Neandertals, Part V:

1.Neandertal Healthcare

2. Neandertal Endgame:
The Neandertal demise

Charles J Vella, PhD
July 2020

Neandertal Healthcare

Zoo Pharmacognosy: Animals who self medicate

- Many animal species have created their own pharmacies from ingredients that commonly occur in nature.
- Birds, bees, lizards, elephants, and chimpanzees all share a survival trait: They self-medicate. These animals eat things that make them feel better, or prevent disease, or kill parasites like flatworms, bacteria, and viruses, or just to aid in digestion. Even creatures with brains the size of pinheads somehow know to ingest certain plants or use them in unusual ways when they need them.
- Anyone who has seen a dog eat grass during a walk has witnessed self-medication. The dog probably has an upset stomach or a parasite. The grass helps them vomit up the problem or eliminate it with the feces.
- Zoo pharmacognosy: The science of animal self-medication

Neighborhood Pharmacies for animals

- A wide range of animals self-prescribe the plants around them when they need a remedy.
- Bears, deer, elk, and various carnivores, as well as great apes, are known to consume medicinal plants apparently to self-medicate.
- Some lizards are believed to respond to a bite by a venomous snake by eating a certain root to counter the venom.
- Baboons in Ethiopia eat the leaves of a plant to combat the flatworms that cause schistosomiasis.
- Fruit flies lay eggs in plants containing high ethanol levels when they detect parasitoid wasps, a way of protecting their offspring.

Neighborhood Pharmacies for animals

- Red and green macaws, along with many animals, eat clay to aid digestion and kill bacteria.
- Female woolly spider monkeys in Brazil add plants to their diet to increase or decrease their fertility.
- Pregnant lemurs in Madagascar nibble on tamarind and fig leaves and bark to aid in milk production, kill parasites, and increase the chances of a successful birth.
- Pregnant elephants in Kenya eat the leaves of some trees to induce delivery.

N sociality

- R. Dunbar: Sociality was a core characteristic in hominin evolution. Sociality & language were primary factor in the increased brain size of *Homo*
- Social collaboration was essential to early human evolution & survival.
- N group size: similar to hunter-gatherers ~30 people (4-6 families) with relations to neighboring clusters

Collaboration was essential to early human adaptation

- 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 defense from predators, increased meat eating, food sharing, collaborative hunting and increased dependence on social learning

- Early examples include the probable care for a hominin from Dmanisi with tooth loss and periodontal disease dated to 1.8 million years ago; for KNM-ER 1808, a *Homo ergaster* with hypervitaminosis and treponemal disease dated to around 1.6 Ma, and for WT1500, Turkana Boy, a *Homo erectus* with juvenile disc herniation dated to 1.6 Ma.

N Healthcare

- Neandertals lead a hard life:
- There are no adult Neanderthal skeletons that don't have at least one fracture,
- In N adults in their 30s, it's common to see multiple healed fractures.
- Few lived to old age of 45.
- Ns clearly cared for the sick and injured. Practiced Medicare for All
- Used plant based medication; knowledge gained over 400 K of experience

Healthcare based on social relatedness

- Ns high caloric energy requirements would have
  - limited group sizes and so
  - increased interdependence and the
  - of any individual hunter mortality.

- The loss of even one adult hunter in such a circumstance may be enough to make any such group more vulnerable, while their high relatedness would act to increase the selective advantages of helping others in the group.

N Medical competence

- Archaeological evidence also supports the notion that Neanderthals had a medical competence, a finding consistent with a pattern of
  - high rates of healing and
  - low levels of infection.
- The presence of interproximal grooves in teeth supports the use of toothpicks to reduce irritation in inflamed gums in cases of periodontal disease.
- The analysis of dental calculus has evidenced the presence of bitter tasting plants with minimal nutritional value, suggesting possible medicinal consumption.

Healthcare

- More speculatively, the mastery of tar production (may suggest an awareness of the health benefits in chewing this substance, both as an antiseptic and in maintaining the teeth.)
- The use of ochre is now well demonstrated (Zilhão et al. 2010) and this substance can be used as an antiseptic when applied to wounds (Velo 1984).
- No good evidence to support an interpretation of Neanderthal healthcare as unusually callous or calculating, i.e. abandonment of injured
- Good evidence for individuals with injuries and impairments being supported and accommodated, often with considerable effort, skill and knowledge.

Healthcare

- For Neanderthals food sharing, hunting, childcare and healthcare are likely to have been inseparable elements of social relationships based on strong social bonds and willingness to take risks and give up time or resources to improve others' survival

- Such investments in others' wellbeing were particularly critical to survival.

- Hunting of large game was notably dangerous, with some individuals inevitably risking serious injury on behalf of others.

How do archeologists identify ancient disease

- 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.

- Only the most severe cases of pathology (such as bone trauma and severe degenerative diseases) are identified in skeletal material

- Only the most severe cases can be attributed to probable care from others with any confidence

Modern comparisons

- % of the injuries requiring medical attention in modern wilderness activities, mostly through hiking with a heavy pack, were moderate (such as sprains and minor lacerations) and only 4% severe, such as fractures;

- In contrast N fossil material:
  - injuries recorded almost all would be classed as ‘severe’, taking the form of fractures and head injuries,
  - but far more common and much less serious pathologies are largely invisible.

(Wu et al. 2011)

Healthcare

- Costly cases of care are highly visible archaeologically whilst more common 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 were
  - predominantly low cost,
  - highly effective in improving health
  - and reducing mortality.

N altruism

- In a 2018 paper in *Quaternary Science Reviews*, Penny Spikins concludes that Neanderthals' medical skills were remarkably similar to our own ancestors' methods, and included
  - wound dressing,
  - fever management,
  - midwifery,
  - and a budding pharmacopeia of herbal remedies.

- Spikins, attempts to debunk the myth that Neanderthals lacked the compassion of modern *Homo sapiens,* listed individuals who could not have lived through their illnesses without the help of others.

Penny Spikins, et al., 2018

Calculated or caring? Neanderthal healthcare in social context

- Despite widespread evidence for recovery from injuries or survival despite impairments, apparent evidence for healthcare is given limited research attention.

- Based on a bioarcheology of care, Neanderthal medical treatment and healthcare was widespread and part of a social context of strong pro-social bonds

Penny Spikins, et al., 2018

Ns were tough and compassionate

- Neandertal skeletons very often show evidence of disease or disfigurement.
- The original 1856 Neandertal suffered and recovered from two serious injuries. 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).
- The La Chapelle N endured, in addition to arthritis, a broken rib and kneecap.
- Both individuals survived into their mid 40s, which indicates that Neandertals had the capacity for social action, or, if you prefer, empathy. They must—at least sometimes—have cared for their wounded.

Living to hunt another day: N healthcare

- Healthcare was a fundamental survival strategy for Neanderthals, not simply something they did—i.e. a cultural practice.

- These behaviors were highly effective at improving health and reducing mortality risk, offering an evolutionary advantage.

- N care for the ill and injured is based on skeletal evidence of recovery from serious illness and injury

- Neanderthal healthcare was widespread, knowledgeable and effective in reducing mortality risk.

Penny Spikins, et al., 2018

N healthcare

- Healthcare,
  - from likely short-term treatment for minor injuries and illnesses
  - as well as long term and significant accommodations,
  - functions to reduce the risks posed by injury, reducing mortality risks.

- N medications were advanced in that they allowed Ns to survive even after severe injuries and infections

N healthcare 2

- Neanderthals cleaned wounds, connected broken bones and midwifed births.

- Injury, rather than disease, was the most common threat: were not at high risk from pathogens because Ns didn't tend to live in large enough communities,

- Midwifery: Neanderthal women were at risk from difficulties arising from childbirth, which would likely have required assistance from midwife-like figures. The pelvic bones of N women and head of N newborns is similar to modern dimensions; without outside help, they would hardly have survived.

Dangerous life of Ns

- Neanderthals are commonly depicted as robust hominins who led stressful, dangerous lives.

- Traumatic injuries, considered to be common among remains of adult Neanderthals, are a major piece of evidence supporting this hypothesis:
  - not only are Neanderthals proposed to suffer from a high prevalence of trauma,
  - but they are also thought to exhibit more traumatic injuries than early modern humans.

Injuries: Rodeo Riders?

- Signs of injury can be found on almost every well-preserved adult Neanderthal skeleton (Trinkaus 1995; Berger and Trinkaus 1995)

- The majority of injuries are healed or partially healed,
  - suggesting that Neanderthals showed some level of compassion:
  - Many of the injured individuals would not have survived the period of convalescence without being cared for by others (Trinkaus 1983).

