus 2012). A reliance on obligate bipedalism will have made lower limb injuries a particularly high mortality risk for early hominins. Furthermore an increasingly lengthy period of infant dependency will have represented greater losses of investments if succumbing to mortality through injury or disease before reaching reproductive age. Added to which a co-evolution of diseases *with* healthcare practices might lead to evolved reliance on healthcare as hominins developed reduced resilience in the presence of care (Hart 2011; Kessler et al. 2017).

The particular circumstances affecting the selection pressures on hominins to reduce the risk of mortality from injury make direct comparisons with apparently notable *independent* recovery from illness and injury in non human primates problematic (Spikins et al. 2018). Non human primates are able to to rely on a forelimb to replace the function of an injured rear limb to move around, and able to use a rear limb to replace an injured forelimb when foraging. In this way injured primates can often forage independently despite injury even though their foraging efficiency is reduced, and for this reason injured chimpanzees can often survive despite injured limbs (Munn 2006). The case of a one armed gibbon able to brachiate effectively by using a rear limb as an 'arm' (Sayer, Whitham, and Margulis 2007) is a particular case in point. However as obligate bipeds hominins could not replace an injured rear limb with a forelimb in order to move around effectively, and rear limbs become far less manipulative and increasing less helpful as a replacement for a forelimb particularly given an increased reliance on tools. Moreover as the diet of early hominins became more dependant on collaborative scavenging and hunting (Domínguez-Rodrigo et al. 2014), foraging independently despite injury would less viable than it is in other primates, particularly in a context with high rates of predation. In comparison to non-human primates hominins will have been more prone to injury, have a higher risk of mortality from injury and been less able to recover independently or find sufficient resources alone.

Both general pressures common to highly social collaborative mammals, as well as selective pressures unique to hominins, will have made healthcare provisioning an increasingly adaptive response to mortality risks from injury, and in turn healthcare provisioning will have influenced the ecological niche which hominins could occupy. Moreover in hominins memory, long term planning and accumulated knowledge and understanding become increasingly evident in healthcare, much as in other complex behaviours such as collaborative hunting. Care appears to have been common In *Homo heidelbergensis*/pre-Neanderthal populations at Sima de Los Huesos around 350,000bp for example. Amongst around 28 individuals interred in a mortuary pit, several provide evidence for care or accomodation. Craniosyntosis in a young child which did not adversely affect her care, despite physical deformity (Gracia et al. 2009) has attracted a certain amount of attention. This case may not be particularly surprising however as this condition does not always affect cognition and behaviour, and care for even extremely disabled infants is known in non-human primates (Matsumoto et al. 2016). However another individual suffered from deafness, probably due to infection (Pérez et al. 1997; Trinkaus and Villotte 2017) which is likely to have needed accomodation from others. Perhaps most notably an elderly individual is likely to have walked with the aid of a stick, with his support likely to have involved a level of planning around his lack of mobility (Bonmatí et al. 2010, 2011).

2.3 Healthcare in Neanderthals as both social behaviour and technical solution

Neanderthals are however the pre-modern humans for whom we have the best evidence for highly effective and knowledgeable healthcare. Despite a limited skeletal sample there are many cases in which recovery from pathology and trauma indicate likely care from others (*table 1*), distributed throughout the period and spatial extent of Neanderthal occupation (*figure 2*), with these cases only the most visible of what seems likely to be extensive, widespread and knowledgeable care. In the case of La Chapelle aux Saints 1, for example, care when most debilitated is likely to have included fever management, hygiene maintenance and repositioning and manipulation (Tilley 2015a). Individuals with systemic diseases (such as La Chapelle aux Saints 1) will have needed to have been kept hydrated to manage fever, whilst though with severe wounds and fractures will have required adequate nutrition and rest. A femoral fracture at the greater trochanter of La Ferrassie 1 for will have been painful and severely restricted mobility requiring care and provisioning (Fennell and Trinkaus 1997), as would chronic osteomyelitis of the hip in La Chapelle aux Saints 1 (Tilley 2015a). High rates and healing and low rates of infection suggest that some form of wound management was common (Trinkaus and Zimmerman 1982, 75). This may have involved using particular dressings and means of reducing blood loss. The Inuit for example killed lemmings to use their skins for dressings wounds and boils, but only rarely ate lemming meat (Mcelroy 2009, 19). Ochre may potentially have been used as an antiseptic when applied to wounds (Zilhão et al. 2010; Velo 1984). There is also evidence for use of the use of medicinal plants in dental calculus (Hardy et al. 2012; Hardy 2018), including poplar, which as salicylic acid may have been used as a painkiller (Weyrich et al. 2017). Healthcare practices are evidence of strong pro-social motivations within groups, but they are also evidence of an adaptation to their environment which also builds on accumulated knowledge, technical ability and complex cognition.

site and date	specimen	age and sex	pathology	impact	care	references
Bau de l'Aubesier, France, c. 180,000 BP	Aubesier 11	Adult, female (?)	1. Extensive antemortem tooth loss 2. Broken teeth 3. Abscesses 4. Mandibular torus and torus lateralis superior	1. – 4. Pain, compromised mastication and incapacity to use teeth and tools, and with increased risk of infection due to broken teeth	1. – 4. Compromised masticatory apparatus may have required accommodation, both in helping with eating and with allowing other tasks to avoid using teeth as tools	(Lebel and Trinkaus 2002)
Šal'a 1, Slovak Republic, c. OIS 5E	Šal'a 1	Prime aged adult, female	traumatic lesion to right supraorbital torus, with evidence of healing	Short term pain and possible cognitive disruption, long term possibly asymptomatic	given its location, short term care in cleaning the wound is likely	(Sladek 2002; Wu et al. 2011)
Regourdou, Montignac-sur-Vézère, France, MIS 5	Regourdou 1	Mid 20s, sex unknown	1. Osteoarthrosis of the spine with osteophytosis 2. abnormal bone growth to C4, 3. T2 ligamentum flavum ossification 4. T9 twisting of spinous process 5. L5 ossification of vertebral ligament	1. – 7. Pain and probable limitation to the range of movement available	1. – 7. Possible accommodation in the range of activities carried out	(Gómez-Olivencia et al. 2012, 2013; Maureille et al. 2015)

			insertion 6. fusion and asymmetry in the sacrum (possible scoliosis) 7. pathology in the femur, possibly linked to 6.			
Krapina rockshelter, Hušnjakovo Hill, northern Zagreb, Croatia, 120-130,000 BP	Krapina 4	Not specified	Blunt force injury marked by an oval depression to the frontal bone, with evidence of healing and a purulent infection	Short term pain and blood loss and possible cognitive disruption, long term possibly asymptomatic	given its location, short term care in cleaning the wound is possible, though perhaps less likely than in other cases given the presence of infection	(Estabrook and Frayer 2013)
Krapina rockshelter, Hušnjakovo Hill, northern Zagreb, Croatia, 120-130,000 BP	Krapina 5	Not specified	1. small blunt force traumas to the skull 2. periosteal reaction across the skull	1. possible short term pain and blood loss and possible cognitive disruption, long term possibly asymptomatic 2. possible pain or asymptomatic	1. given the location, cleaning the wound is possible 2. intervention unlikely	(Estabrook and Frayer 2013)

Krapina rockshelter, Hušnjakovo Hill, northern Zagreb, Croatia, 120-130,000 BP	Krapina 20	Not specified	1. Two blunt force traumas to the frontal bone (possibly occurring at the same time), with no evidence of infection 2. diffuse periostitis, likely caused by a subcutaneous infection	1. possible short term pain and blood loss and possible cognitive disruption, long term possibly asymptomatic 2. possible pain or asymptomatic	1. given the location, cleaning the wound is possible 2. intervention unlikely	(Estabrook and Frayer 2013)
Krapina rockshelter, Hušnjakovo Hill, northern Zagreb, Croatia, 120-130,000 BP	Krapina 31	adult	1. Depression to the frontal bone with evidence of healing 2. mild periostitis	1. possible short term pain and blood loss and possible cognitive disruption, long term possibly asymptomatic 2. possible pain or asymptomatic	1. given the location, cleaning the wound is possible 2. intervention unlikely	(Estabrook and Frayer 2013)
Krapina rockshelter, Hušnjakovo Hill, northern Zagreb, Croatia, 120-130,000 BP	Krapina 34.7	adult	Significant posterior parietal depressed fracture, with some evidence of inflammation of the wound	Pain, blood loss, increased risk of infection and possible short and long term cognitive disturbance	the location of the wound suggests help in dressing and cleaning the wound may have been required over a short term period. If serious cognitive impairments resulted from the injury more substantial long term accommodation may have been required	(Kricun et al. 1999; Wu et al. 2011; Estabrook and Frayer 2013; Monge et al. 2013)

Krapina rockshelter, Hušnjakovo Hill, northern Zagreb, Croatia, 120-130,000 BP	Krapina 106-110	adult	High degree of degeneration to C4-C7, likely caused by trauma	Initial trauma would cause pain and possibly limit the range of mobility and function in the affected area. Possibly caused pain and if advanced may have been more severe and impacted upon nerve function	Possibly accommodation and support in treating the initial trauma. The later degeneration may not have required support or accommodation, unless the nerves were affected, in which instance the level of care might have been high and long term	(Gardner and Smith 2006)
Krapina rockshelter, Hušnjakovo Hill, northern Zagreb, Croatia, 120-130,000 BP	Krapina 120.71	Not specified	Fragment of rib with empty medullary chamber. An osteolytic lesion is present in the posterio-medial aspect of the shaft, corresponding with fibrous dysplasia	Fibrous dysplastic neoplasm can be asymptomatic or it can present with debilitating symptoms. Not possible to differentiate one from the other from the bones alone	If asymptomatic, no care or accommodation would be needed. If symptomatic, care and accommodation may have been significant and long term	(Monge et al. 2013)
Krapina rockshelter, Hušnjakovo Hill, northern Zagreb, Croatia, 120-130,000 BP	Krapina 149	Not specified	Fracture to the right clavicle, well healed, with no evidence of long term disability	Pain and limited or painful motion to the right upper part of the body	Possible short term accommodation for a number of weeks	(Estabrook and Frayer 2013)

Krapina rockshelter, Hušnjakovo Hill, northern Zagreb, Croatia, 120-130,000 BP	Krapina 180	adult	Right distal ulnar fracture and pseudoarthrosis or possible amputation of the limb, with perhaps the latter more likely. No signs of infection.	Pain and restricted movement and use of the affected limb. Amputation would significantly modify the range of activities that could be carried out, though evidence the limb was still actively used	Breaks would require intervention to set the bones and would compromise activities that involved the affected area for a number of weeks and possibly months. An amputated limb would permanently compromise the individual and group behavioural modification would be needed, perhaps including engagement with different tasks or help with tasks	(Radovčić et al. 1988; Wu et al. 2011;Estabrook and Frayer 2013)
Krapina rockshelter, Hušnjakovo Hill, northern Zagreb, Croatia, 120-130,000 BP	Krapina 188.8	adult	Fracture to the proximal end of the left ulna, with some bowing, and no evidence of infection	Pain and restricted movement and use of the affected limb in the short term	Intact radius would provide splinting for a fractured ulna (bowing of the bone suggesting poor alignment before healing). Pain would compromise activities that involved the affected area for a number of weeks.	(Estabrook and Frayer 2013; Trinkaus and Villotte 2017)
North Sea 51º40' northern latitude, 3º20' eastern longitude, c. OIS 5e	Zeeland Ridges	young adult, male	Lesion to the orbital roof with thick sclerotic margin, which lacks periosteal new bone formation but with evidence for osteoclastic action - likely an epidermoid cyst	Typically asymptomatic but can have significant impacts, including: visual problems, pain and swelling, headaches, dizziness, disequilibrium, intracranial	If asymptomatic, no care or accommodation would be needed. If symptomatic, long term care and accommodation would be required.	(Hublin et al. 2009)

				hypertension, convulsions, extradural hematoma, focal neurological signs, seizure. Though rare, these cysts can become malignant.		
Kiik-Koba, Crimea, OIS 4 or OIS 5	Kiik-Koba 1	40-50 years, male	1. Intervertebral ossifications/stiffening of the vertebral column 2. hypercementosis of a mandibular canine linked to extreme wear or possible periodontal disease 3. enthesopathy associated with the quadriceps femoris tendon 4. ossification of intertarsal connective tissue and bony spurs to the left sulcus tali and left intermediate medial cuneiform bone 5. enthesopathies to the triceps surae tendon insertions and left calcaneous 6. possible	1. pain and reduced bending and spinal rotation likely, possibility of trapped nerves 2. pain 3. pain and possibly limited use of the affected area in the short term 4. possibly asymptomatic but can cause pain and limit movement 5. possibly asymptomatic but can cause pain and limit movement 6. pain and may limit movement 7. may be asymptomatic	Short term care and accommodation to help recovery from broken bones and possibly long term support and accommodation to compensate for pain and some limitation to range of movement in the limbs and trunk	(Trinkaus, Maley, and Buzhilova 2008a)

			osteomyelitis to two distal phalanges 7. right distal hallucal phalanx shows a rounded bony growth with possible muscle hypertrophy 8. abnormality to the right fifth proximal phalanx, likely the result of a fracture to the diaphysis 9. The ossification of tendons may be linked to strain and possible old age and over-use or DISH	8. pain and may limit movement for a number of weeks 9. pain and possibly limited mobility		
Shanidar Cave, Iraq, top of layer D, c. 45-70,000 BP	Shanidar 1	35-50 years, male	1. atrophy and limb paralysis in the right arm caused by a nerve injury 2. right humerus fractured in two places, with signs of heavy callus formation and healing, as well as the bone healing at an abnormal angle 3. break to the right humerus from amputation of the limb or pseudoarthrosis	1. – 3. Each would have been painful in the short to medium term, ultimately leading to the probable amputation of the lower portion of the limb 4. short term pain 5. – 9. Mobility was likely compromised - being slow and painful - over a long time period	1. – 4. Breaks and crush injuries would require intervention to set the bones and would compromise activities that involved the affected area for a number of weeks and possibly months. An amputated limb would permanently compromise Shanidar 1 and likely required individual and group behavioural modification, perhaps including engagement with different tasks or help with tasks.	(Trinkaus and Zimmerman 1982; Crubézy and Trinkaus 1992; Tilley 2015b; Trinkaus and Villotte 2017; Kent 2017)

			4. osteomyelitic lesion to the right clavicle, likely the result of a soft tissue injury, with evidence of healed infection 5. abnormalities in the right foot, including a healed fracture to the fifth metatarsal, and degenerative joint disease (DJD), making movement painful 6. DJD in multiple locations and with ossification of connective tissue, lined to trauma 7. hyperostotic disease, based on the presence of otherwise unexplained osteophytes 8. advanced DJD to the right knee 9. broadening of the right talus relative to the left and the left tibia shows significant curvature, likely compensating for trauma in the right leg	10. short term pain and blood loss, probable blindness in the left eye or compromised binocular vision, long term cognitive impairment possible to the cerebral motor cortex 11. possible deafness in this ear or compromised 3D acoustics	5. – 9. Long term compromised mobility may have resulted in behavioural modification by the group to compensate 10. – 11. Compromised sensory and possibly cognitive functions may have similarly necessitated individual and group behaviour modification to compensate	

			and foot 10. the cranium shows a wound to the scalp, as well as a crushing injury to the lateral side of the left orbit, with evidence of full healing prior to death 11. auditory exostoses to the left meatus - grade III, and yet more advanced in the right meatus - grade III, with bridging across the porus			
Layer D, Shanidar Cave, Iraq, c. >45,000 BP	Shanidar 2	20-35 years, male	DJD along the vertebral column	Mobility was possibly compromised, likely being painful	Long term: compromised mobility may have resulted in accommodation by the group to compensate	(Trinkaus and Zimmerman 1982)
Layer D, Shanidar Cave, Iraq, c. >45,000 BP	Shanidar 3	35-50 years, male	1. trauma to the left ninth rib caused by a penetrating wound that likely collapsed the lung 2.right talocrural and talocalcaneal articulations, with signs of healing, 3. extreme DJD to the right foot and bony	1. blood loss and pain for a number of weeks and restricted breathing and reduced exercise tolerance 2-3. pain and restricted mobility in the short term and probable pain and compromised mobility in the long	1. Days to weeks of intense care for projectile injury 2. long term accommodation for limited mobility	(Trinkaus and Zimmerman 1982; Churchill et al. 2009a)

			spurs to the distal fibula and right talus, likely caused by a break or sprain	term		
Layer D, Shanidar Cave, Iraq, c. >45,000 BP	Shanidar 4	35-50 years, male	1. minor DJD to the arms, hands and vertebral column 2. healed fracture of the seventh/eighth rib, evidenced by areas of callus, occurring shortly before the time of death 3. possible hyperostotic disease	1. likely asymptomatic 2. pain and some restriction to breathing, movement and physical tasks for a number of weeks 3. likely asymptomatic	2. probable accommodation for a number of weeks	(Trinkaus and Zimmerman 1982; Crubézy and Trinkaus 1992)
Layer D, Shanidar Cave, Iraq, c. >45,000 BP	Shanidar 5	35-50 years, male	1. scalp wound to the frontal bone with evidence of healing 2. Paramedial endocranial hyperostosis (enplaque type, grade I)	1. blood loss and pain 2. probably asymptomatic	1. the location of the wound suggests help in dressing and cleaning the wound may have been required over a short term period	(Trinkaus and Zimmerman 1982; Wu et al. 2011)