Limited mobility

- There are several N individuals who suffered from severely restricted mobility and possibly complete immobilization for at least some period of time.
- Examples of significant limitation in mobility: La Ferrassie 1 (probably on two occasions), La Ferrassie 2, Tabun 1, La Chapelle-aux-Saints 1 and Shanidar 1.
- Later mobility following such an injury could imply particularly successful care and recovery.
- Consideration of the wider archaeological evidence also casts doubt on interpretations of selective abandonment, such as of those with lower limb injures.

N Pathology: severe osteoarthritis and severe teeth loss

Old Man of La Chapelle-aux-Saint;
an arthritic Neandertal;
Boule's erroneous 1911 reconstruction

La Chapelle-aux-Saints man

Old Man of La Chapelle-aux-Saint: diseased left hip

La Chapelle aux Saints: LCS1

Figure 1. The crania of the La Chapelle aux Saints Neanderthal. Credit: https://upload.wikimedia.org/wikipedia/commons/e/e0/Homo_sapiens_neanderthalensis.jpgBy Luna04 (Own work) [GFDL (http://www.gnu.org/copyleft/fdl.html), CC-BY-SA-3.0

La Ferrassie 1: another N old man

N Mobility: selective abandonment?

- Neanderthals already needed to accommodate slow mobility in young children (Shaw et al. 2016).
- Trinkaus (2012) highlighted an apparent lack of individuals with debilitating lower leg injuries at death as evidence for abandonment.
- Preservation bias is likely to have affected interpretations of selective abandonment of individuals incapacitated by lower limb injuries.
- It is far more probable that the relative absence of those with immobilizing lower leg injury in the archaeological record is a result of these individuals not joining those using difficult to access rock shelters and caves than their selective abandonment.

More injured Ns = dumb Ns

- Estabrook comments: ‘The idea that Neanderthals are more frequently traumatized than modern populations is based on little evidence, but it has been well received because it dovetails nicely with this paradigm [of Neanderthals as “dumb”]’ (2009).

- There is no reason to assume the healthcare practices in Neanderthals were driven by the necessity of a life that was unusually harsh rather than being a caring social and cultural response to illness, injury and vulnerability.

N Healthcare

- Neanderthals were among the first to care for their elderly, ill and injured.

- N medical care: Ian Tattersall, from NY's AMNH, notes that a
  - Shanidar 1 burial reveals Neanderthals took care of an injured individual for years before his death
  - providing "powerful, presumptive evidence for empathy and caring within the social group, and possibly for complex social roles".

Technically competent healthcare

- Healthcare seems to have been knowledgeable and remarkably *technical*ly *competent* in Neanderthals.

- 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) would have needed to have been kept hydrated to manage fever, whilst those with severe wounds and fractures would have required adequate nutrition and rest.

Healthcare: splints, wound dressing

- High rates of healing and low rates of infection suggest that some form of wound management may have been common

- In the vast array of bones that archaeologists have uncovered, the fractures had often healed without significant deformities, suggesting that they had been set with a primitive splint.

- Many of these wounds, such as the severe head traumas and broken ribs, probably would have resulted in significant blood loss and increased risk of infection, yet the injured individuals survived long enough for the bones to heal, and their remains lack signs of severe infection on bone edges

- All of this suggests that Neanderthals had some means of dressing wounds.

N dentistry

- In a cave near the town of Krapina in Croatia, teeth belonged to a 130 Ka Neanderthal.
- Neanderthal dentistry used tools to treat toothache 130 Ka.

- The pattern of grooves on the teeth indicate that Ns attempted to treat dental problems with tools. Identified clear grooves made by some form of toothpick, together with other scratches in the dentin and enamel of the teeth.
- The scratches indicate this individual was pushing something into their mouth to get at that twisted premolar

- The conclusion that Neanderthals used tools as a way of relieving dental pain.

The four Neanderthal teeth showing signs of toothpick use, including the twisted premolar (indicated by the arrow).

- Fossilized El Sidrón Neandertal adolescent with dental abscess

Dietary self medication

- El Sidrón 1 may have been self-medicating a dental abscess.
  - ate poplar, which contains the natural pain-killer salicylic acid (the active ingredient in aspirin),
  - natural antibiotic producing Penicillium from the molded herbaceous material.
  - Also evidence for intracellular eukaryotic pathogen microsporidia (Enterocytozoon bieneusi), which causes acute diarrhea in humans
- Also some evidence that MHs and Ns appeared to swap mouth microbes at one point in time…through kissing or sharing food.

Yarrow use at Shanidar

- Hardy found the chemical signatures of yarrow and chamomile in dental plaque, which is also thought to be an anti-inflammatory agent. Since these plants taste extremely bitter, and have little nutritional value by themselves, it supports idea for self-medication.

- One of the other individuals in the Shanidar Cave was found to be buried with numerous plants that are believed to have medicinal properties, including yarrow, a natural antibacterial and anti-inflammatory agent that appears to accelerate wound healing.

- As a common folk cure, it is also said to reduce fevers and alleviate the symptoms of viral infections such as influenza, and to reduce flatulence and stomach cramps.

Shanidar Cave: Shanidar 1

- In Shanidar cave, partial skeletons of ten individuals, four of them deliberately buried.
- Shanidar 1 is a skeleton of a male who lived to be 40 to 45 years old, a very old age for prehistoric human.
- His height is estimated at 5 feet 7 inches, and his cranial capacity is 1,600 cc. Dated to 45 to 70 Ka
- He had injuries that made it impossible to perform normal activities leading researches to believe he must have been helped by others.

Shanidar I

- Shanidar I: “A one-armed, partially blind, possibly deaf, 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” *(Trinkaus and Shipman 1993)*.

- Perhaps the most famous individual benefitting from N compassion and 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).

Caring for others

- Solecki (1971) and later Trinkaus and Shipman (1993) concluded that someone so badly injured could not have survived without daily provision of food and assistance.

- Neanderthals must have been caring: to survive disabling injury or illness requires the help of fellow clan members.

- Bias in published discussion of a head injury in the St Césaire Neanderthal,
  - focuses almost entirely on implications of violence with
  - only passing mention of recovery from this trauma, which would have taken weeks or months of care

Shanidar 1

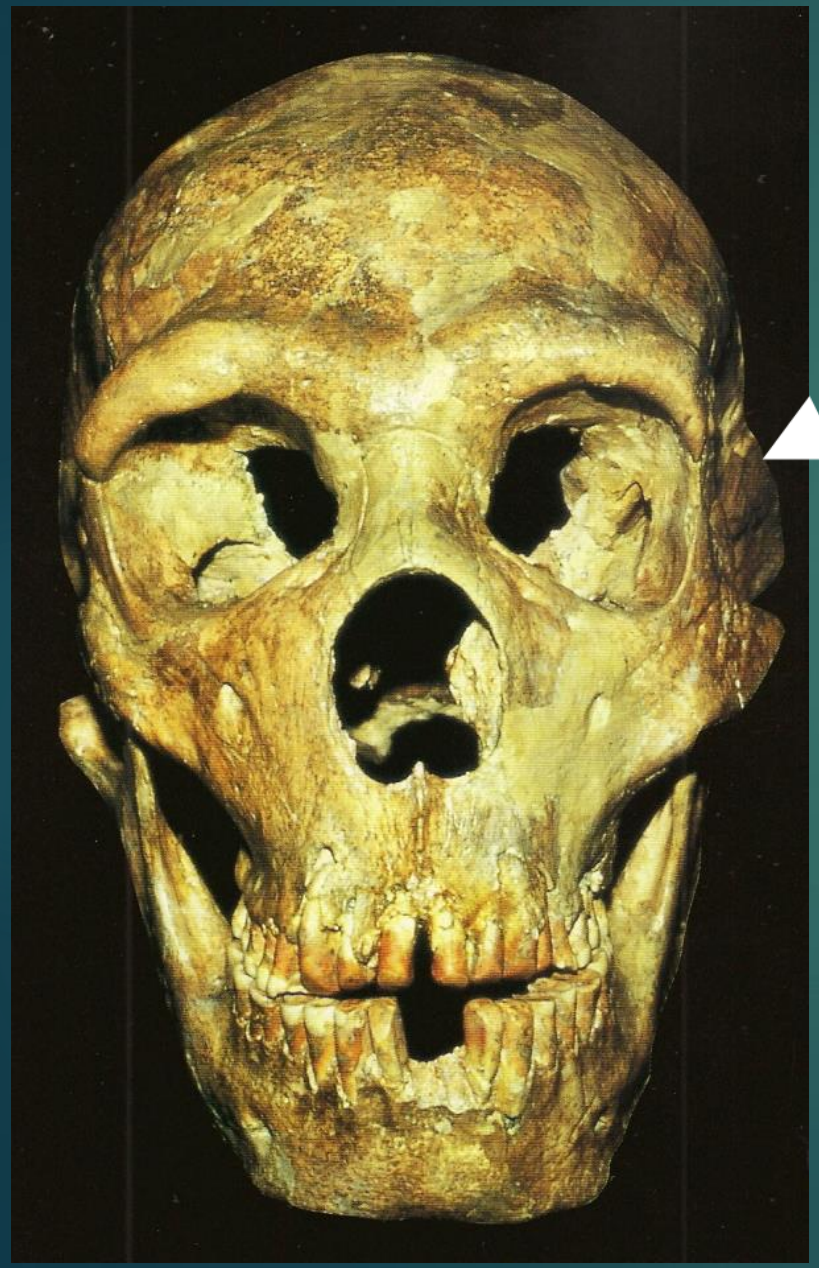
Shanidar 1 injuries

- 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
- 4 osteomyelitic (bone infection) 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

Shanidar 1 injuries

- 7 hyperostotic (excessive bone growth) disease, based on the presence of otherwise unexplained osteophytes
- 8 advanced DJD to the right knee
- 9 broadening of the right talus (ankle bone) relative to the left and the left tibia shows significant curvature, likely compensating for trauma in the right leg 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; probable reduction in vision or blindness
- 11 External auditory exostoses and hearing loss: auditory exostoses to the left meatus - grade III, and yet more advanced in the right meatus - grade III, with bridging across the porus; unilateral conductive hearing loss

Shanidar 1: adult male, 40-45 years, old & injured



- Eye socket crushed- Blinded in that eye
- Had suffered substantial injuries to arms, legs, & head, which had partially healed, suggesting he had been cared for by others

Left arm amputated above the elbow;
Also 1 N at Krapina

Shanidar 1 = He was inspiration for Creb, the disabled shaman in Jean M. Auel's novel *The Clan of the Cave Bear* (1980)

Shanidar 1: severe physical problems

- Shanidar 1:
  - elderly Neanderthal male known as ‘Nandy’
  - He was 1 of 4 reasonably complete skeletons from the cave which displayed trauma-related abnormalities, causing day-to-day life painful.
  - Suffered a violent blow to the left side of his face, causing a crushing fracture to his left orbit, making him partially or totally blind in one eye.
  - Suffered from profound hearing loss, as both ears were blocked by bone spurs.
  - Scars on ankles and ridges on his kneecaps indicated severe arthritis

Shanidar 1: Withered right arm compared to normal arm

Humeri from opposite arms of same male, Shanidar 1

Shanidar 1

- Had a withered right arm which had been fractured in several places that had healed, but which caused the loss of his lower arm and hand.
- This is thought to be either congenital, a result of childhood disease and trauma or due to an amputation later in his life.
- The arm had healed but the injury may have caused some paralysis down his right side, leading to deformities in his lower legs and foot and would have resulted in him walking with a pronounced, painful limp.
- All these injuries were acquired long before death, showing extensive healing.
- This has been used to infer that Neanderthals looked after their sick and aged, denoting implicit group concern.

Shanidar 1

- His right foot and lower right leg had also been broken while he was alive. Abnormal wear in his right knee, ankle and foot shows that he suffered from injury-induced arthritis that would have made walking painful, if not impossible.

- Researchers don't know how he was injured but believe that he could not have survived long without a hand from his fellow Ns.

- “This was really the first demonstration that Neanderthals behaved in what we think of as a fundamentally human way," says Trinkaus,

Shanidar 3, etc.

- Moreover, Shanidar 1 was not alone in surviving trauma: Shanidar 3 similarly sustained injury likely requiring care and many other Neanderthals show evidence of recovery from serious injury.

- Given the prevalence of injury and survival across the skeletal sample of Neanderthals, Trinkaus and Zimmerman commented (1982, 1975) that Neanderthals 'had achieved a level of societal development in which disabled individuals were well cared for by other members of the social group'.

- The Bau de l'Aubesier 11 Neanderthal who had lost nearly all her lower teeth before death, as well as suffering painful abscesses

N Injury and Disease Examples

- There are 30 Neandertals individuals with:
  - extensive tooth loss and abscesses;
  - traumatic lesion to right supraorbital torus, with evidence of healing;
  - osteoarthrosis of the spine with osteophytosis;
  - Blunt force injury marked by an oval depression to the frontal bone, with evidence of healing;
  - small blunt force traumas to the skull;
  - Two blunt force traumas to the frontal bone;
  - Depression to the frontal bone with evidence of healing;
  - Significant posterior parietal depressed fracture;
  - High degree of degeneration to C4-C7, likely caused by trauma; fibrous dysplasia

N Injury and Disease Examples

- Right clavicle fx, well healed,
- Right distal ulnar fracture and pseudoarthrosis or possible amputation;
- Fracture to the proximal end of the left ulna;
- Lesion to the orbital roof;
- Intervertebral ossifications/stiffening of the vertebral column;
- Degenerative disease of vertebral column;
- Trauma to the left ninth rib caused by a penetrating wound that likely collapsed the lung & extreme DJD to the right foot and bony spurs to the distal fibula and right talus;
- Minor DJD to the arms, hands and vertebral column & healed fracture of the seventh/eighth rib;
- Scalp wound to the frontal bone with evidence of healing;

N Injury and Disease Examples

- hypoplasia/atrophy of the left humerus & broken teeth;
- very severe tempero-mandibular osteoarthritis;
- thickening of the inner side of the frontal bone of the skull;
- Myositis ossificans associated with the linea aspera of the femur;
- loss of 15 teeth, abscesses, degeneration;
- Anterosuperior parietal trauma;
- Dental abscess & broken teeth;
- severe periodontal inflammation
- Endocranial hyperostosis limited to the frontal bone, localized to the central portion of the frontal squama & dental abscess

Sites with Neanderthal skeletal material and key sites with probable evidence of recovery through care. Healthcare case studies are in red and numbered: 1) Forbes' Quarry, 2) Cova Negra, 3) Les Pradel les, 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 fAubesier, 12) Saint Césaire, 13) Riparo Mezzena, 14) Guattan, 15) Krapina, 16) Safa, 17) Kiik-Koba, 18) Shanidar. Neanderthal skeletal material (black). Symbols: ▼ cranial/dental material only ▲ postcranial material only near complete or partial skeleton

Healthcare: Midwifery

- At least one form of Neanderthal health care seems more certain: midwifery.
- Skeletal remains demonstrate that, like anatomically modern humans, the size and shape of a Neanderthal baby's head and the mother's pelvis would have made unassisted childbirth dangerous.
- "The only way those heads could have got out of the birth canal is with that characteristic 'twist' which happens with modern humans at birth," says Spikins—a maneuver that presents a high risk without assistance. From this, we can be fairly certain that they had developed some kind of midwifery to reduce the mortality rates, she says.

Healthcare Conclusions

- Neanderthal care for illness and injury, and support of impairments, was widespread, and motivated by similar close social bonds to those in our own species.

- A social perspective on Neanderthal healthcare contributes to our understanding of Neanderthals as living in groups with deep investments in each other's wellbeing and with a competence to apply knowledgeable approaches to preserve health.