La Quina, Charente, France, 65,000 BP	La Quina 5	adult	1. hypoplasia/atrophy of the left humerus 2. Broken teeth	1. affected limb may have been restricted in its range of uses 2. increased likelihood of infection and loss of teeth, possible limitations in using teeth as tools	1. behavioural accommodation may have been required, depending on how quite how limit the individual was in using the affected limb 2. care unlikely	(Condemi et al. 2012)
La Quina, Charente, France, 65,000 BP	La Quina 5/9/18(?)	Adult/juvenile	tempero-mandibular osteoarthritis, described as very severe	May have compromised chewing and eating and the use of teeth as tools	possibly accommodation and support, such as chewing food and facilitating other activities where the teeth were not required, behavioural modification of the individual likely	(Straus and Cave 1957)
Les Pradelles (Marillac) France, c. 60,000 BP	Marillac 3	40-60 years, male	Hyperostosis frontalis interna (type B - mild or grade II)	can be asymptomatic but can be linked to headaches and mental imbalance,	likely to be asymptomatic given its moderate nature but may require care if symptoms were present	(Garralda, Maureille, and Vandermeersch 2014)
Les Pradelles (Marillac), France, c. >58,000 BP	LP femur	adult	Myositis ossificans associated with the linea aspera of the femur	may compromise the function of the affected muscle	given the location, possibly some accommodation linked to mobility	(Mussini et al. 2012)
La Chapelle-aux-Saints,	La Chapelle-aux-Saints 1	25-40 years, male	1. Largely edentulous with advanced anterior alveolar infection - may have lost as many as	1. – 4. Pain, compromised mastication and incapacity to use	1. – 4. Compromised masticatory apparatus may have required accommodation, both in	(Straus and Cave 1957; Trinkaus 1985; Tappen 1985; Dawson and Trinkaus 1997;

France, 47-56,000 BP			15 teeth antemortem 2. Abscesses and resorption to right maxilla 3. DJD right mandibular condyle 4. Minimal DJD to occipital condyles 5. Auditory exostoses 6. Pitting and exostoses to left ulna and right humerus 7. osteoarthritis, especially concentrated in the mid to lower cervical vertebrae and upper thoracic vertebrae, described as very severe 8. Severe DJD to spine with schmorl's nodes to C6-C7 and eburnation to some vertebrae and with ossified ligamenta flava 9. L4-L5 Baastrup disease 10. Ossification of rib cartilage	teeth and tools 5. possibly restriction in hearing 6. pain 7. – 9. Pain and restriction in the range of movement, possibly nerve entrapment or damage 10. pain and restriction of movement while the break heals 11. possibly asymptomatic 12. – 13. Severe pain and restriction in mobility 14. possibly asymptomatic or pain and limited mobility if severe	helping with eating and with allowing other tasks to avoid using teeth as tools 5. likely no accommodation required 7. – 9., 12. long term compromised mobility may have resulted in behavioural modification by the group to compensate 11. likely no accommodation required 13. likely no accommodation required	Gómez-Olivencia 2013; Tilley 2015b)

			11. Break to right thoracic rib broken near the costal cartilage attachment (completely healed) 12. DJD left acetabulum with exostoses and eburnation 13. osteomyelitis and abscess in the left acetabular notch 14. DJD in the toes			
Cove Negra, Valencia, Spain, OIS 3-4, c. 54-51,000 BP	Cova Negra 1	adult	Anterosuperior parietal trauma with external remodeling	possibly pain, bleeding, and short term cognitive impairment	possible short term support linked to the initial trauma	(Lumley 1975; Arsuaga et al. 2007; Wu et al. 2011)
Grotte du Renne, France, c. 50-100,000 BP	Arcy-Sur-Cure 9	Not specifie d	1. Dental abscess 2.broken teeth	1. – 2. pain and may compromise mastication and use of teeth as tools for the duration	1. – 2. compromised masticatory apparatus may have required accommodation, both in helping with eating and with allowing other tasks to avoid using teeth as tools, though only in the short term in this case	(Condemi et al. 2012)
Guattari, Italy, 50-60,000 BP	Guattari 1 / Circeo 1	adult	1. severe periodontal inflammation	1. – 2. Pain, compromised mastication and	1. – 2. Compromised masticatory apparatus may have required	(Sergi, Ascenzi, and Bonucci 1972)

			2. Edentulous with alveolo-palatal remodeling and atrophied bone, suggesting decreased masticatory function. 3. Periosteal osteophytes present on the palate in a symmetrical pattern along both sides of the medial sagittal line, probable torus palatinus.	incapacity to use teeth and tools 3. likely asymptomatic	accommodation, both in helping with eating and with allowing other tasks to avoid using teeth as tools	
Forbes' Quarry, Gibraltar, 45-70,000 BP(?)	Gibraltar 1	60s, female	1. Endocranial hyperostosis (warty/nodular type, grade II) limited to the frontal bone, localised to the central portion of the frontal squama 2. Dental abscess	1. can be asymptomatic but can be linked to headaches and mental imbalance, , seizures in severe cases 2. pain and may compromise mastication and use of teeth as tools for the duration	1. likely to be asymptomatic given its moderate nature but may require significant care if symptoms were present 2. compromised masticatory apparatus may have required accommodation, both in helping with eating and with allowing other tasks to avoid using teeth as tools, though only in the short term in this case	(Condemi et al. 2012)
La Ferrassie, France, 43-45,000 BP	La Ferrassie 1	>50, male	1. temporomandibular osteoarthritis 2. abscesses in the mandible 3. upper limb fracture	1. - 2. pain when chewing 3. pain and short term restricted mobility	1. – 2. behavioural modification and accommodation in eating and using teeth as tools 3. – 4. mid term accommodation and care for	(Straus and Cave 1957; Fennell and Trinkaus 1997; Gómez-Olivencia 2013; Tilley 2015b; Trinkaus and Villotte 2017; Gómez-Olivencia et al. 2018)

			4. healed fracture to the right femoral greater trochanter 5. appendicular symmetrical periostitis (pronounced in the distal femora, proximal tibiae, distal tibiae, distal fibulae) 6. hypertrophic pulmonary osteoarthropathy (likely in the initial stages - estimated 2-14 months duration)	4. pain and significant disruption to mobility weight bearing structures 5. pain and swelling to the limbs and joints, possibly limiting mobility 6. pain and swelling in the joints and clubbing of the digits, possibly limiting mobility and fine motor skills	significant immobility 5. – 6. long term accommodation	
La Ferrassie, France, 43-45,000 BP	La Ferrassie 2	young adult, female	1. healed fracture of the right tibia 2. fractured fibular diaphysis with infection	1. pain and short term restricted mobility for weight bearing bone 2. pain and short term restricted mobility	1. – 2. short term accommodation and care in setting the bones	(Heim 1976; Guérin et al. 2015/6)

Kleine Feldhofer Grotte, Neander Valley, Germany , c. 40,000 BP	Neanderthal 1, Feldhofer	50+ years, male	1. fractured left ulna with evidence of ostoclastic processes 2. Atrophy of left humerus and hypertrophy of right humerus 3. chronic sinusitis and osteoclastic processes in the bone 4. lesion to the right supraorbital arch, likely meningitis or trauma and associated with 3. 5. tumorous process associated with 3.	1. painful and with restricted movement in the limb for a number of weeks 1. reduced use of left arm 3. pain due to persistent infection. 4. pain and severe side effects if meningitis 5. potentially benign but would be serious side effects if malignant	Short term: short term care for lesion on supra-orbital arch? Long term: Long term accommodation for limited movement in left arm, probable care for extensive inflammation of sinuses and metastatic disease leading up to death	(Schmitz et al. 2002; Schultz 2006; Cowgill et al. 2015)
Saint-Césaire, layer E_{J0P}, France, c. 36,000 BP	Saint-Césaire 1	young adult, male	Fractured skull from a wound that penetrated the internal lamina, with evidence of healing	Pain, heavy bleeding, and short term cognitive impairment, with penetration of the internal lamina increasing the risk of infection	the location of the wound suggests help in dressing and cleaning the wound may have been required over a short term period	(Zollikofer et al. 2002)

Table 1. Examples of recovery from pathology suggesting probable care in Neanderthal skeletal material

Figure 2. Sites with Neanderthal skeletal material and key sites with probable evidence of recovery through care. Healthcare case studies (see Table 1) are in red and numbered: 1) Forbes' Quarry, 2) Cova Negra, 3) Les Pradelles, 4) La Quina, 5) La Ferrassie, 6) Regourdou, 7) La Chapelle-aux-Saints, 8) Zeeland Ridges, 9) Kleine Feldhofer, 10) Arcy-sur-Cure, 11) Bau de l'Aubesier, 12) Saint Césaire, 13) Riparo Mezzena, 14) Guattari, 15) Krapina, 16) Šaľa, 17) Kiik-Koba, 18) Shanidar. Neanderthal skeletal material (black) is compiled from Nespos and (Diedrich 2014) with additions). Symbols: ·▼ cranial/dental material only ▲ postcranial material only ·● near complete or partial skeleton.

Healthcare practices in Neanderthals merit discussion alongside those of modern humans and those in later prehistory and history (Spikins et al. 2018). However Neanderthals also occupied unique environments with no known modern analogs and adapted to these environments in distinctive ways. There is good reason to suggest care for the ill and injured amongst Neanderthals was not only evidence of a human desire to care for vulnerable group members but also a response to an ecological context which imposed particular mortality risks.

3. Ecological challenges to Late Pleistocene Neanderthal occupation of the north temperate zone

Neanderthals successfully occupied Western Eurasia from approximately 250ka BP (Marra et al. 2017), being descendents of earlier *Homo heidelbergensis* and pre-Neanderthal populations. They were clearly well adapted to survival in what was a northernmost extension of archaic human occupation. The most securely dated evidence for their presence is limited to below 55° N (Finlayson and Carrión 2007; Slimak et al. 2011; Nielsen et al. 2017) although highly debated Mousterian assemblages have been found as far north as near the Arctic Circle at Byzovaya (Slimak et al. 2011) suggesting that the northernmost latitudes were a limit to their expansion.

Despite surviving for over 200,000 years Neanderthals eventually died out in most of Europe between 35-40 ka BP (Higham et al. 2014; Hublin 2017) with the latest demise probably in Iberia (Finlayson et al. 2006), albeit timing is still strongly debated. A combination of several factors has been argued to have contributed to their extinction (Rey-Rodríguez et al. 2016). The arrival of anatomically modern humans has been suggested as one possible factor in their demise (d'Errico and Sánchez Goñi 2003; Hortolà and Martínez-Navarro 2013). However Neanderthals were adapted to survival within particular ecological contexts and within faunal communities for which we have no modern analogs and climate and environmental changes are often seen as a more significant factor (Finlayson et al. 2004; Stewart 2007; Müller et al. 2011/2; Melchionna et al. 2018), which also led to the extinction of around 35-40% of co-existing megafaunal species (Stuart and Lister 2012).

Surviving in Europe during the Late Pleistocene presented major ecological challenges for human communities. Palaeoecological evidence documents a notable instability in european temperatures, with several harsh climatic events concurring to create a notable deterioration of an already severe glacial environment (Sánchez Goñi et al. 2002; Moreno et al. 2014). During the Last Glacial period a series of Heinrich events, during which large icebergs traversed the North Atlantic causing global climate cooling, followed by rapid warming episodes (ie Dansgaard-Oeschger events) caused abrupt alternations of cold-arid and warm-humid environments. Moreover extended and independent phases of regional drought with significant repercussions on human populations have been documented (Luetscher et al. 2015; Wolf et al. 2018).

Climatic and ecological challenges at less than millennial scale had a substantial impact on human communities during MIS 3, affecting the availability of food resources, changing distributions of plant and animal communities, and forcing costly and repeated mobility and changes in dietary habits (Hodgkins et al. 2016; El Zaatari et al. 2016). Furthermore there were notable contractions of human occupation from north and east Europe and into a few regions with milder climates including southerly Mediterranean refugia (Finlayson et al. 2006; Stewart et al. 2010). There was also a significant fragmentation of Neanderthal distribution and demographic decline in Europe with frequent regional extinctions (Dennell, Martinón-Torres, and Bermúdez de Castro 2011; Sánchez-Quinto and Lalueza-

Fox 2015; Hublin and Roebroeks 2009; Benito et al. 2017; Wolf et al. 2018) and sporadic population replacement (Fabre, Condemi, and Degioanni 2009; Dalén et al. 2012; Melchionna et al. 2018; Hajdinjak et al. 2018).

The north temperate zone is a demanding environment for human originally adapted to more equatorial conditions, and particularly so in glacial periods. Evidence for nutritional stress from enamel hypoplasia is common and within the upper range of that observed within modern hunter-gatherers (Ogilvie, Curran, and Trinkaus 1989; Guatelli-Steinberg, Larsen, and Hutchinson 2004; Hlusko et al. 2013). Contacts between groups may have been limited by low population density, see (Dennell, Martinón-Torres, and Bermúdez de Castro 2011; Bocquet-Appel and Degioanni 2013; Sánchez-Quinto and Lalueza-Fox 2015; French 2016; Simons and Sella 2016; Hajdinjak et al. 2018), driven by low plant productivity and animal biomass, and the energetic costs of movement across large areas of landscape. Low population densities and limited contacts also explains low rates of introgression, with half sibling matings being common (Prüfer et al. 2014; Castellano et al. 2014; Rogers, Bohlender, and Huff 2017; Harris and Nielsen 2016).

These were archaic humans who often lived in very challenging environments, and for whom their capacities to adapt to such challenges played a major factor in individual and group survival.

It might seem that such populations could not afford to waste resources on individuals who were ill or injured however there are good reasons to argue that they could not afford *not to do so*. Far from merely an interesting cultural practice, healthcare provisioning, already part of hominin adaptations, may have been particularly essential to their survival given the significant mortality risks which their ecological context imposed.

4. The selective advantages of Neanderthal healthcare provisioning

4.1 Neanderthal mortality risks in relation to environment and ecology

In ecological terms as environments become cooler, more seasonal and often increasingly arid with increasing latitude (or altitude, or effective latitude during glacial phases), survival becomes increasingly dependant on abilities to cope with the challenges imposed by the environment rather than biotic interactions. Both intra and interspecies competition is affected by this latitudinal gradient (Schemske et al. 2009). Thus survival depends on managing and mitigating the notable risks which these environments bring, particularly at the most northerly limits of occupation and during glaciations where effective latitude (in terms of cold and aridity) increases. With increasing latitude resources become more variable seasonally, increasingly patchy and less reliable placing a challenge on hominin occupation (Pearce et al. 2014). Risks to mortality and survival come from several different sources. There are risks to effective reproduction posed by seasonal variations in the resources needed to support pregnancy and lactation for example, variable resources leading to potential famines, extremes of cold which can threaten infant survival, as well as high requirements for mobility to exploit more patchy resources. Dependance on animal food for survival increases with increasing distance from the equator (Johnson 2014), and moreover average prey size increases with cold and increasing latitude (Rodríguez, Olalla-Tárraga, and Hawkins 2008) bringing elevated risks of injury and mortality through injury from hunting as well as through competition with other predators.

Human health, disease and mortality risk in modern ethnographic contexts is strongly correlated with observed changes in ecology occurring with variations in latitude and aridity (Waguespack 2002; Kelly 2013, 200). In warmer and more equatorial environments the risk of mortality from pathogens as well as the health effects of pathogen loads are highest, both due the diversity of pathogens present and to a greater population density of hosts and greater possibilities for transmission. Hot and humid environments are particularly favourable for the spread of pathogens which are commonly the primary cause of hunter-gatherer mortality (Froment 2001) and continue to influence life history and development in modern contexts in complex ways (Magid et al. 2018). As environments become more cold and seasonal with increasing latitude the mortality risk from pathogens reduces. The risks posed by any possibilities of pathogen transmission from healthcare practices also reduce. However, as risks of infectious diseases reduce with increasing latitude, mortality risks from cold, injury and famine rise significantly. For modern Inuit for example the major risks to mortality come from cold, injury and famine, with injury deriving not only from hunting and mobility in difficult terrain but also from the effect which high endurance demands have on wear and degeneration of bone. Around 50% of Inuit from northern Alaska, Canada and Greenland, both historically and in archaeological contexts have spondylitis of the spine due to fatigue and stress fractures for example (Merbs 2002). Moreover hunting accidents caused 15% of the deaths of an ethnographically documented southern Baffin Island group (Ann Mcelroy 2009) despite complex weaponry. In these cooler and more arid environments, healthcare practices are more focused on treating injuries, which both demands more technical knowledge and has greater returns in terms of recovery than the treatment of pathogens and infectious disease.

4.2 Neanderthal physiological and behavioural adaptations

The physiology and anatomy of Neanderthals as whole reflects the selection pressures placed on them from the specific environmental challenges of Late Pleistocene western Eurasia with its associated cold, seasonal and often arid environments. High endurance requirements, frequent famines and the high meat diets influenced their body shape, proportions and physiology. A similar body shape to other populations adapted to cold environments has been noted for some time for example (Ruff 1994; Holliday 1997) and their facial morphology may also be an adaptation to cold and high energy demands (Wroe et al. 2018). A large thorax may be an adaptation to enhanced physical activity (García-Martínez et al. 2014) and a high protein diet (Ben-Dor, Gopher, and Barkai 2016) and likewise physiological adaptations to conserve resources appear to be an adaptation to highly seasonal resource availability and frequent famine (Vernot and Akey 2014; Sankararaman et al. 2016). Furthermore cognitively Neanderthal's large visual cortex may also be an adaptation to selective pressures on identifying and hunting animals in conditions of potentially low visibility (Pearce, Stringer, and Dunbar 2013).

Neanderthals efficiently exploited the food resources available to them. Since they occupied regions with substantial ecological variation in time and space, their diets will have varied accordingly (Fiorenza et al. 2011; El Zaatari et al. 2016). Plant foods appear to have been exploited as and when available and are likely to have formed some component of diets throughout the region occupied (Henry, Brooks, and Piperno 2011; Power et al. 2018). Coastal populations will have been able to rely on less risky marine and intertidal resources, as seen at Gibraltar in the exploitation of shellfish and seals (Cortés-Sánchez et al. 2011). Fish and birds are likely to have been exploited available. (B. L. Hardy and Moncel 2011). In some Mediterranean regions, particularly in interglacial periods, it will even have been possible to depend significantly on plant resources (Salazar-García et al. 2013), and Neanderthals appear to have particularly flourished in these environments (Benito et al. 2017). At El Sidron the dietary profile from dental calculus suggests that a notable component of plant foods contributed to Neanderthal diets for example (Weyrich et al. 2017; Estalrrich, El Zaatari, and Rosas 2017). Neanderthals in mediterranean contexts provide the only known cases of dental caries due to ingestion of carbohydrates in the form of plant resources (Walker et al. 2011).

There is however good evidence for a heavy dependance on a largely meat based diet in most regions. Stable isotope studies (Bocherens et al. 2005; Richards and Trinkaus 2009; Naito et al. 2016), molar macrowear (Fiorenza et al. 2011; El Zaatari et al. 2016; Estalrrich, El Zaatari, and Rosas 2017) and faecal biomarkers (Sistiaga et al. 2014) suggest that Neanderthals outside of the Mediterranean region depended on a largely meat based diet. Faunal remains on archaeological sites also suggest a reliance on large game, which varied accordingly the ecological context, with faunal assemblages typically dominated predominantly by bison, reindeer and horse (Smith 2015) though Neanderthals also exploited megafauna in the form of woolly rhinoceros and mammoth, such as at La Cotte de Ste Brelade (Scott et al. 2015). They were clearly well able to adapt to the different opportunities which large game provided, sometimes hunting individual animals, and at other times focusing on herds, including the hunting of prime age individuals. At Jonsac (Laura Niven et al. 2012) and La Pradelles (Rendu et al. 2012) hunting seems to have focused solely on reindeer for example. Close range hunting with wooden or stone tipped spears seems to have been the norm given environments in which 'running down' prey through heat exhaustion would not have been a feasible strategy (Rhodes and Churchill 2009; Shea and Sisk 2010). Evidence from characteristic impact patterns on fallow deer at Neumark-Nord during the last interglacial confirms the use of close range spears for example (Gaudzinski-Windheuser et al. 2018). A combination of thrusting and close range throwing seems the most likely hunting technique as Neanderthals would have been physically capable of using thrown projectiles (Roach et al. 2013). Repeated throwing behaviour is also the most likely explanation humeral abnormalities in a Neanderthal from Tourville-la-Riviere (Faivre et al. 2014).

Neanderthal's lack of projectile technology has been seen as a potential adaptive disadvantage (Shea and Sisk 2010). However, close encounter hunting, taking advantage of landscape features, despite the high rates of injury, may simply have been the most effective hunting method for the faunal communities which Neanderthals exploited. For many of the larger species exploited by Neanderthals neither long distance spears nor even bow and arrow technology would have had the kinetic energy required to sufficiently pierce skin and flesh. For larger body size prey hand delivered spears and use of physiographic features are the typical means of hunting in modern hunter-gatherer contexts (Churchill 1993), as well as many Upper Palaeolithic contexts such as archaic period bison hunting sites in north americas. Close encounter hunting, using landscape features against which to drive animals explains patterns of mammoths and woolly rhinoceros exploited by Neanderthals at La Cotte de Ste Brelade (Scott et al. 2015). Neanderthals also exploited game which were dangerous to exploit in other ways, such as ibex (*Capra ibex*) and chamois (*Rupicapra rupicapra*), found in particularly difficult terrain (de los Terreros et al. 2014; Yravedra and Cobo-Sánchez 2015).

That the pressures of reliance on meat from large game animals were a pressing adaptive problem in many regions is clear. Whilst plant foods and other resources were undoubtedly a component of diets everywhere, meat as the dominant resource outside of the mediterranean region, and probably to the most extreme degree in late winter and early spring imposes physiological challenges. In open environments, as recorded at Spy, Neanderthals survived on a largely carnivorous diet for example (Weyrich et al. 2017; Estalrrich, El Zaatari, and Rosas 2017). A high protein diet can have serious physiological consequences (Hardy 2010; Hockett 2012; Fiorenza et al. 2015) as is clear from palaeopathologies in Inuit populations (Bishop 2011) which include anaemia caused by excess consumption of meat (Jamieson and Kuhnlein 2008). Likewise a Neanderthal infant from Kiik-Koba appears to have been a victim of vitamin C deficiency for example (Mednikova 2017). What plant materials and fats were available are likely to have been important. Mammoths may have provided important fat from their brain material for example (Agam and Barkai 2016) and Neanderthals may also have diversified their diet by eating vegetable matter from the stomachs of the prey (Buck and Stringer 2014). Selective pressures to adapt to the strains imposed by a high protein diet has also been argued to be the explanation for the large lower thorax of Neanderthals (Ben-Dor, Gopher, and Barkai 2016).

4.3 Neanderthal mortality risk through injury

Given most available biomass in the form of large herbivores in many regions (Daura et al. 2017) a common reliance on hunting large game would clearly be an inevitable part of Neanderthal adaptation in most regions. Requirements for high levels of mobility driven by relying on highly dispersed game (Laura Niven et al. 2012) bring risks of injury in itself, whilst hunting of any animal prey is dangerous, however close encounter hunting of large game demands a high level of collaboration and brings particularly high injury risks (Gaudzinski-Windheuser et al. 2018). The elevated injury rates from close range hunting compared to the use of long range projectiles is evident in ethnographic and archaeological contexts for example (Churchill 1993). Amongst neighbouring prehistoric groups at Point Hope Alaska, the Tigara, reliant on close encounter hunting of bowhead whale, had twice the rates of severe injury than the Ipiutak who were reliant on projectile hunting of caribou (22% vs 12% of skeletal remains showing traumatic injury) (Dabbs 2011). The faunal communities of Late Pleistocene Western Eurasia also brought additional mortality risks for which we have no modern analogs however. The guild of large prey and megafauna present during Neanderthal occupation, including mammoths and woolly rhinoceros would be particularly dangerous prey, easily able to overcome an individual human assailant.

Neanderthals also faced the presence of large carnivores which in turn were dangerous as competitors and as predators and for which we have no modern analogs (Wang et al. 2004). Hyenas (*Crocuta crocuta*), lions (*Panthera spelaea*) and cave bears (*Ursus spelaeus*) would have been the most common large carnivore threats, due to their overlapping habitats and prey choices (Ardèvol and López 2009; Blasco et al. 2010; Dusseldorp 2011). Dangerous encounters with leopards (*Panthera pardus*) and wolves (*Canis lupus*) seem to have been less frequent (Camarós et al. 2017)). Unfortunately, it is not an easy task to determine from the archaeological record whether the carnivore damage discovered in several sites are the result of scavenging activity or from a direct confrontation, but the latter is reliably recognised in several cases (Fernández-Lomana, López, and Moreno 2010; Camarós, Cueto, et al. 2016; Camarós et al. 2017). Conflicts with such predators were extremely dangerous and could lead to death or severe injuries, as also demonstrated by forensic studies on current-day carnivore attacks (Camarós, Cueto, et al. 2016). The effects of carnivore attacks can be significant and in modern contexts are more likely to lead to mortality in women and children (Treves and Naughton-Treves 1999).

Interactions between hominin and large carnivores will have occured in a variety of contexts, and across the whole range of Neanderthal occupation, not only through competition for resources, but also potential occupation sites in caves (Conard 2011; Stiner 2012; Camarós, Münzel, et al. 2016; E. Camarós et al. 2017). Neanderthals occupied cave sites also favoured by carnivores, with faunal accumulations in these locations deriving from both (Rufà et al. 2017). Equally cave bears often occupy caves also frequented by Neanderthals, such as in the Swabian Jura for example (Conard, Bolus, and Münzel 2012). Neanderthals may have been unlikely to have been a chosen prey, with other animals bringing a lower risk of mortality and it also seems unlikely that large carnivores were hunted to obtain hides (Camarós, Münzel, et al. 2016) or to produce bone ornaments and bone tools

(Abrams et al. 2014; L. Niven 2006). Nonetheless close interactions with large carnivores brought considerable injury risks (Camarós, Münzel, et al. 2016).

The nature and impact of injury risks may have varied according age or gender. The extent to which any particular individuals may have been protected from the mortality risk imposed through hunting large game and competing with large carnivorans, or indeed differentially exposed to such risks, remains in debate however. Inexperienced adolescents are likely have been at particular risk of injury in close encounter hunting, with their loss particularly costly in terms of energetic investments against future returns. Whether Neanderthals had a gender based division of labour also remains an area of debate (Kuhn et al. 2006; Balme and Bowdler 2006; Estalrrich and Rosas 2015). A gender based division of labour exists in modern ethnographic contexts, however this doesn't preclude women's hunting and women in many such contexts are expert hunters, albeit of smaller and less dangerous game than men (Goodman et al. 1985; Kelly 2013). Women may however equally have been more involved in hide preparation, as suggested by dental wear studies (Estalrrich and Rosas 2015). The reduced mobility of a pregnant female from Isernia inferred from strontium isotope studies (Lugli et al. 2017) suggests that pregnant women (perhaps alongside infants and the injured) may have protected from the costs of travelling long distances in search of food resources, and perhaps also mortality risks from hunting. Nonetheless some involvement of females as well as males in dangerous hunting has been argued to explain the limited evidence for similar injuries across both genders (Kuhn et al. 2006).

The broader impact of mortality risks through injury in to Neanderthal ecology is rarely considered. However in other species reliant on hunting such risks are highly significant and drive biological and behavioural adaptations. Mortality risks from injury typically play a significant role in prey choice of predators in general (Mukherjee and Heithaus 2013). African wild dogs can be killed or severely injured by the herbivores which they hunt for example (Creel and Creel 2002). Predators such as lions are not only less efficient foragers when injured but also can be killed by their competitors (Mukherjee and Heithaus 2013). Severe injuries bring a high risk of mortality, and predators will avoid not only dangerous prey, but habitats which are dangerous, either because of the risks of being killed by other predators or because of the risk of injury in moving through complex terrain. Few predators prey on ibex for example as they reduce their predation risks by occupying steep shelves and rugged habitats in which predators run a notable risk of injury (Kotler, Gross, and Mitchell 1994). Wolves often avoid dangerous prey, particularly if lacking older animals with necessary knowledge and skills to avoid injury (MacNulty 2002; Stahler, Smith, and Guernsey 2006), and wolf packs which have lost older members tend to no longer be able to hunt dangerous prey such as bison or moose (Dutcher and Dutcher 2018; Sand et al. 2006). Perhaps most significantly it is in those packs which hunt dangerous prey, and rely on accumulated knowledge, that wolves are most likely to compensate for mortality risk through injury by caring for and provisioning the injured (Barber-Meyer et al. 2016). In comparison hominins are more naturally vulnerable to injury than carnivores, faced more significant adaptive pressures to improve the survival of their own injured group members and moreover had a far greater cognitive capacity to find the means to reduce mortality risks.

4.4 The influence of behavioural adaptations on selective pressures to reduce mortality risks

Various elements of their unique behavioural ecology will have increased the significance of reducing mortality risks through healthcare to Neanderthals, perhaps even progressively so as they become more adapted to a niche which may have *depended* on healthcare provisioning. Most notably their robust body sizes and high energy requirements (Churchill 2014) will have placed additional pressures on ensuring adequate resources through hunting success. These same high energy requirements will also have limited group sizes and so increased interdependence, and the significance of any individual mortality to survival. Evidence from El Sidron of a group apparently made up of around thirteen individuals, three related males, four females, three adolescent boys and three infants is one potentially good example (Lalueza-Fox et al. 2011). The loss of even one adult hunter in such a circumstance may be enough to make any such group unviable, whilst their high relatedness would act to increase the selective advantages of helping others in the group. High levels of relatedness, with half sibling matings common (Prüfer et al. 2014), also brings with it other pressures on healthcare provisioning. Low genetic fitness, caused by high levels of inbreeding (Sánchez-Quinto and Lalueza-Fox 2015; Simons and Sella 2016) brings higher incidences of pathologies which are likely to have required care and support (Dean et al. 2013; Juric, Aeschbacher, and Coop 2016; Simons and Sella 2016). Whether prion diseases from cannibalistic practices added to the disease load remains unclear (Mead et al. 2003).

A particular dependance on the high levels of skill and the technological competence required in acquiring difficult resources in colder and more seasonal environments (Bamforth and Bleed 1997; Bleed 1986) will also have increased the advantages of survival of older and even partially disabled group members to Neanderthals. Hunting efficiency, and thus resource acquisition, increases with age in modern hunter-gatherer contexts even where prey are not particularly dangerous (Walker et al. 2002), and this ‘learning curve’ is likely to have been even steeper for Neanderthals, particularly where variable environments also adds to the relative advantage of knowledge built up over long periods. The knowledge, skills and experience required both in healthcare in general and in care related to assisting births, and keeping babies and infants alive in cold conditions should also not be underestimated. By extending life expectancies through healthcare following injuries the group knowledge and experience of how to deal with many different challenges, particularly in difficult or unusual circumstances, will have increased. Moreover any increased dependence on the knowledge of older members with the greatest life experience will have made care practices all the more necessary to survival.