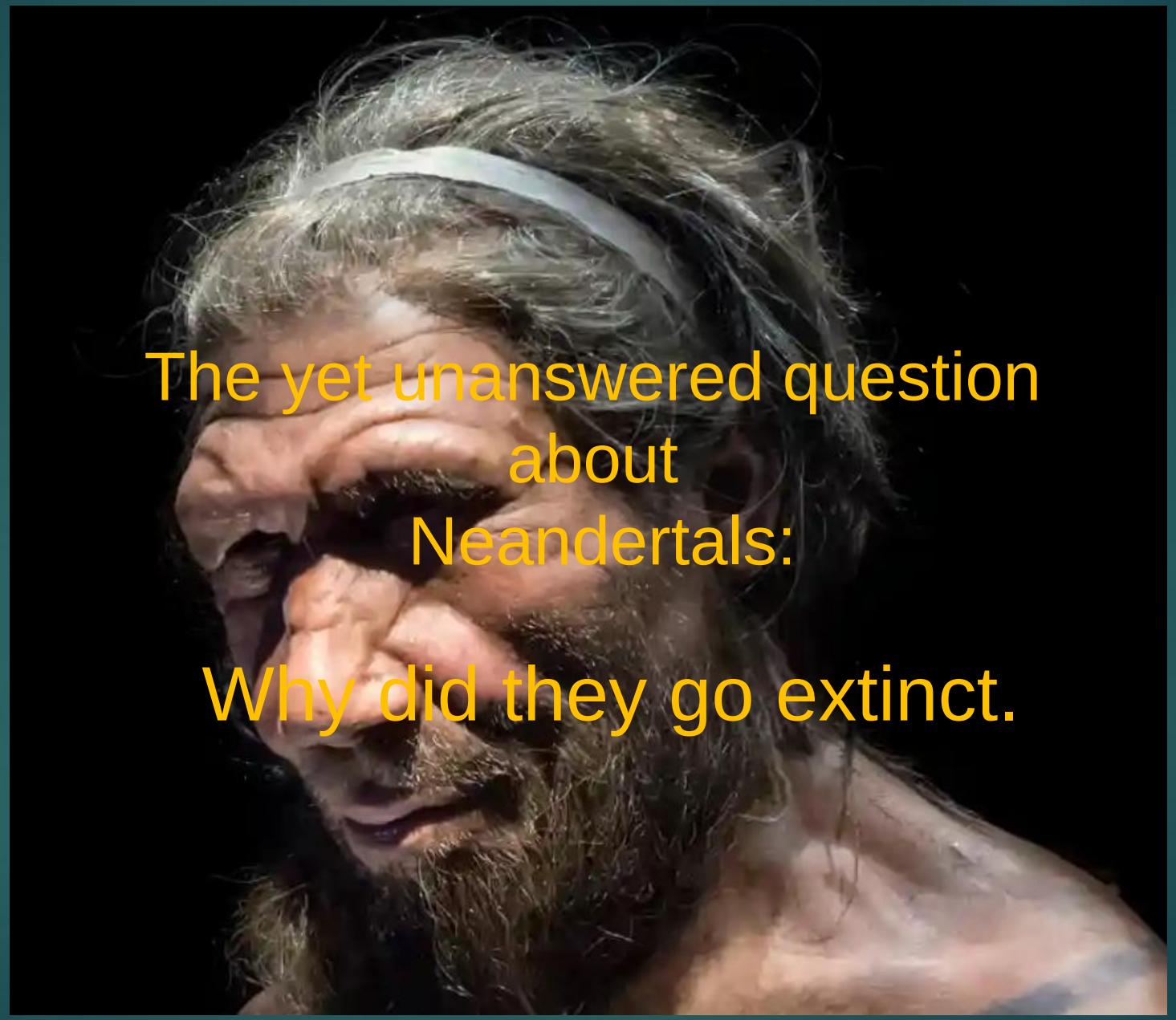
Healthcare

- Neanderthals appear to share a common human emotional and practical response to vulnerability and suffering of those that they were close to, attitudes also reflected in care of children, attitudes to the body at death through burial practice.

- Neanderthals were capable of caring for individuals who were ill or injured, from the provisioning of food, water and protection to active treatment for injuries

(Hublin 2009; Thorpe 2016; Trinkaus and Villotte 2017).


EXTINCT?! I'VE BEEN MARRIED TO ONE FOR 30 YEARS!
News
SCIENTISTS MAY CLONE EXTINCT NEANDERTHALS
BEER
DAVE GRANLUND © www.davegranlund.com


The yet unanswered question
about
Neandertals:
Why did they go extinct.

Our interest in N demise: Our own demise

- Part of the reason we're so intrigued is that on one level we wonder as a species whether we could disappear in the same way—gone but for a few instances in the fossil record.

- Our current existential choices: pandemics, global warming, nuclear war

- Rick Potts: our species didn't outsmart the Neanderthals, we simply out survived them.

Extinction is the norm for all animal species

- Average age of extinction of all species is ~1 million years.
- In the end, Neanderthals, though handy, big-brained, brawny and persistent, went the way of every human species but one.
- Rick Potts: "There have been a great many experiments at being human preceding us and none of them made it, so we should not think poorly of Neanderthal just because they went extinct"
- "Given that Neanderthal possessed the very traits that we think guarantee our success should make us pause about our place here on earth."

Demise of Ns

- Dr. Chris Stringer & Dr. Gamble: “There was **nothing inevitable** about the triumph of the Moderns, and a twist of Pleistocene fate could have left the Neandertals occupying Europe to this day. It was luck.”

- Until recently, the intellectual superiority of AMHs over Neandertals was cited as the major cause of Neandertal extinction.

- This hypothesis is of questionable merit as recent discoveries and our review in this interest group has shown that Neandertals were capable of behaviors that must be regarded as behaviorally and cognitively modern.

Pestera cu Oase: oldest MH in Europe

- Zilhão and Trinkaus labored on. In 2002, cavers found a human mandible in Pestera cu Oase, a bear cave in the Carpathian Mountains of Romania,

- Carbon-dating determined the mandible was 38 Ka.

- Like the Lagar Velho child, the find presented a mosaic of early modern human and possible Neanderthal ancestry.

- In 2015, DNA analysis showed that the owner of the jawbone had a Neanderthal in his lineage as recently as four generations back.

The earliest evidence for AMH in northwestern Europe: 45 Ka

- Historic theory: The earliest MHs appeared in Europe around 43–42 ka, by association with Aurignacian sites and lithic tools; actual physical evidence for MHs is extremely rare, and direct dates are ~41–39 ka.

- Higham, et al., 2011: A fragment of human maxilla (KC4) the Kent's Cavern site, UK, directly associated with two Aurignacian blades: collagen analysis of KC4, dates to 44–42 ka, making KC4 the oldest known anatomically modern human fossil in northwestern Europe

- Current data: Bacho Kiro Cave, Bulgaria, evidence MH starts ~45 Ka

T. Higham et al., 2011

Higham: N demise in different times and places

- T. Higham et al. 2014: statistical models plot changing spatial distributions of Neanderthals and modern humans

- The disappearance of Neanderthals occurred at different times in different regions. First in eastern Europe, then in Western Europe.

- Study: 40 key Mousterian and Neanderthal archaeological sites, ranging from Russia to Spain. Conclusion: the N Mousterian ended by 41,030–39,260 Ka across Europe

- The temporal overlap between the two groups was 2,600–5,400 years

T. Higham, 2014: Model of N demise

- Higham: In human terms, these transitions spanned some 130 to 270 generations,
  - There was a restriction of the Neanderthal presence in Europe to France at 40 Ka and their eventual extinction.
  - The survey did not include sites in Asia, where Ns may have survived longer
- Higham suggests that there was ample time for the transmission of cultural and symbolic behaviors, as well as possible genetic exchanges, between the two groups.

T. Higham, et al., 2014

Neandertal extinction

- **Neanderthal extinction** happened between 41 to 39 Ka in Europe, after MHs had reached the continent ~ 45 Ka.

- The last of the Neandertals are thought to have died out around 28 Ka at Gibraltar; but this date is debated

- No one knows why Neanderthals disappeared.

- It is unclear what role – if any – modern humans played in their demise.

Difficulty in estimating Extinction Dates

- Neandertal fossil record is strongly biased toward Neandertals from Western Europe, which is 20% of the size of their estimated total range but containing about three-quarters of all of the sites which yielded Neandertal remains.
- This pattern is partly related to
  - the preservation of fossils in caves and rock shelters in the limestone areas of France, Spain, and Italy
  - Is an artifact of the large amount of fieldwork done in the western tip of Eurasia.
  - In actual fact, the northern, eastern, and southern limits to their distribution are poorly documented, because of striking imbalances in research intensity
  - No unambiguous Neandertal sites are known from areas above 53° north in western Europe (Scandinavian countries), as well as in the eastern parts of their range

N Extinction theories

Hypotheses on the fate of the Neanderthals include:

- violence from encroaching anatomically modern humans
- parasites and pathogens
- competitive replacement (MH aggression)
- competitive exclusion (two species competing for the same limited resource cannot coexist)
- extinction by interbreeding with early modern human populations
- natural catastrophes
- failure or inability to adapt to climate change
- It is unlikely that any one of these hypotheses is sufficient on its own; rather, multiple factors probably contributed to the demise of an already small population.

Demise of N: complex factors

- Interbreeding and assimilation (a model first proposed by Fred Smith) are now supported by genetic data

- Interbreeding of Neandertals and modern humans may have helped modern humans to adapt to non-African environments but also introduced alleles that were not tolerated and contributed to N male hybrid sterility

Not MH superiority

- Those who see Ns as an inferior species suspect that smarter, more talkative, more social and adaptable early modern humans were to blame, outcompeting Neanderthals in terms of resource use, organization and reproductive success, if not direct confrontation.
- MH superiority theory: No significant data supports the supposed technological, social and cognitive inferiority of Neandertals compared to their AMH contemporaries.
- Single-factor explanations for the disappearance of the Neandertals are not warranted any more, and N demise was clearly more complex than many archaeology-based scenarios of “cognitive inferiority” seem to suggest.