4.5 Interpersonal violence as an additional pressure on healthcare provisioning to reduce mortality risk

Other social factors which may also have influenced the relative adaptive advantages of healthcare provisioning but remain as yet difficult to define. Most particularly any interpersonal violence will also have increased the risk of mortality from injury. Lethal interpersonal violence has been recorded in pre-Neanderthal populations at Sima de los Huesos where cranium 16 shows evidence of several blunt force trauma blows to the frontal bone (Sala et al. 2015). For Neanderthals themselves there are two recorded instances of likely interpersonal violence, one individual from St Cesaire (Zollikofer et al. 2002) and one from Shanidar (Shanidar 3) (Churchill et al. 2009b). The former suffered a blunt force head wound (from which they recovered) and the latter a projectile point injury, most probably from modern human projectiles, which appear to have led to death several days later. Interpersonal violence may of course also elevate the pressure to provide effective healthcare from injury, however whether interpersonal violence was a significant mortality risk remains unclear. Rates of violence in modern hunter-gatherers are notoriously variable, with some African groups having no recorded cases, whilst violence is far more frequent in others (Hill, Hurtado, and Walker 2007; Wrangham, Wilson, and Muller 2006; Lee 2014; Lomas 2009). Very low population densities (Bocquet-Appel and Degioanni 2013; Sánchez-Quinto and Lalueza-Fox 2015) would argue against any significant territorial aggression (it would be quite simply impossible to ‘police’ a territory and accidental encounters with other groups would be rare) whilst high genetic relatedness (Prüfer et al. 2014; Harris and Nielsen 2016) argues against excessive intragroup aggression.

Some attention has been given to injury profiles, the distribution of injuries across the skeleton, as potential source of evidence for the injury risks from different activities. A greater prevalence of injuries to the head and upper body in Neanderthal skeletal material, appeared to be similar to that seen in adult rodeo riders and supported an interpretation of the majority of injuries being sustained through direct engagement with large and dangerous prey (Berger and Trinkaus 1995). This interpretation remains debated however (Trinkaus 2012), Different physiologies make such comparisons difficult, particularly as the injury profile in adolescent rodeo riding is notably different (Stoneback, Trizno, and Albright 2018). Similar injury profiles also characterise pathologies in skeletal remains throughout the Pleistocene (Wu et al. 2011) suggesting the differential preservation may be a more likely explanation for this pattern. Injury profiles warrant further research, and whilst engagements with prey undoubtedly played an important role in injury risk, moving across difficult terrain (such as when hunting ibex, (de los Terreros et al. 2014; Yravedra and Cobo-Sánchez 2015) are also likely to have had a part to play in Neanderthal injury rates, alongside interactions with carnivores and any interpersonal violence. Thus whilst the significance of close range hunting and engagements with dangerous predators to neanderthal mortality risks remains clear, that of interpersonal violence is still an issue of debate.

Whatever the precise relative contribution of injury risks from interpersonal violence, risk of mortality from injury was clearly significant to Neanderthal survival.

4.6 Healthcare provisioning as an adaptive response to mortality risks

By improving their survival from injuries through healthcare provisioning Neanderthals would have been able to mitigate the effects of these significant injury risks. Deaths of productive adults would pose serious consequences in small groups with young who would be dependant for long periods as well as affecting reproductive capacity. Moreover surviving any injury which reduced mobility in the context of such highly efficient predators would be unlikely if isolated from group support. In simple terms healthcare, even for only a few days or weeks, would be the difference between death and survival for a Neanderthal with an injured arm or leg, and who would unable to hunt or easily escape predators alone.

Few would question that a human occupation of much of Western Eurasia was reliant on hunting technology, shelter, fire or clothing, nor that Neanderthals relied on knowledge, skill and technological understanding to acquire the large herbivores which made up much of their diet in most of the regions occupied. However the implications of reducing mortality risks through healthcare provisioning has yet to be seen in adaptive terms, even though Neanderthals will have experienced notable selective pressures to reduce mortality risk from several causes (see *table 2*). In cooler and more arid environments in particular it is difficult to imagine any greater pressures on abilities to buffer injury risks through whatever means, including through healthcare provisioning. However pressures from predation and hunting in difficult terrain will also have lead to high risks of injury and mortality in even the most favourable environments.

Caring for ill and injured group members is part of being human. However such healthcare may have been key to particularly key to making the injury risks imposed by high mobility, hunting of large game, and engagements with predators within small groups of robustly built and closely related archaic humans sustainable.

Environmental pressures on reducing mortality risk from injury	**Neanderthal adaptations increasing selective pressures to reduce mortality risk from injury**
North temperate environments > ● Increased mortality risk from cold including risk to vulnerable infants ● Increased injury and mortality risks from high mobility in cold environments ● Injury risks from hunting large mammals ● Stress related injuries from endurance activities ● Risky, seasonal and unreliable resources, placing pressures on hunting success (few second chances) and on ensuring sustained resources for pregnancy, lactation and young infants *Contemporary environments in Western Eurasia >* ● Low plant biomass and higher animal biomass leading to dependence on hunting (placing hunters under risk of injury) ● Megafaunal herbivores (such as bison, mammoth and woolly rhinoceros) are more dangerous than smaller animals ● Exceptionally large carnivorans (such as sabre cats) increase injury risk from competition and from predator attacks	*Demography >* ● Small group sizes imply increased interdependence (the loss of one individual has a greater effect within a smaller group) ● High degree of relatedness within groups favours greater investments in the wellbeing of others. ● High degree of relatedness increases risk of certain genetic diseases and conditions *Resource exploitation >* ● Close encounter hunting increases risk of injury through direct engagement with prey ● Reliance on skilled hunting implies that hunting efficiency increases with age, increasing relative payoffs for survival of older members of the group ● Vulnerability of offspring to cold and predation increases reliance on infant care skills and knowledge of older group members

Table 2. The effects of environment and adaptation on pressures to reduce mortality risk from injury in Neanderthals

5. The implications of healthcare provisioning as an adaptive response to mortality risks

A strategy of mitigating injury and mortality risk through healthcare provisioning would explain several previously enigmatic elements of Neanderthal behaviour.

Most obviously healthcare provisioning explains how Neanderthals were able to occupy a predatory niche in competition with large carnivores from which the risk of mortality from injury would otherwise have precluded them. Neanderthal's 'punch above their weight' as a predator and tackle far larger game than ecological models would suggest should be possible for example (Dusseldorp 2012). Moreover recorded injury rates in other predators are significantly lower and injuries typically less severe than those seen in Neanderthals. Injury rates in birds of prey (such as broken toes, talons, flight feathers and injured eyes) vary between around 6-19%, whilst around 5-10% of large cats have fractured canines (see Mukherjee and Heithaus 2013). In contrast almost almost all Neanderthals seem to have suffered at least one severe injury, with many suffering several instances of injury or illness. It even seems to have been rare to reach adulthood without a significant injury (Trinkaus and Zimmerman 1982; Berger and Trinkaus 1995; Pettitt 2000). Nakahashi estimates that the rate of individuals suffering serious traumatic injury before death may have been as high as 80-95% of the population (Nakahashi 2017). Since injury rates for other predators are limited by a lack of actualistic studies of injuries occurring in wild populations, and the estimates for Neanderthal injury are based on a skeletal record which is inevitably biased through selective mortuary practices and survival (see (Spikins et al. 2014)), we may be cautious about using specific estimates. Nonetheless Neanderthals appear to have used healthcare provisioning to sustain an injury rate which is *unusually high* within a broader evolutionary context.

By 'living to fight another day' after injury Neanderthals will have accumulated their characteristic pattern of several episodes of severe injury on a scale which is not recorded in either other predators or in other primates. Modern humans whose environments also impose high rates of injuries and who provide healthcare similarly reflect this pattern albeit on a less extreme scale. Lessa for example notes that 27% of coastal hunter-gather-fishers in pre-colonial contexts in Brazil showed evidence of severe fractures which had healed, most commonly caused by falls in difficult coastal terrain, and 11.5% had multiple instances of fractures (Lessa 2011). Surviving injuries from which they might otherwise have died has far reaching effects. Such survival for example extends the age profile of modern hunter-gatherers, allowing a third generation to have an influence on the communication of culture (Hill, Hurtado, and Walker 2007) and may have had similarly notable effects on Neanderthals.

Neanderthal's ability to take on more risk than any similar predator may even explain their apparently daring (or blazé) attitudes to tackling prime adult adults at various sites (White, Pettitt, and Schreve 2016), whilst other predators by necessity would focus on the weak and vulnerable.

6. The wider evolutionary significance of healthcare provisioning

Healthcare provisioning clearly affects the ecology and evolution of hominins, as perhaps seen most clearly in Neanderthals. It might be tempting to further conclude that these archaic humans further displayed some kind of cognitive adaptation to a high risk, high injury niche. Genes regulating dopamine production, and influencing patterns of risk taking, have been influenced by patterns of palaeolithic migration (Chen et al. 1999; Matthews and Butler 2011) and even historical subsistence practices (Kidd, Pakstis, and Yun 2014) for example. However a broader perspective on pro-social behaviour would instead suggest that pro-sociality has been integral to human adaptation from much earlier periods, with substantial behavioural plasticity of pro-social behaviour according to context part of that adaptation (House et al. 2013; Rajhans et al. 2016). In modern contexts high risk environments increase propensities to altruism though normal behavioural plasticity according to context (Li et al. 2013) as does dependance on collaborative hunting of very large and dangerous game (whale hunting, (Heinrich et al. 2004)). In cognitive terms, Neanderthal's willingness to care for injured and ill group members, apparently regardless of costs, most likely reflects simply that they were humans coping with the particular challenges that their lifestyles entailed.

The longer evolutionary history of healthcare provisioning is nonetheless likely to have influenced the path of human evolution in various different ways (Bastir 2018). Healthcare can have a direct effect, such as in the relationship between foetal brain size and pelvis shape in Neanderthals, implying a characteristic half turn of a foetus at birth which is unlikely to have evolved without assisted births (de León et al. 2008). However even provision of moderate care can influence the selective advantages and disadvantages of genes linked to several traits, such as local adaptation of the TRPM8 cold receptor gene with increasing latitude, which whilst protecting from effects of cold is also associated with migraine susceptibility (Key et al. 2018). Care can also have subtle and complex effects of selection pressures, such as pressures to be pro-social and affiliative (Hare 2017), or to express subtle indicators of friendliness and vulnerability (Godinho, Spikins, and O'Higgins 2018). Positive selection for autism genes may also imply a level of social support for those who bring additional skills but may need more support (Spikins, Wright, and Hodgson 2016; Polimanti and Gelernter 2017). Healthcare provisioning is likely to have affected many realms, from anatomy to physiology to cognition and further research might help us to understand these wider evolutionary implications of healthcare provisioning both in Neanderthal populations and beyond.

7. Conclusions

Care for ill and injured group members is likely to have been part of human adaptation since at least the emergence of the genus Homo. Like food sharing, collaborative defence, collaborative hunting and collaborative parenting, healthcare provisioning will have functioned to mitigate risks in highly collaborative and interdependent groups.

For Neanderthals healthcare provisioning may have been essential to survival. They will have faced unique ecological challenges, not only directly from risky and unreliable environments but also from the injury risks imposed by the need to exploit large and dangerous game animals in competition with exceptionally large predators. Particularly high pressures will have been placed on the means to reduce mortality risk, including through healthcare provisioning. Added to which Neanderthal adaptations, including high energy requirements, small closely related groups, and a dependence on skills and knowledge to exploit resources, will also have elevated the risks from loss of any group members and the relative benefits of healthcare provisioning. Visible cases of 'costly' care in the archaeological record are likely to be the tip of the iceberg of far more common cases of more minor injuries requiring care and provisioning to ensure survival.

We argue that healthcare provisioning is a previously unrecognised and significant adaptation which improved survival in hominins in general, influenced human evolution in other realms, and was particularly significant to the viability of Neanderthal occupation.

8. Acknowledgements

This work was partially supported by the John Templeton Foundation [59475] (contributions by Penny Spikins and Andrew Needham)

References

Abrams, Grégory, Silvia M. Bello, Kévin Di Modica, Stéphane Pirson, and Dominique Bonjean. 2014. “When Neanderthals Used Cave Bear (Ursus Spelaeus) Remains: Bone Retouchers from Unit 5 of Scladina Cave (Belgium).” *Quaternary International: The Journal of the International Union for Quaternary Research* 326-327 (April): 274–87.

Agam, Aviad, and Ran Barkai. 2016. “Not the Brain Alone: The Nutritional Potential of Elephant Heads in Paleolithic Sites.” *Quaternary International: The Journal of the International Union for Quaternary Research* 406, Part B (June): 218–26.

Ann Mcelroy, Patricia K. Townsend. 2009. *Medical Anthropology in Ecological Perspective: Fifth Edition*.

Ardèvol, Jordi Rosell, and Ruth Blasco López. 2009. “Home Sharing: Carnivores in Anthropogenic Assembalges of the Middle Pleistocene.” *Journal of Taphonomy* 7 (4): 305–24.

Arsuaga, J. L., V. Villaverde, R. Quam, I. Martínez, J. M. Carretero, C. Lorenzo, and A. Gracia. 2007. “New Neandertal Remains from Cova Negra (Valencia, Spain).” *Journal of Human Evolution* 52 (1): 31–58.

Bailey, R. C. 1991. “The Behavioral Ecology of Efe Pygmy Men in the Ituri Forest, Zaire, Anthropological Papers, Museum of Anthropology, University of Michigan No. 86.” *Ann Arbor*.

Balme, Jane, and Sandra Bowdler. 2006. “Spear and Digging Stick: The Origin of Gender and Its Implications for the Colonization of New Continents.” *Journal of Social Archaeology* 6 (3): 379–401.

Bamforth, D. B., and P. Bleed. 1997. “Technology, Flaked Stone Technology, and Risk.” *Archeological Papers of the American*. http://onlinelibrary.wiley.com/doi/10.1525/ap3a.1997.7.1.109/full.

Barber-Meyer, Shannon M., L. David Mech, Wesley E. Newton, and Bridget L. Borg. 2016. “Differential Wolf-Pack-Size Persistence and the Role of Risk When Hunting Dangerous Prey.” *Behaviour* 153 (12): 1473–87.

Bastir, Markus. 2018. “Pulling Faces.” *Nature Ecology & Evolution*, April. https://doi.org/10.1038/s41559-018-0550-2.

Ben-Dor, Miki, Avi Gopher, and Ran Barkai. 2016. “Neandertals’ Large Lower Thorax May Represent Adaptation to High Protein Diet.” *American Journal of Physical Anthropology* 160 (3): 367–78.

Benito, Blas M., Jens-Christian Svenning, Trine Kellberg-Nielsen, Felix Riede, Graciela Gil-Romera, Thomas Mailund, Peter C. Kjaergaard, and Brody S. Sandel. 2017. “The Ecological Niche and Distribution of Neanderthals during the Last Interglacial.” *Journal of Biogeography* 44 (1): 51–61.

Berger, L. R., and W. S. McGraw. 2007. “Further Evidence for Eagle Predation Of, and Feeding Damage On, the Taung Child.” *South African Journal of Science* 103 (11-12): 496–98.

Berger, Thomas D., and Erik Trinkaus. 1995. “Patterns of Trauma among the Neandertals.” *Journal of Archaeological Science* 22 (6): 841–52.

Bishop, K. 2011. “Thule Palaeopathology: The Health Concerns of an Arctic Lifestyle.” *Totem: The University of Western Ontario Journal of*. http://ir.lib.uwo.ca/cgi/viewcontent.cgi?article=1115&context=totem.

Blasco, Ruth, Jordi Rosell, Juan Luis Arsuaga, José M. Bermúdez de Castro, and Eudald Carbonell. 2010. “The Hunted Hunter: The Capture of a Lion (Panthera Leo Fossilis) at the Gran Dolina Site, Sierra de Atapuerca, Spain.” *Journal of Archaeological Science* 37 (8): 2051–60.

Bleed, Peter. 1986. “The Optimal Design of Hunting Weapons: Maintainability or Reliability.” *American Antiquity* 51 (4): 737–47.

Bocherens, Hervé, Dorothée G. Drucker, Daniel Billiou, Marylène Patou-Mathis, and Bernard Vandermeersch. 2005. “Isotopic Evidence for Diet and Subsistence Pattern of the Saint-Césaire I Neanderthal: Review and Use of a Multi-Source Mixing Model.” *Journal of Human Evolution* 49 (1): 71–87.

Bocquet-Appel, Jean-Pierre, and Anna Degioanni. 2013. “Neanderthal Demographic Estimates.” *Current Anthropology* 54 (S8): S202–13.

Bonmatí, Alejandro, Asier Gómez-Olivencia, Juan-Luis Arsuaga, José Miguel Carretero, Ana Gracia, Ignacio Martínez, Carlos Lorenzo, José María Bérmudez de Castro, and Eudald Carbonell. 2010. “Middle Pleistocene Lower Back and Pelvis from an Aged Human Individual from the Sima de Los Huesos Site, Spain.” *Proceedings of the National Academy of Sciences* 107 (43): 18386–91.

Bonmatí, Alejandro, Asier Gómez Olivencia, Juan Luis Arsuaga, José Miguel Carretero, Ana Gracia, Ignacio Martínez, and Carlos Lorenzo. 2011. “El Caso de Elvis El Viejo de La Sima de Los Huesos.” *Dendra Médica. Revista de Humanidades* 10 (2): 138–46.

Brantingham, P. Jeffrey. 1998. “Hominid–Carnivore Coevolution and Invasion of the Predatory Guild.”

Journal of Anthropological Archaeology 17 (4): 327–53.
Buck, Laura T., and Chris B. Stringer. 2014. “Having the Stomach for It: A Contribution to Neanderthal Diets?” *Quaternary Science Reviews* 96: 161–67.
Burkart, Judith M., Carel van Schaik, and Michael Griesser. 2017. “Looking for Unity in Diversity: Human Cooperative Childcare in Comparative Perspective.” *Proceedings. Biological Sciences / The Royal Society* 284 (1869). https://doi.org/10.1098/rspb.2017.1184.
Camarós, E., M. Cueto, L. Teira, Susanne C. Münzel, F. Plassard, P. Arias, and F. Rivals. 2017. “Bears in the Scene: Pleistocene Complex Interactions with Implications Concerning the Study of Neanderthal Behavior.” *Quaternary International: The Journal of the International Union for Quaternary Research*. https://doi.org/10.1016/j.quaint.2015.11.027.
Camarós, Edgard, Marián Cueto, Carlos Lorenzo, Valentín Villaverde, and Florent Rivals. 2016. “Large Carnivore Attacks on Hominins during the Pleistocene: A Forensic Approach with a Neanderthal Example.” *Archaeological and Anthropological Sciences*, 1–12.
Camarós, Edgard, Susanne C. Münzel, Marián Cueto, Florent Rivals, and Nicholas J. Conard. 2016. “The Evolution of Paleolithic Hominin–carnivore Interaction Written in Teeth: Stories from the Swabian Jura (Germany).” *Journal of Archaeological Science: Reports* 6 (April): 798–809.
Castellano, Sergi, Genís Parra, Federico A. Sánchez-Quinto, Fernando Racimo, Martin Kuhlwilm, Martin Kircher, Susanna Sawyer, et al. 2014. “Patterns of Coding Variation in the Complete Exomes of Three Neandertals.” *Proceedings of the National Academy of Sciences of the United States of America* 111 (18): 6666–71.
Chen, Chuansheng, Michael Burton, Ellen Greenberger, and Julia Dmitrieva. 1999. “Population Migration and the Variation of Dopamine D4 Receptor (DRD4) Allele Frequencies Around the Globe.” *Evolution and Human Behavior: Official Journal of the Human Behavior and Evolution Society* 20 (5): 309–24.
Churchill, Steven E. 1993. “Weapon Technology, Prey Size Selection, and Hunting Methods in Modern Hunter-Gatherers: Implications for Hunting in the Palaeolithic and Mesolithic.” *Archeological Papers of the American Anthropological Association* 4 (1): 11–24.
———. 2014. *Thin on the Ground: Neandertal Biology, Archeology and Ecology*. John Wiley & Sons.
Churchill, Steven E., Robert G. Franciscus, Hilary A. McKean-Peraza, Julie A. Daniel, and Brittany R. Warren. 2009a. “Shanidar 3 Neandertal Rib Puncture Wound and Paleolithic Weaponry.” *Journal of Human Evolution* 57 (2): 163–78.
———. 2009b. “Shanidar 3 Neandertal Rib Puncture Wound and Paleolithic Weaponry.” *Journal of Human Evolution* 57 (2): 163–78.
Clay, Zanna, and Frans B. M. de Waal. 2013. “Bonobos Respond to Distress in Others: Consolation across the Age Spectrum.” *PloS One* 8 (1): e55206.
Conard, Nicholas J. 2011. “The Demise of the Neanderthal Cultural Niche and the Beginning of the Upper Paleolithic in Southwestern Germany.” In *Neanderthal Lifeways, Subsistence and Technology: One Hundred Fifty Years of Neanderthal Study*, edited by Nicholas J. Conard and Jürgen Richter, 223–40. Dordrecht: Springer Netherlands.
Conard, Nicholas J., Michael Bolus, and Susanne C. Münzel. 2012. “Middle Paleolithic Land Use, Spatial Organization and Settlement Intensity in the Swabian Jura, Southwestern Germany.” *Quaternary International: The Journal of the International Union for Quaternary Research* 247 (January): 236–45.
Condemi, Silvana, Aurélien Mounier, Paolo Giunti, Martina Lari, David Caramelli, and Laura Longo. 2013. “Possible Interbreeding in Late Italian Neanderthals? New Data from the Mezzena Jaw (Monti Lessini, Verona, Italy).” *PloS One* 8 (3): e59781.
Condemi, Silvana, Delphine Tardivo, Bruno Foti, Stefano Ricci, Paolo Giunti, and Laura Longo. 2012. “A Case of an Osteolytic Lesion on an Italian Neanderthal Jaw.” *Comptes Rendus. Palevol* 11 (1): 79–83.
Cortés-Sánchez, Miguel, Arturo Morales-Muñiz, María D. Simón-Vallejo, María C. Lozano-Francisco, José L. Vera-Peláez, Clive Finlayson, Joaquín Rodríguez-Vidal, et al. 2011. “Earliest Known Use of Marine Resources by Neanderthals.” *PloS One* 6 (9): e24026.
Cowgill, L. W., M. B. Mednikova, A. P. Buzhilova, and Erik Trinkaus. 2015. “The Sunghir 3 Upper Paleolithic Juvenile: Pathology versus Persistence in the Paleolithic.” *International Journal of Osteoarchaeology* 25 (2): 176–87.
Creel, Scott, and Nancy Marusha Creel. 2002. *The African Wild Dog: Behavior, Ecology, and Conservation*. Princeton University Press.
Crubézy, Eric, and Erik Trinkaus. 1992. “Shanidar 1: A Case of Hyperostotic Disease (DISH) in the Middle Paleolithic.” *American Journal of Physical Anthropology* 89 (4): 411–20.
Cunha, Eugénia. 2016. “Compassion between Humans since When? What the Fossils Tell Us.”

Etnografica: Revista Do Centro de Estudos de Antropologia Social, no. vol. 20 (3) (October): 653–57.
Dabbs, Gretchen R. 2011. “Health Status among Prehistoric Eskimos from Point Hope, Alaska.” *American Journal of Physical Anthropology* 146 (1): 94–103.
Dalén, Love, Ludovic Orlando, Beth Shapiro, Mikael Brandström-Durling, Rolf Quam, M. Thomas P. Gilbert, J. Carlos Díez Fernández-Lomana, Eske Willerslev, Juan Luis Arsuaga, and Anders Götherström. 2012. “Partial Genetic Turnover in Neandertals: Continuity in the East and Population Replacement in the West.” *Molecular Biology and Evolution* 29 (8): 1893–97.
Daura, J., M. Sanz, E. Allué, M. Vaquero, J. M. López-García, A. Sánchez-Marco, R. Domènech, et al. 2017. “Palaeoenvironments of the Last Neanderthals in SW Europe (MIS 3): Cova Del Coll Verdaguer (Barcelona, NE of Iberian Peninsula).” *Quaternary Science Reviews* 177 (December): 34–56.
Dawson, James E., and Erik Trinkaus. 1997. “Vertebral Osteoarthritis of the La Chapelle-Aux-Saints 1 Neanderthal.” *Journal of Archaeological Science* 24 (11): 1015–21.
Dean, M. C., A. Rosas, A. Estalrrich, A. García-Tabernero, R. Huguet, C. Lalueza-Fox, M. Bastir, and M. de la Rasilla. 2013. “Longstanding Dental Pathology in Neandertals from El Sidrón (Asturias, Spain) with a Probable Familial Basis.” *Journal of Human Evolution* 64 (6): 678–86.
DeHaven, K. E., and D. M. Lintner. 1986. “Athletic Injuries: Comparison by Age, Sport, and Gender.” *The American Journal of Sports Medicine* 14 (3): 218–24.
Demuru, Elisa, Pier Francesco Ferrari, and Elisabetta Palagi. 2018. “Is Birth Attendance a Uniquely Human Feature? New Evidence Suggests That Bonobo Females Protect and Support the Parturient.” *Evolution and Human Behavior: Official Journal of the Human Behavior and Evolution Society*, May. https://doi.org/10.1016/j.evolhumbehav.2018.05.003.
Dennell, Robin W., María Martinón-Torres, and José M. Bermúdez de Castro. 2011. “Hominin Variability, Climatic Instability and Population Demography in Middle Pleistocene Europe.” *Quaternary Science Reviews* 30 (11): 1511–24.
Diedrich, C. 2014. “Ice Age Spotted Hyenas as Neanderthal Exhumers and Scavengers in Europe.” *Chronicles Sci* 1: 1–34.
Domínguez-Rodrigo, M., H. T. Bunn, A. Z. P. Mabulla, E. Baquedano, D. Uribelarrea, A. Pérez-González, A. Gidna, et al. 2014. “On Meat Eating and Human Evolution: A Taphonomic Analysis of BK4b (Upper Bed II, Olduvai Gorge, Tanzania), and Its Bearing on Hominin Megafaunal Consumption.” *Quaternary International: The Journal of the International Union for Quaternary Research* 322–323 (February): 129–52.
Doolan, Sean Gregory. 2011. “A Critical Examination of the Bone Pathology of KNM-ER 1808, a 1.6 Million Year Old Homo Erectus from Koobi Fora, Kenya.” New Mexico State University.
Dusseldorp, Gerrit Leendert. 2011. “Studying Pleistocene Neanderthal and Cave Hyena Dietary Habits: Combining Isotopic and Archaeozoological Analyses.” *Journal of Archaeological Method and Theory* 18 (3): 224–55.
———. 2012. “Studying Prehistoric Hunting Proficiency: Applying Optimal Foraging Theory to the Middle Palaeolithic and Middle Stone Age.” *Quaternary International: The Journal of the International Union for Quaternary Research* 252 (February): 3–15.
Dutcher, Jim, and Jamie Dutcher. 2018. *The Wisdom of Wolves*. Simon and Schuster.
El Zaatari, Sireen, Frederick E. Grine, Peter S. Ungar, and Jean-Jacques Hublin. 2016. “Neandertal versus Modern Human Dietary Responses to Climatic Fluctuations.” *PloS One* 11 (4): e0153277.
Errico, Francesco d’, and María Fernanda Sánchez Goñi. 2003. “Neandertal Extinction and the Millennial Scale Climatic Variability of OIS 3.” *Quaternary Science Reviews* 22 (8): 769–88.
Estabrook, V. Hutton, and David W. Frayer. 2013. “Trauma in the Krapina Neandertals: Violence in the Middle Palaeolithic?” In *The Routledge Handbook of the Bioarchaeology of Human Conflict*, edited by Christopher Knüsel And Martin. taylorfrancis.com.
Estabrook, Virginia Hutton. 2009. “Sampling Biases and New Ways of Addressing the Significance of Trauma in Neandertals.” University of Michigan. http://search.proquest.com/openview/d7e6160b60b5fbc39d0d6faa00c5b978/1?pq-origsite=gscholar&cbl=18750&diss=y.
Estalrrich, Almudena, Sireen El Zaatari, and Antonio Rosas. 2017. “Dietary Reconstruction of the El Sidrón Neandertal Familial Group (Spain) in the Context of Other Neandertal and Modern Hunter-Gatherer Groups. A Molar Microwear Texture Analysis.” *Journal of Human Evolution* 104 (March): 13–22.
Estalrrich, Almudena, and Antonio Rosas. 2015. “Division of Labor by Sex and Age in Neandertals: An Approach through the Study of Activity-Related Dental Wear.” *Journal of Human Evolution* 80 (March): 51–63.

Fabrega, H., Jr. 1997. “Earliest Phases in the Evolution of Sickness and Healing.” *Medical Anthropology Quarterly* 11 (1): 26–55.
Fabre, Virginie, Silvana Condemi, and Anna Degioanni. 2009. “Genetic Evidence of Geographical Groups among Neanderthals.” *PloS One* 4 (4): e5151.
Faivre, Jean-Philippe, Bruno Maureille, Priscilla Bayle, Isabelle Crevecoeur, Mathieu Duval, Rainer Grün, Céline Bemilli, et al. 2014. “Middle Pleistocene Human Remains from Tourville-La-Rivière (Normandy, France) and Their Archaeological Context.” *PloS One* 9 (10): e104111.
Fashing, Peter J., and Nga Nguyen. 2011. “Behavior toward the Dying, Diseased, or Disabled among Animals and Its Relevance to Paleopathology.” *International Journal of Paleopathology* 1 (3–4): 128–29.
Fennell, Karen J., and Erik Trinkaus. 1997. “Bilateral Femoral and Tibial Periostitis in the La Ferrassie 1 Neanderthal.” *Journal of Archaeological Science* 24 (11): 985–95.
Fernández-Lomana, Juan Carlos Díez, Sandra Pérez López, and Jorge Martínez Moreno. 2010. “Restos de Neandertales Y Hiénidos En La Península Ibérica.” *Zona Arqueológica*, no. 13: 230–44.
Finlayson, Clive, and José S. Carrión. 2007. “Rapid Ecological Turnover and Its Impact on Neanderthal and Other Human Populations.” *Trends in Ecology & Evolution* 22 (4): 213–22.
Finlayson, Clive, Darren A. Fa, Geraldine Finlayson, Francisco Giles Pacheco, and Joaquin Rodríguez Vidal. 2004. “Did the Moderns Kill off the Neanderthals? A Reply to F. d’Errico and Sánchez Goñi.” *Quaternary Science Reviews* 23 (9-10): 1205–9.
Finlayson, Clive, Francisco Giles Pacheco, Joaquín Rodríguez-Vidal, Darren A. Fa, José María Gutierrez López, Antonio Santiago Pérez, Geraldine Finlayson, et al. 2006. “Late Survival of Neanderthals at the Southernmost Extreme of Europe.” *Nature* 443 (7113): 850–53.
Fiorenza, Luca, Stefano Benazzi, Amanda G. Henry, Domingo C. Salazar-García, Ruth Blasco, Andrea Picin, Stephen Wroe, and Ottmar Kullmer. 2015. “To Meat or Not to Meat? New Perspectives on Neanderthal Ecology.” *American Journal of Physical Anthropology* 156 Suppl 59 (February): 43–71.
Fiorenza, Luca, Stefano Benazzi, Jeremy Tausch, Ottmar Kullmer, Timothy G. Bromage, and Friedemann Schrenk. 2011. “Molar Macrowear Reveals Neanderthal Eco-Geographic Dietary Variation.” *PloS One* 6 (3): e14769.
Fisk, G. R., and G. A. Macho. 1992. “Evidence of a Healed Compression Fracture in a Plio-Pleistocene Hominid Talus from Sterkfontein, South Africa.” *International Journal of Osteoarchaeology* 2 (4): 325–32.
Frank, Erik T., and K. Eduard Linsenmair. 2017. “Saving the Injured: Evolution and Mechanisms.” *Communicative & Integrative Biology* 10 (5-6): e1356516.
French, Jennifer C. 2016. “Demography and the Palaeolithic Archaeological Record.” *Journal of Archaeological Method and Theory* 23 (1): 150–99.
Froment, Alain. 2001. “Evolutionary Biology and Health of Hunter-Gatherer Populations.” *Hunter-Gatherers: An Interdisciplinary Perspective*, 239–66.
Fuentes, Agustín, Matthew A. Wyczalkowski, and Katherine C. MacKinnon. 2010. “Niche Construction through Cooperation: A Nonlinear Dynamics Contribution to Modeling Facets of the Evolutionary History in the Genus Homo.” *Current Anthropology* 51 (3): 435–44.
García-Martínez, Daniel, Alon Barash, Wolfgang Recheis, Cristina Utrilla, Isabel Torres Sánchez, Francisco García Río, and Markus Bastir. 2014. “On the Chest Size of Kebara 2.” *Journal of Human Evolution* 70 (May): 69–72.
Gardner, Janet C., and Fred H. Smith. 2006. “The Paleopathology of the Krapina Neandertals.” *Periodicum Biologorum* 108 (4): 471.
Garralda, María Dolores, Bruno Maureille, and Bernard Vandermeersch. 2014. “Hyperostosis Frontalis Interna in a Neandertal from Marillac (Charente, France).” *Journal of Human Evolution* 67 (February): 76–84.
Gaudzinski-Windheuser, Sabine, Elisabeth S. Noack, Eduard Pop, Constantin Herbst, Johannes Pfleging, Jonas Buchli, Arne Jacob, et al. 2018. “Evidence for Close-Range Hunting by Last Interglacial Neanderthals.” *Nature Ecology & Evolution*, June. https://doi.org/10.1038/s41559-018-0596-1.
Godinho, Ricardo Miguel, Penny Spikins, and Paul O’Higgins. 2018. “Supraorbital Morphology and Social Dynamics in Human Evolution.” *Nature Ecology & Evolution*, April. https://doi.org/10.1038/s41559-018-0528-0.
Gómez-Olivencia, A. 2013. “The Presacral Spine of the La Ferrassie 1 Neandertal: A Revised Inventory.” *Bulletins et Memoires de La Societe D’anthropologie de Paris* 25 (1): 19–38.
Gómez-Olivencia, Asier. 2013. “Back to the Old Man’s Back: Reassessment of the Anatomical