N Endgame: 60 to 30 Ka

- N's final period (60-30 Ka) had wild swings of climate, and intrusion of a rival hominin
- Three phases
  - 1 - Classic N phase: began 60 Ka, during mild but highly variable, but colder, interglacial; N increased their range within Europe & eastwards into Asia
  - 2 – Overlap with *H. sapiens*; MHs did not initially have much of an advantage over the Ns
  - 3 – Final phase starts around 41 Ka
  - MH Culture called the Gravettian (33-21 Ka), probably a new influx of MHs, appears & was more successful than both N & earlier wave of MH was in Europe for 10 k; N was extinct in this period

Reasons for N demise

- For many years, climate change or MH competition have been the leading hypotheses.

- Recently these hypotheses have somewhat fallen out of favor due to the recognition that Neandertals were a highly developed species with complex social structure, culture and technical skills.

N Extinction Theoretical Models: causes of N demise at 40 Ka

- Neanderthals disappeared from the fossil record ~ 41-39 Ka and were replaced in Europe by anatomically modern forms.
- Models of possible causation of N demise: from least likely to most likely
- I) Early MH alliance with wolves resulting in domination of the food chain
- II) Volcanic eruptions: Mt. Toba or Campanian Ignimbrite volcanic eruption
- III) Genocide: Intergroup violence: Ns were killed off by MHs: localized quarrels for food or territory a la Colonial Europeans vs Native Americans

Causes of Extinction Theories

- IV) Spread of MH pathogens/disease to Ns
- V) Resource Competition:
  - Out competed by anatomically modern *H. sapiens*
  - Better energy extraction methods; Shorter gestation period
- VI) Effects of severe climate change
  - Sudden or repetitive climatic change
  - Large game dying out and Neandertals hunting methods not suitable?
- VII) Population Demographics: N population became too small
  - Family interbreeding; decline in genetic diversity; reduced fertility

Causes of Extinction Theories

- VIII. Genetic assimilation: Interbreeding & Hybridization with MHs
  - Genetically absorbed into *Homo sapiens* without significant genetic contributions to modern populations
  - Continuity? Evolved into MHs: Genetically absorbed
  - Interbred with anatomically modern *H. sapiens* to produce modern Europeans?
  - Evidence of MH Hybrids

Neandertal demise: MH Superiority Complex

- Villa P, Roebroeks W (2014) *Neandertal Demise: An Archaeological Analysis of the Modern Human Superiority Complex*. PLoS ONE 9(4)

- Modern humans in the MP and early UP are usually hypothesized as being superior to Ns in a wide range of domains,

- Their systematic review of the archaeological records of Ns and MH contemporaries finds no support for such an interpretation.

Paola Villa, Wil Roebroeks, 2014 See also **Neandertals revised -** Wil Roebroeks& Marie Soressi, 2016

N Demise: Nine MH Superiority Complex hypotheses

- 1. Ns did not have “complex symbolic communication systems” or “fully syntactic language”, while AMH did.
- 2 Neandertals had limited capacity for innovations.
- 3. Neandertals were less efficient hunters.
- 4. Neandertal weaponry was inferior to AMH projectile technology.
- 5. Neandertals had a narrow diet, unsuccessful in competition with AMH with their more diverse diets.

MH Superiority Complex hypotheses

- 6. Ns did not use of traps and snares to capture animals
- 7. Ns had smaller social networks.
- 8. Ns had smaller regional populations when AMH entered Neandertal territory
- 9. Hafting by AMH required complex procedures indicative of modern cognition, while Neandertals hafting was a simple procedure using naturally available glues.

Modern Human Superiority?: Conclusions

- All the 11 “archaeology-based” explanations for the demise of the Neandertals reviewed here are flawed.

- They were historical theories based on much less data than we now have available today and often based on comparisons with the later Upper Paleolithic of Europe

- Use of ocher, of personal ornaments, production of specialized bone tools, complex hafting techniques, and some art were already part of the Neandertal repertoire before the arrival of AMH in western Eurasia.

Modern Human Superiority?: Conclusions

- Production of bladelets has been securely identified in French Mousterian assemblages. Neandertals & late MSA humans had bladelet production by 60 Ka. It is their frequency, not cognition or technical competence, that distinguishes AMH bladelet production from that of Neandertals.

- The Neandertal archaeological record was not different enough to explain their demise in terms of inferiority in archaeologically visible domains.

- Thus, if Neandertals were not technologically and cognitively "disadvantaged", how can we explain that they did not survive?

N demise = complex process, not just 1 factor

- Villa & Roebroeks:
- Neandertal demise appears to have resulted from a complex and protracted process including multiple factors such as:
  - low Neandertal population density,
  - interbreeding with some cultural contact,
  - possible male hybrid sterility,
  - contraction in geographic distribution,
  - followed by genetic swamping and assimilation by modern human immigrants.

Villa & Roebroeks

Strangest theories of N demise

- Among the farther out theories:
- Ns got fried by increased UV-B radiation from temporary reduction in the ozone layer (Valet & Valladeas, 2010)
- Baked in their own skin thanks to mitochondria that leaked heat (Hudson et al. 2008)
- Transmissible spongiform encephalopathies, perpetrated by their cannibalistic habit of eating one another's brains (Chiarelli 2004): "Mad Neanderthal disease"
- Ns could not hunt rabbits.
- With all of the above, Ns may have welcomed extinction!

N Division of Labor: N women hunting a hinderance?

- In 2006, an efficiency explanation for the demise of the Neanderthals.
- In an article titled "What's a Mother to Do? The Division of Labor among Neanderthals and Modern Humans in Eurasia", it was posited that Neanderthal division of labor between the sexes was less developed than Middle paleolithic *Homo sapiens*.
- Both male and female Neanderthals participated in the single occupation of hunting big game, such as bison, deer, gazelles and wild horses.
- This hypothesis proposes that the Neanderthal's relative lack of labor division resulted in less efficient extraction of resources from the environment as compared to *Homo sapiens*.

Earth’s magnetic field and N demise: UV radiation

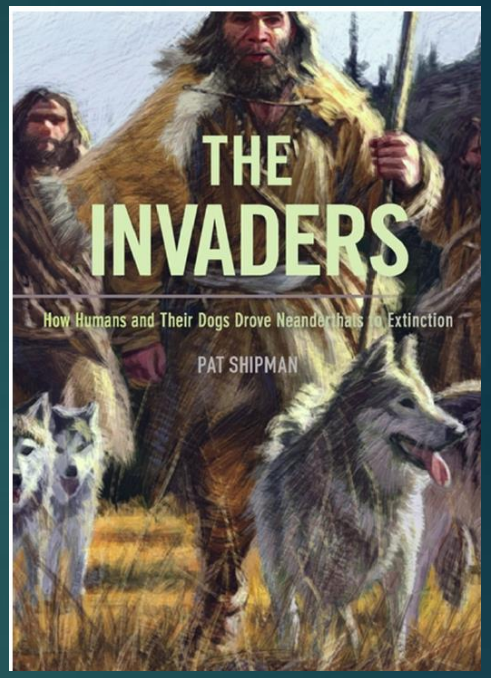
- 2019: journal *Reviews of Geophysics*, James Channell, from the University of Florida, and Luigi Vigliotti, from Italy's Institute of Marine Sciences, have linked changes in Earth's geomagnetic field to the evolution and extinction of mammals, claiming that periods where the field weakens appear to correlate to extinction episodes across the world.
- Earth's magnetic field extends from the planet's interior far into space. It protects the planet from the solar wind—a stream of charged particles coming from the Sun. If these particles were able to impact our atmosphere it could strip away the ozone layer that protects the planet from UV radiation.
- When the field reverses its poles, magnetic field gets weaker. During one reversal that took place around 41,000 years ago—known as the Laschamp event—the magnetic field is estimated to have fallen to just five percent of its current strength.