Determination of the Vertebrae of the Neandertal Individual of La Chapelle-Aux-Saints." *Annales de Paléontologie* 99 (1): 43–65.
Gómez-Olivencia, Asier, Christine Couture-Veschambre, Stéphane Madelaine, and Bruno Maureille. 2013. "The Vertebral Column of the Regourdou 1 Neandertal." *Journal of Human Evolution* 64 (6): 582–607.
Gómez-Olivencia, Asier, Robert G. Franciscus, Christine Couture-Veschambre, Bruno Maureille, and Juan Luis Arsuaga. 2012. "The Mesosternum of the Regourdou 1 Neandertal Revisited." *Journal of Human Evolution* 62 (4): 511–19.
Gómez-Olivencia, Asier, Rolf Quam, Nohemi Sala, Morgane Bardey, James C. Ohman, and Antoine Balzeau. 2018. "La Ferrassie 1: New Perspectives on a 'Classic' Neandertal." *Journal of Human Evolution* 117 (April): 13–32.
Goodman, Madeleine J., P. Bion Griffin, Agnes A. Estioko-Griffin, and John S. Grove. 1985. "The Compatibility of Hunting and Mothering among the Agta Hunter-Gatherers of the Philippines." *Sex Roles* 12 (11): 1199–1209.
Gracia, Ana, Juan Luis Arsuaga, Ignacio Martínez, Carlos Lorenzo, José Miguel Carretero, José María Bermúdez de Castro, and Eudald Carbonell. 2009. "Craniosynostosis in the Middle Pleistocene Human Cranium 14 from the Sima de Los Huesos, Atapuerca, Spain." *Proceedings of the National Academy of Sciences of the United States of America* 106 (16): 6573–78.
Griffin, R., K. D. Peterson, J. R. Halseth, and B. Reynolds. 1987. "Injuries in Professional Rodeo: An Update." *The Physician and Sportsmedicine* 15 (2): 104–15.
Guatelli-Steinberg, Debbie, Clark Spencer Larsen, and Dale L. Hutchinson. 2004. "Prevalence and the Duration of Linear Enamel Hypoplasia: A Comparative Study of Neandertals and Inuit Foragers." *Journal of Human Evolution* 47 (1-2): 65–84.
Guérin, Guillaume, Marine Frouin, Sahra Talamo, Vera Aldeias, Laurent Bruxelles, Laurent Chiotti, Harold L. Dibble, et al. 2015/6. "A Multi-Method Luminescence Dating of the Palaeolithic Sequence of La Ferrassie Based on New Excavations Adjacent to the La Ferrassie 1 and 2 Skeletons." *Journal of Archaeological Science* 58: 147–66.
Gurven, M., W. Allen-Arave, K. Hill, and M. Hurtado. 2000. "'It's a Wonderful Life'. Signaling Generosity among the Ache of Paraguay." *Evolution and Human Behavior: Official Journal of the Human Behavior and Evolution Society* 21 (4): 263–82.
Haeusler, Martin, Regula Schiess, and Thomas Boeni. 2013. "Evidence for Juvenile Disc Herniation in a Homo Erectus Boy Skeleton." *Spine* 38 (3): E123–28.
Hajdinjak, Mateja, Qiaomei Fu, Alexander Hübner, Martin Petr, Fabrizio Mafessoni, Steffi Grote, Pontus Skoglund, et al. 2018. "Reconstructing the Genetic History of Late Neanderthals." *Nature* 555 (7698): 652–56.
Hardy, Bruce L. 2010. "Climatic Variability and Plant Food Distribution in Pleistocene Europe: Implications for Neanderthal Diet and Subsistence." *Quaternary Science Reviews* 29 (5): 662–79.
Hardy, Bruce L., and Marie-Hélène Moncel. 2011. "Neanderthal Use of Fish, Mammals, Birds, Starchy Plants and Wood 125-250,000 Years Ago." *PloS One* 6 (8): e23768.
Hardy, Karen. 2018. "Plant Use in the Lower and Middle Palaeolithic: Food, Medicine and Raw Materials." *Quaternary Science Reviews* 191 (July): 393–405.
Hardy, Karen, Stephen Buckley, Matthew J. Collins, Almudena Estalrrich, Don Brothwell, Les Copeland, Antonio García-Tabernero, et al. 2012. "Neanderthal Medics? Evidence for Food, Cooking, and Medicinal Plants Entrapped in Dental Calculus." *Die Naturwissenschaften* 99 (8): 617–26.
Hare, Brian. 2017. "Survival of the Friendliest: Homo Sapiens Evolved via Selection for Prosociality." *Annual Review of Psychology* 68 (January): 155–86.
Harris, Kelley, and Rasmus Nielsen. 2016. "The Genetic Cost of Neanderthal Introgression." *Genetics* 203 (2): 881–91.
Hart, Benjamin L. 2011. "Behavioural Defences in Animals against Pathogens and Parasites: Parallels with the Pillars of Medicine in Humans." *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 366 (1583): 3406–17.
Heggie, Travis W., and Thomas Küpper. 2018. "Pediatric and Adolescent Injury in Wilderness and Extreme Environments." *Research in Sports Medicine* 26 (sup1): 186–98.
Heim, Jean-Louis. 1976. "Les Hommes Fossiles de La Ferrassie, Tomo I." *Archives de l'Institut de Paléontologie Humaine* 35. http://ci.nii.ac.jp/naid/10003965119/.
Heinrich, Joseph, Robert Boyd, Samuel Bowles, Colin Camerer, Ernst Fehr, and Herbert Gintis. 2004. "Foundations of Human Sociality." Oxford University Press, Oxford.
Henry, Amanda G., Alison S. Brooks, and Dolores R. Piperno. 2011. "Microfossils in Calculus Demonstrate Consumption of Plants and Cooked Foods in Neanderthal Diets (Shanidar III, Iraq;

Spy I and II, Belgium).” *Proceedings of the National Academy of Sciences of the United States of America* 108 (2): 486–91.
Higham, Tom, Katerina Douka, Rachel Wood, Christopher Bronk Ramsey, Fiona Brock, Laura Basell, Marta Camps, et al. 2014. “The Timing and Spatiotemporal Patterning of Neanderthal Disappearance.” *Nature* 512 (7514): 306–9.
Hill, Kim, and A. Magdalena Hurtado. 2009. “Cooperative Breeding in South American Hunter-Gatherers.” *Proceedings. Biological Sciences / The Royal Society* 276 (1674): 3863–70.
Hill, Kim, A. M. Hurtado, and R. S. Walker. 2007. “High Adult Mortality among Hiwi Hunter-Gatherers: Implications for Human Evolution.” *Journal of Human Evolution* 52 (4): 443–54.
Hlusko, Leslea J., Joshua P. Carlson, Debbie Guatelli-Steinberg, Kristin L. Krueger, Ben Mersey, Peter S. Ungar, and Alban Defleur. 2013. “Neanderthal Teeth from Moula-Guercy, Ardèche, France.” *American Journal of Physical Anthropology* 151 (3): 477–91.
Hockett, Bryan. 2012. “The Consequences of Middle Paleolithic Diets on Pregnant Neanderthal Women.” *Quaternary International: The Journal of the International Union for Quaternary Research* 264 (June): 78–82.
Hodgkins, Jamie, Curtis W. Marean, Alain Turq, Dennis Sandgathe, Shannon J. P. McPherron, and Harold Dibble. 2016. “Climate-Mediated Shifts in Neandertal Subsistence Behaviors at Pech de l’Azé IV and Roc de Marsal (Dordogne Valley, France).” *Journal of Human Evolution* 96 (July): 1–18.
Holliday, T. W. 1997. “Postcranial Evidence of Cold Adaptation in European Neandertals.” *American Journal of Physical Anthropology* 104 (2): 245–58.
Hortolà, Policarp, and Bienvenido Martínez-Navarro. 2013. “The Quaternary Megafaunal Extinction and the Fate of Neanderthals: An Integrative Working Hypothesis.” *Quaternary International: The Journal of the International Union for Quaternary Research* 295 (May): 69–72.
House, Bailey, Joseph Henrich, Barbara Sarnecka, and Joan B. Silk. 2013. “The Development of Contingent Reciprocity in Children.” *Evolution and Human Behavior: Official Journal of the Human Behavior and Evolution Society* 34 (2): 86–93.
Hublin, Jean-Jacques. 2009. “The Prehistory of Compassion.” *Proceedings of the National Academy of Sciences of the United States of America* 106 (16): 6429–30.
———. 2017. “The Last Neanderthal.” *Proceedings of the National Academy of Sciences of the United States of America* 114 (40): 10520–22.
Hublin, Jean-Jacques, and Wil Roebroeks. 2009. “Ebb and Flow or Regional Extinctions? On the Character of Neandertal Occupation of Northern Environments.” *Comptes Rendus. Palevol* 8 (5): 503–9.
Hublin, Jean-Jacques, Darlene Weston, Philipp Gunz, Mike Richards, Wil Roebroeks, Jan Glimmerveen, and Luc Anthonis. 2009. “Out of the North Sea: The Zeeland Ridges Neandertal.” *Journal of Human Evolution* 57 (6): 777–85.
Jamieson, Jennifer A., and Harriet V. Kuhnlein. 2008. “The Paradox of Anemia with High Meat Intake: A Review of the Multifactorial Etiology of Anemia in the Inuit of North America.” *Nutrition Reviews* 66 (5): 256–71.
Johnson, Amber L. 2014. “Exploring Adaptive Variation among Hunter-Gatherers with Binford’s Frames of Reference.” *Journal of Archaeological Research* 22 (1): 1–42.
Jordan, Jillian J., Moshe Hoffman, Martin A. Nowak, and David G. Rand. 2016. “Uncalculating Cooperation Is Used to Signal Trustworthiness.” *Proceedings of the National Academy of Sciences of the United States of America* 113 (31): 8658–63.
Juric, Ivan, Simon Aeschbacher, and Graham Coop. 2016. “The Strength of Selection against Neanderthal Introgression.” *PLoS Genetics* 12 (11): e1006340.
Kelly, Robert L. 2013. *The Lifeways of Hunter-Gatherers*. Cambridge: Cambridge University Press.
Kent, Laura. 2017. “Health-Related Care for the Neanderthal Shanidar.” *ANU Undergraduate Research Journal: 2016* 8: 83–91.
Kessler, Sharon E., Tyler R. Bonnell, Richard W. Byrne, and Colin A. Chapman. 2017. “Selection to Outsmart the Germs: The Evolution of Disease Recognition and Social Cognition.” *Journal of Human Evolution* 108 (July): 92–109.
Key, Felix M., Muslihudeen A. Abdul-Aziz, Roger Mundry, Benjamin M. Peter, Aarthi Sekar, Mauro D’Amato, Megan Y. Dennis, Joshua M. Schmidt, and Aida M. Andrés. 2018. “Human Local Adaptation of the TRPM8 Cold Receptor along a Latitudinal Cline.” *PLoS Genetics* 14 (5): e1007298.
Kidd, Kenneth K., Andrew J. Pakstis, and Libing Yun. 2014. “An Historical Perspective on ‘The World-Wide Distribution of Allele Frequencies at the Human Dopamine D4 Receptor Locus.’” *Human Genetics* 133 (4): 431–33.

Kotler, Burt P., John E. Gross, and William A. Mitchell. 1994. “Applying Patch Use to Assess Aspects of Foraging Behavior in Nubian Ibex.” *The Journal of Wildlife Management* 58 (2): 299–307.

Kricun, Morrie, Janet Monge, Alan Mann, Gerald Finkel, Michelle Lampl, and J. Radovčić. 1999. “The Krapina Hominids. A Radiographic Atlas of the Skeletal Collection.” *Zagreb: Croatian Natural History Museum*.

Kuhn, Steven L., Mary C. Stiner, Guy BarOz, Mina WeinsteinEvron, Jean-Pierre BocquetAppel, Erella Hovers, Katharine MacDonald, Wil Roebroeks, Kenneth Martnez, and John J. Shea. 2006. “What’s a Mother to Do? The Division of Labor among Neandertals and Modern Humans in Eurasia.” *Current Anthropology* 47 (6): 953–81.

L’Abbé, Ericka N., Steven A. Symes, James T. Pokines, Luis L. Cabo, Kyra E. Stull, Sharon Kuo, David E. Raymond, Patrick S. Randolph-Quinney, and Lee R. Berger. 2015. “Evidence of Fatal Skeletal Injuries on Malapa Hominins 1 and 2.” *Scientific Reports* 5 (October): 15120.

Lalueza-Fox, Carles, Antonio Rosas, Almudena Estalrrich, Elena Gigli, Paula F. Campos, Antonio García-Tabernero, Samuel García-Vargas, et al. 2011. “Genetic Evidence for Patrilocal Mating Behavior among Neandertal Groups.” *Proceedings of the National Academy of Sciences of the United States of America* 108 (1): 250–53.

Lambrecht, C. J., and S. W. Hargarten. 1993. “Hunting-Related Injuries and Deaths in Montana: The Scope of the Problem and a Framework for Prevention.” *Journal of Wilderness Medicine* 4 (2): 175–82.

Lebel, Serge, and Erik Trinkaus. 2002. “Middle Pleistocene Human Remains from the Bau de l’Aubesier.” *Journal of Human Evolution* 43 (5): 659–85.

Leemon, Drew, and Tod Schimelpfenig. 2003. “Wilderness Injury, Illness, and Evacuation: National Outdoor Leadership School’s Incident Profiles, 1999–2002.” *Wilderness & Environmental Medicine* 14 (3): 174–82.

Lee, Richard B. 2014. “Hunter-Gatherers on the Best-Seller List: Steven Pinker and the ‘Bellicose School’s’ Treatment of Forager Violence.” *Journal of Aggression, Conflict and Peace Research* 6 (4): 216–28.

León, Marcia S. Ponce de, Lubov Golovanova, Vladimir Doronichev, Galina Romanova, Takeru Akazawa, Osamu Kondo, Hajime Ishida, and Christoph P. E. Zollikofer. 2008. “Neanderthal Brain Size at Birth Provides Insights into the Evolution of Human Life History.” *Proceedings of the National Academy of Sciences* 105 (37): 13764–68.

Lessa, Andrea. 2011. “Daily Risks: A Biocultural Approach to Acute Trauma in Pre-Colonial Coastal Populations from Brazil.” *International Journal of Osteoarchaeology* 21 (2): 159–72.

Li, Yiyuan, Hong Li, Jean Decety, and Kang Lee. 2013. “Experiencing a Natural Disaster Alters Children’s Altruistic Giving.” *Psychological Science* 24 (9): 1686–95.

Lomas, William. 2009. “Conflict, Violence, and Conflict Resolution in Hunting and Gathering Societies.” *Totem: The University of Western Ontario Journal of Anthropology* 17 (1): 5.

Lordkipanidze, David, Abesalom Vekua, Reid Ferring, G. Philip Rightmire, Jordi Agusti, Gocha Kiladze, Alexander Mouskhelishvili, et al. 2005. “Anthropology: The Earliest Toothless Hominin Skull.” *Nature* 434 (7034): 717–18.

Luetscher, M., R. Boch, H. Sodemann, C. Spötl, H. Cheng, R. L. Edwards, S. Frisia, F. Hof, and W. Müller. 2015. “North Atlantic Storm Track Changes during the Last Glacial Maximum Recorded by Alpine Speleothems, Nat. Commun., 6, 6344.”

Lugli, Federico, Anna Cipriani, Julie Arnaud, Marta Arzarello, Carlo Peretto, and Stefano Benazzi. 2017. “Suspected Limited Mobility of a Middle Pleistocene Woman from Southern Italy: Strontium Isotopes of a Human Deciduous Tooth.” *Scientific Reports* 7 (1): 8615.

Lumley, Marie-Antoinette D. E. 1975. “Ante-Neanderthals of Western Europe.” In *Paleoanthropology*, edited by Russell H. Tuttle. Berlin, New York: DE GRUYTER MOUTON.

MacNulty, D. R. 2002. “The Predatory Sequence and the Influence of Injury Risk on Hunting Behavior in the Wolf.” St. Paul (MN): University of Minnesota. https://www.researchgate.net/profile/Daniel_Macnulty/publication/35938430_The_predatory_sequence_and_the_influence_of_injury_risk_on_hunting_behavior_in_the_wolf/links/54da40e20cf261ce15cc1885.pdf.

Magid, Kesson, Robert T. Chatterton, Farid Uddin Ahamed, and Gillian R. Bentley. 2018. “Childhood Ecology Influences Salivary Testosterone, Pubertal Age and Stature of Bangladeshi UK Migrant Men.” *Nature Ecology & Evolution*, June. https://doi.org/10.1038/s41559-018-0567-6.

Maguire, Brian J., Katherine L. Hunting, Tee L. Guidotti, and Gordon S. Smith. 2005. “Occupational Injuries among Emergency Medical Services Personnel.” *Prehospital Emergency Care: Official Journal of the National Association of EMS Physicians and the National Association of State EMS Directors* 9 (4): 405–11.

Manapat, Michael L., Martin A. Nowak, and David G. Rand. 2013. “Information, Irrationality, and the Evolution of Trust.” *Journal of Economic Behavior & Organization* 90, Supplement: S57–75.
Marra, Fabrizio, Piero Ceruleo, Luca Pandolfi, Carmelo Petronio, Mario F. Rolfo, and Leonardo Salari. 2017. “The Aggradational Successions of the Aniene River Valley in Rome: Age Constraints to Early Neanderthal Presence in Europe.” *PloS One* 12 (1): e0170434.
Marsh, Abigail A. 2016. “Neural, Cognitive, and Evolutionary Foundations of Human Altruism.” *Wiley Interdisciplinary Reviews. Cognitive Science* 7 (1): 59–71.
Matsumoto, Takuya, Noriko Itoh, Sana Inoue, and Michio Nakamura. 2016. “An Observation of a Severely Disabled Infant Chimpanzee in the Wild and Her Interactions with Her Mother.” *Primates; Journal of Primatology* 57 (1): 3–7.
Matthews, Luke J., and Paul M. Butler. 2011. “Novelty-Seeking DRD4 Polymorphisms Are Associated with Human Migration Distance out-of-Africa after Controlling for Neutral Population Gene Structure.” *American Journal of Physical Anthropology* 145 (3): 382–89.
Maureille, Bruno, Asier Gómez-Olivencia, Christine Couture-Veschambre, Stéphane Madelaine, and Trenton Holliday. 2015. “New Hominin Remains from the Site of Regourdou (Montignac-Sur-Vézère, Dordogne, France).” *PALEO. Revue D’archéologie Préhistorique*, no. 26 (December): 117–38.
McIntosh, Scott E., Drew Leemon, Joshua Visitacion, Tod Schimelpfenig, and David Fosnocht. 2007. “Medical Incidents and Evacuations on Wilderness Expeditions.” *Wilderness & Environmental Medicine* 18 (4): 298–304.
Mead, Simon, Michael P. H. Stumpf, Jerome Whitfield, Jonathan A. Beck, Mark Poulter, Tracy Campbell, James B. Uphill, et al. 2003. “Balancing Selection at the Prion Protein Gene Consistent with Prehistoric Kurulike Epidemics.” *Science* 300 (5619): 640–43.
Mednikova, Maria. 2017. “Neanderthal Infant Kiik-Koba 2 and a Possible Pathology in the Context of Bioarchaeology.” In *PESHE Proceedings of the European Society for Human Evolution*.
Melchionna, Marina, Mirko Di Febbraro, Francesco Carotenuto, Lorenzo Rook, Alessandro Mondanaro, Silvia Castiglione, Carmela Serio, et al. 2018. “Fragmentation of Neanderthals’ Pre-Extinction Distribution by Climate Change.” *Palaeogeography, Palaeoclimatology, Palaeoecology* 496 (May): 146–54.
Merbs, C. F. 2002. “Spondylolysis in Inuit Skeletons from Arctic Canada.” *International Journal of Osteoarchaeology*. http://onlinelibrary.wiley.com/doi/10.1002/oa.623/full.
Monge, Janet, Morrie Kricun, Jakov Radovčić, Davorka Radovčić, Alan Mann, and David W. Frayer. 2013. “Fibrous Dysplasia in a 120,000+ Year Old Neandertal from Krapina, Croatia.” *PloS One* 8 (6): e64539.
Moreno, Ana, Anders Svensson, Stephen J. Brooks, Simon Connor, Stefan Engels, William Fletcher, Dominique Genty, et al. 2014. “A Compilation of Western European Terrestrial Records 60–8 Ka BP: Towards an Understanding of Latitudinal Climatic Gradients.” *Quaternary Science Reviews* 106 (December): 167–85.
Mukherjee, Shomen, and Michael R. Heithaus. 2013. “Dangerous Prey and Daring Predators: A Review: Daring Predators.” *Biological Reviews* 88 (3): 550–63.
Müller, Ulrich C., Jörg Pross, Polychronis C. Tzedakis, Clive Gamble, Ulrich Kotthoff, Gerhard Schmiedl, Sabine Wulf, and Kimon Christanis. 2011/2. “The Role of Climate in the Spread of Modern Humans into Europe.” *Quaternary Science Reviews* 30 (3–4): 273–79.
Munn, Julie. 2006. “Effects of Injury on the Locomotion of Free-Living Chimpanzees in the Budongo Forest Reserve, Uganda.” *Primates of Western Uganda*, 259–80.
Mussini, Celimene, Isabelle Crevecoeur, Maria Dolores Garralda, Alan Mann, and Bruno Maureille. 2012. “A New Neandertal Femoral Diaphysis from Les Pradelles (Marillac-Le-Franc, Charente, France).” *Periodicum Biologorum* 114 (1): 117–23.
Naito, Yuichi I., Yoshito Chikaraishi, Dorothée G. Drucker, Naohiko Ohkouchi, Patrick Semal, Christoph Wißing, and Hervé Bocherens. 2016. “Ecological Niche of Neanderthals from Spy Cave Revealed by Nitrogen Isotopes of Individual Amino Acids in Collagen.” *Journal of Human Evolution* 93 (April): 82–90.
Nakahashi, Wataru. 2017. “The Effect of Trauma on Neanderthal Culture: A Mathematical Analysis.” *Homo: Internationale Zeitschrift Fur Die Vergleichende Forschung Am Menschen*, February. https://doi.org/10.1016/j.jchb.2017.02.001.
Nielsen, Trine Kellberg, Blas M. Benito, Jens-Christian Svenning, Brody Sandel, Luseadra McKerracher, Felix Riede, and Peter C. Kjærgaard. 2017. “Investigating Neanderthal Dispersal above 55°N in Europe during the Last Interglacial Complex.” *Quaternary International: The Journal of the International Union for Quaternary Research* 431: 88–103.
Niven, L. 2006. “The Palaeolithic Occupation of Vogelherd Cave.” *Tübingen: Kerns Verlag*.

Niven, Laura, Teresa E. Steele, William Rendu, Jean-Baptiste Mallye, Shannon P. McPherron, Marie Soressi, Jacques Jaubert, and Jean-Jacques Hublin. 2012. “Neandertal Mobility and Large-Game Hunting: The Exploitation of Reindeer during the Quina Mousterian at Chez-Pinaud Jonzac (Charente-Maritime, France).” *Journal of Human Evolution* 63 (4): 624–35.

Ogilvie, M. D., B. K. Curran, and Erik Trinkaus. 1989. “Incidence and Patterning of Dental Enamel Hypoplasia among the Neandertals.” *American Journal of Physical Anthropology* 79 (1): 25–41.

Pearce, Eiluned, Andrew Shuttleworth, Matt Grove, and R. Layton. 2014. “The Costs of Being a High Latitude Hominin.” *Lucy to Language: The Benchmark Papers*, 356–79.

Pearce, Eiluned, Chris Stringer, and Robin Dunbar. 2013. “New Insights into Differences in Brain Organization between Neanderthals and Anatomically Modern Humans.” *Proceedings. Biological Sciences / The Royal Society* 280 (1758): 20130168.

Pérez-Manrique, Ana, and Antoni Gomila. 2017. “The Comparative Study of Empathy: Sympathetic Concern and Empathic Perspective-Taking in Non-Human Animals.” *Biological Reviews of the Cambridge Philosophical Society*, May. https://doi.org/10.1111/brv.12342.

Pérez, P. J., A. Gracía, I. Martínez, and J. L. Arsuaga. 1997. “Paleopathological Evidence of the Cranial Remains from the Sima de Los Huesos Middle Pleistocene Site (Sierra de Atapuerca, Spain). Description and Preliminary Inferences.” *Journal of Human Evolution* 33 (2-3): 409–21.

Pettitt, P. B. 2000. “Neanderthal Lifecycles: Developmental and Social Phases in the Lives of the Last Archaics.” *World Archaeology* 31 (3): 351–66.

Pickering, Robyn, and Jan D. Kramers. 2010. “Re-Appraisal of the Stratigraphy and Determination of New U-Pb Dates for the Sterkfontein Hominin Site, South Africa.” *Journal of Human Evolution* 59 (1): 70–86.

Pickering, Travis Rayne, Manuel Domínguez-Rodrigo, Charles P. Egeland, and C. K. Brain. 2004. “Beyond Leopards: Tooth Marks and the Contribution of Multiple Carnivore Taxa to the Accumulation of the Swartkrans Member 3 Fossil Assemblage.” *Journal of Human Evolution* 46 (5): 595–604.

Polimanti, Renato, and Joel Gelernter. 2017. “Widespread Signatures of Positive Selection in Common Risk Alleles Associated to Autism Spectrum Disorder.” *PLoS Genetics* 13 (2): e1006618.

Power, Robert C., Domingo C. Salazar-García, Mauro Rubini, Andrea Darlas, Katerina Harvati, Michael Walker, Jean-Jacques Hublin, and Amanda G. Henry. 2018. “Dental Calculus Indicates Widespread Plant Use within the Stable Neanderthal Dietary Niche.” *Journal of Human Evolution* 119 (June): 27–41.

Prüfer, Kay, Fernando Racimo, Nick Patterson, Flora Jay, Sriram Sankararaman, Susanna Sawyer, Anja Heinze, et al. 2014. “The Complete Genome Sequence of a Neanderthal from the Altai Mountains.” *Nature* 505 (7481): 43–49.

Radovčić, J., F. H. Smith, Erik Trinkaus, and M. H. Wolpoff. 1988. “The Krapina Hominids: An Illustrated Catalog of Skeletal Remains.” Zagreb.

Rajhans, Purva, Nicole Altvater-Mackensen, Amrisha Vaish, and Tobias Grossmann. 2016. “Children’s Altruistic Behavior in Context: The Role of Emotional Responsiveness and Culture.” *Scientific Reports* 6 (May): 24089.

Randolph-Quinney, Patrick S., Scott A. Williams, Maryna Steyn, Marc R. Meyer, Jacqueline S. Smilg, Steven E. Churchill, Edward J. Odes, Tanya Augustine, Paul Tafforeau, and Lee R. Berger. 2016. “Osteogenic Tumour in Australopithecus Sediba: Earliest Hominin Evidence for Neoplastic Disease.” *South African Journal of Science* 112 (7-8): 1–7.

Rasa, O. Anne E. 1983. “A Case of Invalid Care in Wild Dwarf Mongooses.” *Zeitschrift Für Tierpsychologie* 62 (3): 235–40.

Reishus, Allan D. 2007. “Injuries and Illnesses of Big Game Hunters in Western Colorado: A 9-Year Analysis.” *Wilderness & Environmental Medicine* 18 (1): 20–25.

Rendu, William, Sandrine Costamagno, Liliane Meignen, and Marie-Cécile Soulier. 2012. “Monospecific Faunal Spectra in Mousterian Contexts: Implications for Social Behavior.” *Quaternary International: The Journal of the International Union for Quaternary Research* 247 (January): 50–58.

Rey-Rodríguez, Iván, Juan-Manuel López-García, Maria Bennasar, Sandra Bañuls-Cardona, Hugues-Alexandre Blain, Ángel Blanco-Lapaz, Xosé-Pedro Rodríguez-Álvarez, et al. 2016. “Last Neanderthals and First Anatomically Modern Humans in the NW Iberian Peninsula: Climatic and Environmental Conditions Inferred from the Cova Eirós Small-Vertebrate Assemblage during MIS 3.” *Quaternary Science Reviews* 151: 185–97.

Rhodes, Jill A., and Steven E. Churchill. 2009. “Throwing in the Middle and Upper Paleolithic: Inferences from an Analysis of Humeral Retroversion.” *Journal of Human Evolution* 56 (1): 1–10.