Earth’s magnetic field

- It is this reversal event that Channell and Vigliotti believe helped wipe out a number of mammal species in Australia and Eurasia—including Neanderthals.
- It caused an increase in detrimental mutations. In the study, the researchers say two extinction events—one 40,000 years ago and another 13,000 years ago—both appear to have coincided with periods where Earth's magnetic field had weakened
- The study suggests that modern humans were better protected from the harmful effects than Neanderthals due to differences in the aryl hydrocarbon receptor (AhR), which controls sensitivity to UV radiation

I - The Invaders. How Humans and Their Dogs Drove Neanderthals to Extinction – Pat Shipman, 2015: Wrong

- Her theory: coevolution of MHs with wolves (*Canis lupus*) had a great impact on the extinction of Neanderthals.
- She cites research on mtDNA lineages, suggests that between 36 and 26 Ka humans were able to breed a doglike animal.
- Problem: modern dog DNA = only at 16 Ka (Nova, 2020); all at MH sites; past N extinction time
- Wolves have now been shown to do cooperative rope pull for food and response to pointing



MH advantage in hunting warm climate animals

- Pat Shipman, argues that the domestication of the dog gave modern humans an advantage when hunting.
- The oldest disputed remains of domesticated dogs were found in Belgium (32 Ka) and in Siberia (33 Ka).
- In 2013, DNA testing on the 33 Ka "Altai dog", a paleolithic dog's remains from the Razboinichya Cave (Altai Mountains), has linked this dog with the present lineage of *Canis lupus familiaris.*
- 2017 study indicates it was a wolf.
- The archaeological record and genetic analysis show the remains of the Bonn–Oberkassel dog buried beside humans 14,200 years ago to be the first undisputed dog

Survival of the Friendliest: MH evolved via prosociality selection

- SciAmer, 2020: It was MH friendliness that was reason for MH superiority; developed via self domestication (a la 50 generations of Russian silver foxes)
- Ability to cooperatively communicate with others
- Evidence of self domestication: with more testosterone, thicker brow ridges, longer face, more aggression: MHs after 80Ka, MHs had 40% reduction brow ridges & 10% shorter faces; also skull & brain size decrease
- Increase in serotonin: SSRIs make people more cooperative
- Lower testosterone & higher serotonin increase oxytocin effects on social bonding
- Increased social networks and increased technological innovation as consequence
- But increased oxytocin can increase violence potential

B. Hare & V. Woods, 2020

Dogs are wolves that self domesticated themselves

- Dogs can read our gestures and our gaze better than any other species

- Dogs did not descend from wolves. Dogs and wolves shared a wolf like ancestor, the Ice Age Wolves, who survived when other large predators (giant hyenas, saber-tooth lions) did not. Dogs are not genetically close to any living wolf population; wild ancestor of the dog is extinct. Modern dogs were not descended from the same *Canis* lineage as modern wolves;

- Dog-wolf divergence occurring between 37-41 Ka; domestication much later; dog domestication preceded the emergence of agriculture

Who domesticated the dog

- Folklore that humans brought wolf puppies into camp & domesticated them. Theory has not held up.
- Taming occurs over a lifetime. Domestication takes generations & involves genome changes.
- Wolves eat too much meat (20 lbs a feeding) to be good co-hunters. Ice Age wolves were much larger than current wolves; you would not leave them at camp guarding your kids.

Siberian Silver fox domestication project

- Dogs: shorter snout and canine teeth; varying coat colors; curled tails; have floppy ears; breed throughout year = what unites all these traits? All the result of generations of self domestication
- 1959, Dmitry Belyeav: Siberian silver fox domestication experiment – 1 breeding criteria = whether fox would approach a human hand; selected the tamest, least aggressive individuals to breed
- Over the next 40 years (50 generations), he succeeded in producing foxes with traits that were never directly selected for, including piebald coats floppy ears, upturned tails, shortened snouts, and shifts in developmental timing; in effect, a fox that was a dog; foxes were only bred to be unafraid and attracted to humans; social intelligence happened by accident: They can read our intentions from our gestures
- Domestic phenotypic traits could arise through selection for a behavioral trait, and domestic behavioral traits could arise through the selection for a phenotypic trait: Shown in foxes, fallow deer, quail, mink

How did wolves turn into dogs

- Humans became more sedentary and produced more trash dumped outside of camps
- Trash leavings would be appealing to hungry wolves
- But only friendlier wolves would have been allowed to scavenge nearby. Would have to have been unafraid of humans. If they displayed aggression toward us, they would be killed.
- The wolves most likely drawn to human camps were the less-aggressive, subdominant pack members with lowered flight response, higher stress thresholds, & less wary of humans. Wolf population could have begun following mobile hunter-gatherers.
- This produced wolves with a reproductive advantage due to more food availability. Scavenging together probably lead to breeding together.

Wolves into dogs

- After generations of selection for friendliness to humans without intentional selection by humans, this friendlier group of wolves would begin to look different (coat coloring, teeth, ears). Humans became more tolerant of these wolves. We began to note their unique capacity to read us.

- 3 genes of Williams Syndrome (hyper-sociality, gaze fixation) are present in dogs; when dogs and their owners interact, extended eye contact (mutual gaze) increases oxytocin levels in both the dog and its owner.

- Such wolves could be joint hunters and guards, with warmth & companionship. Allowed into our camps.

- We did not domesticate wolves. The friendliest wolves self domesticated themselves.

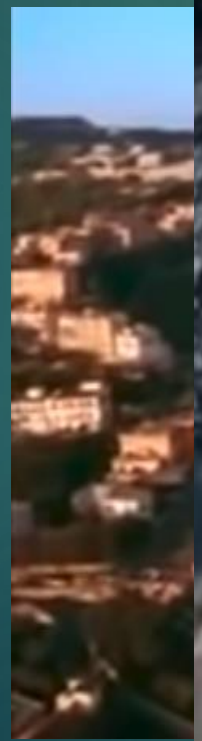
II. Volcanoes: extended volcanic winters

- 2 Volcanic events: Mt. Toba and Campi Flegrei
- Studies show that neither Neandertals nor modern humans were adversely affected by these climatic coolings. The decline of Neandertals was not associated with any volcanic eruption.

- Mt. Toba at 74 Ka: too early
  - There is no associated evidence of mammal decline or extinction even in environmentally-sensitive species. There is no evidence of habitat reduction at that time in Africa or Eurasia.
  - The Toba eruption did not have a significant effect on the climate of East Africa and was not the cause of a human bottleneck in Africa at around 75 ka, nor the later N extinction.
  - Likewise, there is archeological evidence that the Toba eruption did not affect the behavior of populations inhabiting peninsular India.

Campi Flegrei Volcanic eruption, 39 Ka

- Largest caldera in Europe; near Naples; largest eruption in 200 Ky; went S and E (eastward to Greece, Bulgaria and into Russia); ash over 5 million km
- But only 4 degree
- Most do not think



Natural catastrophe: Campanian Ignimbrite Eruption

- A number of researchers have argued that the Campanian Ignimbrite/ Campi Flegrei Eruption, a volcanic eruption near Naples, Italy, about 39,280 ± 110 years ago, erupting about 200 km^3 (48 cu mi) of magma (500 km^3 (120 cu mi) bulk volume) contributed to the extinction of Neanderthal man. Reduction of 1.8-3.6 degrees Fahrenheit for a period of 2 to 3 years.
- The hypothesis posits that although Neanderthals had encountered several Interglacials during 250,000 years in Europe, inability to adapt their hunting methods caused their extinction facing *H. sapiens* competition when Europe changed into a sparsely vegetated steppe and semi-desert during the last Ice Age.
- Studies of sediment layers at Mezmaiskaya Cave suggest a reduction of plant pollen. The damage to plant life would have led to a corresponding decline in plant-eating mammals hunted by the Neanderthals.

(Fedele *et al.* 2008; Golovanova *et al.* 2010

III. Genocide Model

- Fortress Europe: N prevalence until 45 Ka; MHs went East 1st (Israel at 120 Ka; China at 80 Ka; Australia at 65 Ka), then to Europe at 45 Ka

- Conflict between MH & Ns for territory: projectiles vs N physical strength & and klg of territory

- Shea speculates that modern humans were superior warriors and wiped out the Neanderthals. "Modern humans are very competitive and really good at using projectile weapons to kill from a distance," he says, adding they also probably worked together better in large groups, providing a battlefield edge.

Violence: No evidence

- Theory: Neanderthal extinction was either precipitated or hastened by violent conflict with *Homo sapiens*.
- The hypothesis that early humans violently replaced Neanderthals was first proposed by French paleontologist Marcellin Boule (the first researcher to publish an analysis of a Neanderthal) in 1911.
- Violence in early hunter-gatherer societies usually occurred as a result of resource competition following natural disasters. It is therefore plausible to suggest that violence, including primitive warfare, would have transpired between the two human species.
- Problem with theory: There is no archeological evidence of direct combat between the two species,

Violence: Shanidar 3

- Steven Churchill, 2009:
- In an experiment Churchill's team aimed to re-create the conditions of Shanidar 3's death using a crossbow, Stone Age projectiles and a pig carcass (pig skin and bones are thought to have the same toughness as Neanderthal skin and bones).
- When the projectiles were fired at a velocity consistent with that of a thrown spear the punctures left on the pig's ribs resembled those found on the Shanidar 3's ribs.
- By contrast when the ribs were stabbed with a thrusting spear Churchill found the ribs “were busted al to hell. The high kinetic energy cased a lot of damage on the area."
- In addition, the angle of entry of Shanidar 3's wound is “consistent with the ballistic trajectory of a thrown weapon."

IV. Pathogens: Neandertal pandemic

- Once Neandertal ancestors left Africa, their immune system adapted gradually to the pathogens in their new Eurasian environment.

- In contrast, AMHs continued to co-evolve with east African pathogens. More than 200,000 years later, AMHs carried pathogens that would have been alien to pre-historic Europe. First contact between long separated populations can be devastating.

- Theory: The introduction of viral, protozoan or bacterial pathogens to immunologically naïve populations leads to mass mortality and local population extinction.

The ecological challenges faced by Late Pleistocene Ns

- In warmer and more equatorial environments the risk of dying from pathogens as well as the health effects of pathogen loads are highest,
  - due to the diversity of pathogens present and
  - to a greater population density of hosts and greater possibilities for transmission.

- Hot and humid environments are particularly favorable for the spread of pathogens which are commonly the primary cause of hunter-gatherer mortality

Infectious disease: Africa to Europe

- Ns would have limited immunity to diseases they had not been exposed to, so diseases carried into Europe by *Homo sapiens* could have been particularly lethal to them.

- On the other hand, the same mechanism could work in reverse, and the resistance of *Homo sapiens* to Neanderthal pathogens and parasites would need explanation.

Gili Greenbaum, et al.,

Parasites and pathogens

- There is good reason to suppose that the net movement of novel human pathogens would have been overwhelmingly uni-directional, from Africa into the Eurasian landmass.

- The most common source of novel human pathogens (like HIV1 today) would have been our closest phylogenetic relatives, namely other primates, of which there were many in Africa but only one known species in Europe, the Barbary Macaque, and only a few species in Southern Asia.

Pathogens

- As a result, African populations of humans would have been exposed to, and developed resistance to, and become carriers of, more novel pathogens than their Eurasian cousins

- The unidirectional movement of pathogens would have enforced a unidirectional movement of human populations out of Africa, and doomed the immunologically naïve indigenous populations of Eurasia

Pathogens

- This putative "African advantage" would have persisted until the agricultural revolution 10,000 years ago in Eurasia, after which domesticated animals overtook other primates species as the most common source of novel human pathogens, replacing the "African advantage" with a "Eurasian advantage".

- The devastating effect of Eurasian pathogens on Native American populations in the historical era gives us some idea of the effect that modern humans may have had on the precursor populations of hominins in Eurasia 40,000 years ago.

Pathogens

- Rosenburg Study: modeled what would happen if the suite of tropical diseases MHs harbored were deadlier or more numerous than those carried by Neanderthals.

- The hypothesis is that the disease burden of the tropics was larger than the disease burden in temperate regions.

- An asymmetry of disease burden in the contact zone might have favored modern humans, who arrived there from the tropics

Noah Rosenberg

Pathogens: a la European contact with Indigenous Americans

- According to the models, even small differences in disease burden between the two groups at the outset would grow over time, eventually giving our ancestors the edge.

- As modern humans expanded deeper into Eurasia, they would have encountered Neanderthal populations that did not receive any protective immune genes via hybridization.

Disease burden

- Greenbaum propose that complex disease transmission patterns can explain how modern humans were able to wipe out Neanderthals in Europe and Asia in just a few thousand years

- Modeling of disease transmission and gene flow to show that when two species with unique disease burdens and immunities start to co-mingle, there is often a period of “stasis” where they both survive, trailed by a collapse of one species — like what befell modern human and Neanderthals.
- Ironically, what may have broken this stalemate and ultimately allowed our ancestors to supplant Neanderthals was the coming together of our two species through interbreeding.

Wolff and Greenwood, 2010

MH pathogens

- The hybrid humans born of these unions may have carried immune-related genes from both species, which would have slowly spread through modern human and Neanderthal populations.

- As these protective genes spread, the disease burden or consequences of infection within the two groups gradually lifted.

- Eventually, a tipping point was reached when modern humans acquired enough immunity that they could venture beyond the Levant and deeper into Neanderthal territory with few health consequences.

Pathogen demise theory

- Problem with theory:
  - Social Distancing –
  - Given N separation into smaller groups, pathogens would be less likely to spread widely
  - Genetic studies indicate MHs got immunological benefit from interbreeding from MHs
  - We have no evidence that MH pathogens wiped out the Ns

V. Most frequent theory of N demise: MH superiority

- Majority of N demise hypotheses revolve around the concepts of MH competition and competitive exclusion –
  - either exploitative competition (where both groups were contending for same resources) or
  - interference competition (direct, aggressive encounters) or both.

- MHs have history of ecological domination: note fate of megafaunal like mammoths or invading colonists eliminating indigenous peoples (Native American decimation) or loss of biodiversity.

N vs MH: competition

- This theory sees the advent of modern humans, perhaps with better cultural buffering and more effective social networks, as providing the coup de grâce to the highly stressed Neanderthal populations through competition for severely limited resources during the critical time interval of their co-existence in Europe (Stringer et al. 2003; Lahr and Foley 2003; Harvati 2007).

- In this view, it is the interaction between the effects of fluctuating climate and environment and of competition with modern humans that led to the eventual Neanderthal demise.

“Their bad luck was us."

- Elizabeth Kolbert wrote in The New Yorker:
- “Over the decades, many theories have been offered to explain what caused the demise of the Neanderthals, ranging from climate change to simple bad luck. In recent years, though, it's become increasingly clear that, as Svante Pääbo put it to me, “Their bad luck was us."
- Again and again, the archeological evidence in Europe indicates, once modern humans showed up in a region where Neanderthals were living, the Neanderthals in that region vanished. Perhaps the Neanderthals were actively pursued, or perhaps they were just outcompeted.
- The Neanderthals’ “bad luck” is presumably the same misfortune that the hobbits and the Denisovans encountered, and similar to the tragedy suffered by the giant marsupials that once browsed Australia, and the varied megafauna that used to inhabit North America, and the moas that lived in New Zealand.
- And it is precisely the same bad luck that today has brought so many species—including every one of the great apes—to the edge of oblivion.

MH competitive advantages

- Proposed modern human competitive advantages include demographic and subsistence factors, such as
  - larger group sizes ?
  - slightly higher birth rates,
  - lower mortality rates ?
  - shorter interbirth spacing,
  - greater dietary diversity ?
  - more complex social networks
  - better tools, clothing and shelter in modern humans ?

(Zubrow 1989; Skinner 1997; Flores 1998; Gat 1999; Richards et al. 2001; Stringer et al. 2003; Hockett and Haws 2005).

Competition

- Since the Protoaurignacians first appeared in Europe about 45,000 years ago and the Neanderthals disappeared from Europe between about 41,000 and 39,000 years ago, these new findings suggest that Protoaurignacians "caused, directly or indirectly, the demise of Neanderthals.
- It remains unclear just how modern humans might have driven Neanderthals into extinction.
- Modern humans might have competed with Neanderthals, or they might simply have assimilated Neanderthals into their populations.
- Moreover, prior research suggests that Neanderthals in Europe might have been headed toward extinction before modern humans even arrived on the continent. Neanderthals apparently experienced a decline in genetic diversity about the time when modern humans began turning up in Europe.

MH arrival in Europe

- At Bacho Kiro Cave, Bulgaria, evidence MH starts ~45 Ka
- The expansion of modern human population is thought to have begun 45,000 years ago, and it may have taken 15,000–20,000 years for Europe to be colonized, based on mitochDNA evidence.
- Almost no evidence of MH population sizes in Europe between 45 and 20 Ka
- Almost no evidence of their weapons in this time period; certainly no MH use of bows and arrows until after 20 Ka
- Both Ns and MHs just had spears

Competition with modern humans

- Archaeologists argue that the replacement of Neanderthals by modern humans was driven by interspecific competition due to a difference in culture level.
- Ecocultural niche modeling and radiocarbon dating suggest a causal role for interspecies competition in the extinction of Neanderthals.

- Most archaeologists argue that the advantage to modern humans lay in a higher culture level (a sizable minority dispute this view).

W. Gilpin, et al., 2016

Competitive replacement

- Competitive advantage on the part of modern humans has accounted for Neanderthals' decline on a timescale of thousands of years.

- Generally small and widely-dispersed fossil sites suggest that Neanderthals lived in less numerous and socially more isolated groups than contemporary *Homo sapiens*.