Richards, Michael P., and Erik Trinkaus. 2009. “Isotopic Evidence for the Diets of European Neanderthals and Early Modern Humans.” *Proceedings of the National Academy of Sciences of the United States of America* 106 (38): 16034–39.
Roach, Neil T., Madhusudhan Venkadesan, Michael J. Rainbow, and Daniel E. Lieberman. 2013. “Elastic Energy Storage in the Shoulder and the Evolution of High-Speed Throwing in Homo.” *Nature* 498 (7455): 483–86.
Rodríguez, Miguel Á., Miguel Á. Olalla-Tárraga, and Bradford A. Hawkins. 2008. “Bergmann’s Rule and the Geography of Mammal Body Size in the Western Hemisphere.” *Global Ecology and Biogeography: A Journal of Macroecology* 17 (2): 274–83.
Rogers, Alan R., Ryan J. Bohlender, and Chad D. Huff. 2017. “Early History of Neanderthals and Denisovans.” *Proceedings of the National Academy of Sciences of the United States of America* 114 (37): 9859–63.
Romero, Teresa, Miguel A. Castellanos, and Frans B. M. de Waal. 2010. “Consolation as Possible Expression of Sympathetic Concern among Chimpanzees.” *Proceedings of the National Academy of Sciences of the United States of America* 107 (27): 12110–15.
Rufà, Anna, Ruth Blasco, Thierry Roger, Mathieu Rué, and Camille Daujeard. 2017. “A Rallying Point for Different Predators: The Avian Record from a Late Pleistocene Sequence of Grotte Des Barasses II (Balazuc, Ardèche, France).” *Archaeological and Anthropological Sciences*, January. https://doi.org/10.1007/s12520-017-0469-6.
Ruff, Christopher B. 1994. “Morphological Adaptation to Climate in Modern and Fossil Hominids.” *American Journal of Physical Anthropology* 37 (S19): 65–107.
Sala, Nohemi, Juan Luis Arsuaga, Ana Pantoja-Pérez, Adrián Pablos, Ignacio Martínez, Rolf M. Quam, Asier Gómez-Olivencia, José María Bermúdez de Castro, and Eudald Carbonell. 2015. “Lethal Interpersonal Violence in the Middle Pleistocene.” *PloS One* 10 (5): e0126589.
Salazar-García, Domingo C., Robert C. Power, Alfred Sanchis Serra, Valentín Villaverde, Michael J. Walker, and Amanda G. Henry. 2013. “Neanderthal Diets in Central and Southeastern Mediterranean Iberia.” *Quaternary International: The Journal of the International Union for Quaternary Research* 318 (December): 3–18.
Sánchez Goñi, M., I. Cacho, J. Turon, J. Guiot, F. Sierro, J. Peypouquet, J. Grimalt, and N. Shackleton. 2002. “Synchroneity between Marine and Terrestrial Responses to Millennial Scale Climatic Variability during the Last Glacial Period in the Mediterranean Region.” *Climate Dynamics* 19 (1): 95–105.
Sánchez-Quinto, Federico, and Carles Lalueza-Fox. 2015. “Almost 20 Years of Neanderthal Palaeogenetics: Adaptation, Admixture, Diversity, Demography and Extinction.” *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 370 (1660): 20130374.
Sand, Håkan, Camilla Wikenros, Petter Wabakken, and Olof Liberg. 2006. “Effects of Hunting Group Size, Snow Depth and Age on the Success of Wolves Hunting Moose.” *Animal Behaviour* 72 (4): 781–89.
Sankararaman, Sriram, Swapan Mallick, Nick Patterson, and David Reich. 2016. “The Combined Landscape of Denisovan and Neanderthal Ancestry in Present-Day Humans.” *Current Biology: CB* 26 (9): 1241–47.
Sayer, Emily C., Jessica C. Whitham, and Susan W. Margulis. 2007. “Who Needs a Forelimb Anyway? Locomotor, Postural and Manipulative Behavior in a One-Armed Gibbon.” *Zoo Biology* 26 (3): 215–22.
Schaller, George B. 2009. *The Serengeti Lion: A Study of Predator-Prey Relations*. University of Chicago Press.
Schemske, Douglas W., Gary G. Mittelbach, Howard V. Cornell, James M. Sobel, and Kaustuv Roy. 2009. “Is There a Latitudinal Gradient in the Importance of Biotic Interactions?” *Annual Review of Ecology, Evolution, and Systematics* 40 (1): 245–69.
Schiess, Regula, Thomas Boeni, Frank Rühli, and Martin Haeusler. 2014. “Revisiting Scoliosis in the KNM-WT 15000 Homo Erectus Skeleton.” *Journal of Human Evolution* 67 (February): 48–59.
Schmitz, Ralf W., David Serre, Georges Bonani, Susanne Feine, Felix Hillgruber, Heike Krainitzki, Svante Pääbo, and Fred H. Smith. 2002. “The Neandertal Type Site Revisited: Interdisciplinary Investigations of Skeletal Remains from the Neander Valley, Germany.” *Proceedings of the National Academy of Sciences of the United States of America* 99 (20): 13342–47.
Schultz, M. 2006. “Der Neandertaler Aus Der Kleinen Feldhofer Grotte—Versuch Eine Rekonstruktion Seines Geshundheitsstatus.” *Neanderthal* 2006: 277–318.
Scott, Beccy, Martin Bates, Richard Bates, Chantal Conneller, Matt Pope, Andrew Shaw, and Geoff Smith. 2015. “A New View from La Cotte de St Brelade, Jersey.” *Antiquity* 88 (339): 13–29.

Sergi, S., A. Ascenzi, and E. Bonucci. 1972. “Torus Palatinus in the Neandertal Circeo I Skull. A Histologic, Microradiographic and Electron Microscopic Investigation.” *American Journal of Physical Anthropology* 36 (2): 189–97.
Shea, John J., and Matthew L. Sisk. 2010. “Complex Projectile Technology and Homo Sapiens Dispersal into Western Eurasia.” *PaleoAnthropology* 2010: 100–122.
Simons, Yuval B., and Guy Sella. 2016. “The Impact of Recent Population History on the Deleterious Mutation Load in Humans and Close Evolutionary Relatives.” *Current Opinion in Genetics & Development* 41 (December): 150–58.
Sistiaga, Ainara, Carolina Mallol, Bertila Galván, and Roger Everett Summons. 2014. “The Neanderthal Meal: A New Perspective Using Faecal Biomarkers.” *PloS One* 9 (6): e101045.
Skinner, Mark. 1991. “Bee Brood Consumption: An Alternative Explanation for Hypervitaminosis A in KNM-ER 1808 (Homo Erectus) from Koobi Fora, Kenya.” *Journal of Human Evolution* 20 (6): 493–503.
Sladek, V. 2002. “Morphological Affinities of the Sala 1 Frontal Bone.” *Journal of Human Evolution* 43 (6): 787–815.
Slimak, Ludovic, John Inge Svendsen, Jan Mangerud, Hugues Plisson, Herbjørn Presthus Heggen, Alexis Brugère, and Pavel Yurievich Pavlov. 2011. “Late Mousterian Persistence near the Arctic Circle.” *Science* 332 (6031): 841–45.
Smith, Geoff M. 2015. “Neanderthal Megafaunal Exploitation in Western Europe and Its Dietary Implications: A Contextual Reassessment of La Cotte de St Brelade (Jersey).” *Journal of Human Evolution* 78 (January): 181–201.
Spikins, Penny. 2012. “Goodwill Hunting? Debates over the ‘meaning’of Lower Palaeolithic Handaxe Form Revisited.” *World Archaeology* 44 (3): 378–92.
———. 2015. “How Compassion Made Us Human.” *Barnsley, UK: Pen and Sword.*
Spikins, Penny, Gail Hitchens, Andy Needham, and Holly Rutherford. 2014. “The Cradle of Thought: Growth, Learning, Play and Attachment in Neanderthal Children.” *Oxford Journal of Archaeology* 33 (2): 111–34.
Spikins, Penny, Andy Needham, Lorna Tilley, and Gail Hitchens. 2018. “Calculated or Caring? Neanderthal Healthcare in Social Context.” *World Archaeology*, February, 1–20.
Spikins, Penny, Barry Wright, and Derek Hodgson. 2016. “Are There Alternative Adaptive Strategies to Human pro-Sociality? The Role of Collaborative Morality in the Emergence of Personality Variation and Autistic Traits.” *Time and Mind* 9 (4): 289–313.
Stahler, Daniel R., Douglas W. Smith, and Debra S. Guernsey. 2006. “Foraging and Feeding Ecology of the Gray Wolf (Canis Lupus): Lessons from Yellowstone National Park, Wyoming, USA.” *The Journal of Nutrition* 136 (7 Suppl): 1923S – 1926S.
Steinkopf, Leander. 2017. “Disgust, Empathy, and Care of the Sick: An Evolutionary Perspective.” *Evolutionary Psychological Science* 3 (2): 149–58.
Stewart, John R. 2007. “Neanderthal Extinction as Part of the Faunal Change in Europe during Oxygen Isotope Stage 3.” *Acta Zoologica Cracoviensia - Series A: Vertebrata* 50 (1-2): 93–124.
Stewart, John R., Adrian M. Lister, Ian Barnes, and Love Dalén. 2010. “Refugia Revisited: Individualistic Responses of Species in Space and Time.” *Proceedings. Biological Sciences / The Royal Society* 277 (1682): 661–71.
Stiner, Mary. 2012. “Competition Theory and the Case for Pleistocene Hominin-Carnivore Co-Evolution.” *Journal of Taphonomy* 10 (3): 129–45.
Stoneback, Jason W., Anastasiya A. Trizno, and Jay C. Albright. 2018. “Pediatric and Adolescent Injury in Rodeo.” *Research in Sports Medicine* 26 (sup1): 114–28.
Straus, W. L., Jr, and J. E. Cave. 1957. “Pathology and the Posture of Neanderthal Man.” *The Quarterly Review of Biology* 32 (4): 348–63.
Stuart, Anthony J., and Adrian M. Lister. 2012. “Extinction Chronology of the Woolly Rhinoceros Coelodonta Antiquitatis in the Context of Late Quaternary Megafaunal Extinctions in Northern Eurasia.” *Quaternary Science Reviews* 51 (September): 1–17.
Sugiyama, Lawrence S. 2001. “Implications of Pathology Risk and Disability Care for Human Life History Evolution: Evidence from Shiwiar Forager-Horticulturalists.” *Institute of Cognitive and Decision Sciences, University of Oregon*. https://pdfs.semanticscholar.org/f8e3/00d9497204a1b6e702ee00b9363f0a23aa07.pdf.
———. 2004. “Illness, Injury, and Disability among Shiwiar Forager-Horticulturalists: Implications of Health-Risk Buffering for the Evolution of Human Life History.” *American Journal of Physical Anthropology* 123 (4): 371–89.
Tappen, N. C. 1985. “The Dentition of the ‘old Man’ of La Chapelle-Aux-Saints and Inferences Concerning Neandertal Behavior.” *American Journal of Physical Anthropology* 67 (1): 43–50.

Terreros, José Yravedra Sáinz de los, Alberto Gómez-Castanedo, Julia Aramendi Picado, and Javier Baena Preysler. 2014. “Specialised Hunting of Iberian Ibex during Neanderthal Occupation at El Esquilleu Cave, Northern Spain.” *Antiquity* 88 (342): 1035–49.
Thorpe, Nick. 2016. “The Palaeolithic Compassion Debate--Alternative Projections of Modern-Day Disability into the Distant Past.” *Care in the Past: Archaeological and Interdisciplinary Perspectives*, 93.
Tilley, Lorna. 2015a. “Care Among the Neandertals: La Chapelle-Aux-Saints 1 and La Ferrassie 1 (Case Study 2).” In *Theory and Practice in the Bioarchaeology of Care*, 219–57. Bioarchaeology and Social Theory. Springer International Publishing.
———. 2015b. *Theory and Practice in the Bioarchaeology of Care:* Bioarchaeology and Social Theory . Springer International Publishing.
Treves, A., and L. Naughton-Treves. 1999. “Risk and Opportunity for Humans Coexisting with Large Carnivores.” *Journal of Human Evolution* 36 (3): 275–82.
Trinkaus, Erik. 1985. “Pathology and the Posture of the La Chapelle-Aux-Saints Neandertal.” *American Journal of Physical Anthropology* 67 (1): 19–41.
———. 2012. “Neandertals, Early Modern Humans, and Rodeo Riders.” *Journal of Archaeological Science* 39 (12): 3691–93.
———. 2014. *The Shanidar Neandertals*. Academic Press.
Trinkaus, Erik, Blaine Maley, and Alexandra P. Buzhilova. 2008a. “Brief Communication: Paleopathology of the Kiik-Koba 1 Neandertal.” *American Journal of Physical Anthropology: The Official Publication of the American Association of Physical Anthropologists* 137 (1): 106–12.
———. 2008b. “Brief Communication: Paleopathology of the Kiik-Koba 1 Neandertal.” *American Journal of Physical Anthropology* 137 (1): 106–12.
Trinkaus, Erik, and Pat Shipman. 1993. *The Neandertals: Changing the Image of Mankind*. Alfred a Knopf Inc.
Trinkaus, Erik, and Sébastien Villotte. 2017. “External Auditory Exostoses and Hearing Loss in the Shanidar 1 Neandertal.” *PloS One* 12 (10): e0186684.
Trinkaus, Erik, and M. R. Zimmerman. 1982. “Trauma among the Shanidar Neandertals.” *American Journal of Physical Anthropology* 57 (1): 61–76.
Trinkaus, E., and M. R. Zimmerman. 1982. “Trauma among the Shanidar Neandertals.” *American Journal of Physical Anthropology* 57 (1): 61–76.
Underdown, S. 2004. “Freezing, Fighting and Falling; an Exploration of Trauma Causality in the Neanderthals, Fuegians, Eskimo and Aleut.” In *American Journal of Physical Anthropology*, 198–198. WILEY-BLACKWELL COMMERCE PLACE, 350 MAIN ST, MALDEN 02148, MA USA.
Velo, Joseph. 1984. “Ochre as Medicine: A Suggestion for the Interpretation of the Archaeological Record.” *Current Anthropology* 25 (5): 674–674.
Vernot, Benjamin, and Joshua M. Akey. 2014. “Resurrecting Surviving Neandertal Lineages from Modern Human Genomes.” *Science* 343 (6174): 1017–21.
Waguespack, Nicole M. 2002. “Colonization of the Americas: Disease Ecology and the Paleoindian Lifestyle.” *Human Ecology* 30 (2): 227–43.
Walker, Alan, Michael R. Zimmerman, and Richard E. Leakey. 1982. “A Possible Case of Hypervitaminosis A in Homo Erectus.” *Nature* 296 (5854): 248–50.
Walker, Michael J., J. Zapata, A. V. Lombardi, and Erik Trinkaus. 2011. “New Evidence of Dental Pathology in 40,000-Year-Old Neandertals.” *Journal of Dental Research* 90 (4): 428–32.
Walker, Robert, Kim Hill, Hillard Kaplan, and Garnett McMillan. 2002. “Age-Dependency in Hunting Ability among the Ache of Eastern Paraguay.” *Journal of Human Evolution* 42 (6): 639–57.
Wang, Xiaoming, Richard H. Tedford, Blaire Van Valkenburgh, and Robert K. Wayne. 2004. “Evolutionary History, Molecular Systematics, and Evolutionary Ecology of Canidae.” *Biology and Conservation of Wild Canids (DW Macdonald and C. Sillero-Zubiri, Eds.). Oxford University Press, Oxford, United Kingdom*, 39–54.
Weyrich, Laura S., Sebastian Duchene, Julien Soubrier, Luis Arriola, Bastien Llamas, James Breen, Alan G. Morris, et al. 2017. “Neanderthal Behaviour, Diet, and Disease Inferred from Ancient DNA in Dental Calculus.” *Nature*, March. https://doi.org/10.1038/nature21674.
White, Mark, Paul Pettitt, and Danielle Schreve. 2016. “Shoot First, Ask Questions Later: Interpretative Narratives of Neanderthal Hunting.” *Quaternary Science Reviews* 140 (May): 1–20.
Wolf, D., T. Kolb, M. Alcaraz-Castaño, S. Heinrich, P. Baumgart, R. Calvo, J. Sánchez, et al. 2018. “Climate Deteriorations and Neanderthal Demise in Interior Iberia.” *Scientific Reports* 8 (1): 7048.
Wrangham, Richard W., Michael L. Wilson, and Martin N. Muller. 2006. “Comparative Rates of Violence in Chimpanzees and Humans.” *Primates; Journal of Primatology* 47 (1): 14–26.
Wroe, Stephen, William C. H. Parr, Justin A. Ledogar, Jason Bourke, Samuel P. Evans, Luca

Fiorenza, Stefano Benazzi, et al. 2018. “Computer Simulations Show That Neanderthal Facial Morphology Represents Adaptation to Cold and High Energy Demands, but Not Heavy Biting.” *Proceedings. Biological Sciences / The Royal Society* 285 (1876). https://doi.org/10.1098/rspb.2018.0085.

Wu, Xiujie, Ralph L. Holloway, Lynne A. Schepartz, and Song Xing. 2011. “A New Brain Endocast of Homo Erectus from Hulu Cave, Nanjing, China.” *American Journal of Physical Anthropology* 145 (3): 452–60.

Wu, Xiu-Jie, Lynne A. Schepartz, Wu Liu, and Erik Trinkaus. 2011. “Antemortem Trauma and Survival in the Late Middle Pleistocene Human Cranium from Maba, South China.” *Proceedings of the National Academy of Sciences of the United States of America* 108 (49): 19558–62.

Yravedra, José, and Lucía Cobo-Sánchez. 2015. “Neanderthal Exploitation of Ibex and Chamois in Southwestern Europe.” *Journal of Human Evolution* 78 (January): 12–32.

Zilhão, João, Diego E. Angelucci, Ernestina Badal-García, Francesco d’Errico, Floréal Daniel, Laure Dayet, Katerina Douka, et al. 2010. “Symbolic Use of Marine Shells and Mineral Pigments by Iberian Neandertals.” *Proceedings of the National Academy of Sciences of the United States of America* 107 (3): 1023–28.

Zollikofer, Christoph P. E., Marcia S. Ponce de León, Bernard Vandermeersch, and François Lévêque. 2002. “Evidence for Interpersonal Violence in the St. Césaire Neanderthal.” *Proceedings of the National Academy of Sciences* 99 (9): 6444–48.