- Ns were cognitively inferior claim: Tools such as Mousterian flint stone flakes and Levallois points are remarkable but have a slow rate of variability and general technological inertia is noticeable during the entire fossil period. Artifacts are of utilitarian nature, and symbolic behavioral traits are undocumented before the arrival of modern humans in Europe around 40,000 to 35,000 years ago.

Claim: MHs had advanced technology

- Jared Diamond, supporter of competitive replacement, points out in his book *The Third Chimpanzee* that the replacement of Neanderthals by modern humans is comparable to patterns of behavior that occur whenever people with advanced technology clash with less advanced people.

Competitive exclusion

- Replacement of one species (or population) by another is ultimately a matter of numbers.
- One competing species survives while the other is reduced to, or approaches, zero in size. In the classical Lotka–Volterra model of interspecific competition, this process is called competitive exclusion.
- If Neanderthals were indeed outcompeted by modern humans, the question arises: Wherein lay the advantage to the latter species?
- Many suggestions have been made, including better tools, better clothing, and better economic organization. These hypotheses share the premise that modern humans were culturally more advanced than the coeval Neanderthals.

Supercomputer model: Competitive exclusion

- Supercomputer model both hominin groups compete for the same food resources and a small fraction is allowed to interbreed.
- Timmermann demonstrated that a realistic extinction in the computer model is only possible if Homo sapiens had significant advantages over Neanderthals in terms of exploiting existing food resources.
- Even though the model does not specify the details, possible reasons for the superiority of Homo sapiens could have been associated with better hunting techniques, stronger resistance to pathogens or higher fertility level.
- Identifies competitive exclusion as the likely reason for the disappearance of our cousins.

Timmermann et al., 2020

VI. Climate? Unlikely sole reason, but a clear stressor

- Climate theory of N demise: Worsening climatic and contingent environmental changes were a major driving forces in the Neanderthal extinction

- Recently available detailed paleoclimatic records have shown that the time period of the Neanderthal disappearance was prior to the Last Glacial Maximum (33 to 14 Ka), but was dominated by a period of very unstable climatic conditions

- While climate may not have been sole cause of N demise, it clearly acted as a population stressor.

(van Andel and Davies 2003; Tzedakis et al. 2007). .

Fate of Ns

- It is widely accepted that modern humans first arrived in Europe from the southeast, bearing the Aurignacian culture, and replaced the Neanderthals.

- The last Neandertal MP tool assemblages have been documented in the Iberian peninsula at sites such as **Gorham's Cave**, Gibraltar at 28 Ka, and it has been suggested that the Neanderthals were "pushed" to this cul-de-sac by the invading modern humans, deteriorating climatic conditions, or both.

(Finlayson 2006; but see Zilhao and Pettitt 2006 for a critique of these dates), Monnier, G. (2012) Neanderthal Behavior. Nature Education Knowledge 3(10):11

Climate

- Finlayson: suggests that a combination of climate change and the cumulative effect of repeated population busts eventually did them in.

- "I think it's the culmination of 100,000 years of climate hitting Neanderthals hard, their population diving during the cold years, rebounding some during warm years, then diving further when it got cold again," Finlayson says.

Demise: Climate

- In *The Humans Who Went Extinct* (Oxford University Press, 2009), for example, Clive Finlayson argues that the Neanderthals' stocky build and close-in hunting style limited them to a shrinking environment and made them increasingly vulnerable to a deteriorating climate, inbreeding, disease and competition.

- Chris Stringer at the Natural History Museum in London thinks the last Neanderthals were just unlucky. "It was one of the most unstable periods in terms of Earth's climate. They had to cope with those changes and they had a competing species alongside them," he says. "It was a kind of double whammy."

Potts and Finlayson: Climate was the culprit

- According to Potts, climate change was the instrument of their demise.
- Around 33 Ka, the Neanderthal, who migrated south from their northernmost range in Central Europe as glaciers advanced, settled in the wooded regions of Iberia (present-day Spain and Portugal) and Gibraltar.
- There, they flourished, possibly until 28,000 years ago, when they were supplanted by MHs.
- The Neanderthals lived in ever smaller and more isolated areas—suffering what we now call loss of habitat—eventually vanishing from the earth.

Demise Climate: effect on ecosystem

- Climate determines ecosystem survival

- Climate Theory: Neanderthals were better adapted to hunting in woodland environments than modern humans.

- But when Europe's climate began fluctuating, the forests became more open, becoming more like the African savannahs that modern humans were used to.
- The forests, which provided most of Neanderthals' food, dwindled and could no longer sustain them.

Finlayson: Climate was chief factor in N demise

- Finlayson:
  - MH Gravettian culture starts c 37K, with flint blades & bone points; more dense population, with more sites in an area; long term settlements & food storage; river fishing; hunted seasonal migrating animals; was first to exploit this environment; MHs better at pursuit long distance hunting;
  - Ns were in rivers and forest edges using ambush hunting of more sedentary animals; as steppes expanded, Ns contracted along with their preferred habitat; Iberian Peninsula as final refuge

C. Finlayson 2004

Biological and anatomical environmental responses

- The effects of selection pressures from challenging environments on Neanderthal biology and anatomy are well accepted.

- High endurance requirements and frequent famines influenced their body shape, proportions and physiology.

  - N had a similar body shape to other populations adapted to cold environments has been noted for some time

  - their facial morphology may also be an adaptation to cold and high energy demands.

Ecological change

- Finlayson:
  - originally thought that decline of forest regions (ambush hunting specialty; need for cover) to treeless steppe-tundra was cause of N decline
  - but Ns sites are also found in Central Europe with steppe-tundra fauna

- 30 % of N sites had reindeer, red deer, aurochs (forest); 25% were tundra (wooly mammoths, rhinoceros)

- More tundra related animals related to MHs in Europe

Preservation bias

- Did Ns live primarily in forests which disappeared with colder climate?

- Preservation Bias: Yet because
  - many more sites were preserved from glacial periods than warm climates,
  - scientists concluded that Neanderthals must have lived predominantly in harsher forest environments, where they barely clung on.

- Climate demise theory Fails to explain extinction in Middle East/ SW Asia

The ecological challenges faced by Late Pleistocene Ns

- Ns occupied challenging environments in the North Temperate zone

- Securely dated evidence for Neanderthal occupation stretches as far north as 55° N/ (At this latitude the sun is visible for 17 hours, 22 minutes during the summer solstice and 7 hours, 10 minutes during the winter solstice)

- Although highly debated Mousterian assemblages have been found as far north as near the Arctic Circle at Byzovaya. Neanderthals were not the first hominins to successfully occupy Western Eurasia but they nonetheless occupied the most northerly regions.

The ecological challenges faced by Late Pleistocene Ns

- Risks to mortality and survival:
- There are risks to effective reproduction posed by seasonal variations in the resources needed to support pregnancy and lactation
  - i.e. variable resources leading to potential famines,
  - extremes of cold which can threaten infant survival,
- Dependence on animal food for survival
  - increases with increasing distance from the equator,
  - average prey size increases with cold and increasing latitude bringing elevated risks of injury and mortality through injury from hunting
  - as well as through competition with other predators.

The ecological challenges faced by Late Pleistocene Ns

- While risks of infectious diseases reduce with increasing latitude, mortality risks from cold, injury and famine rise significantly.

- For modern Inuit, 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.

The ecological challenges faced by Late Pleistocene Ns

- Around 50% of Inuit from northern Alaska, Canada and Greenland, both historically and in archaeological contexts have spondylitis of the spine (Inflammatory back pain and fusing) due to fatigue and stress fractures.

- Climatic and ecological challenges in under a 1000 years had a substantial impact on Neanderthal communities during MIS 3

- Potential effects would include:
  - affecting the availability of food resources,
  - changing distributions of plant and animal communities,
  - and forcing costly and repeated mobility and changes in dietary habits.

N challenges

- During the last 10 K of N existence, there were contractions of N occupation from north and east Europe and into a few regions with milder climates including southerly Mediterranean refugia

- There was likely a significant fragmentation of Neanderthal distribution and demographic decline in Europe with frequent regional extinctions and sporadic population replacement

- Evidence for nutritional stress from enamel hypoplasia amongst Neanderthals was common

- Low N population densities and limited intergroup N contacts

Finlayson et al. 2004.

Climatic stress: Ns processed more bones, even toe bones

- Jamie Hodgkins: examined bones discovered in caves once inhabited by Neanderthals in southwestern France for marks demonstrating how the carcasses of deer and other animals were butchered and used for food.
- During colder, glacial periods, the bones were more heavily processed. In particular, they showed higher frequencies of percussion marks to consume all of the marrow, probably signaling reduced food availability.
- Cold, harsh environments were stressful for Neanderthals. As the climate got colder, Neanderthals had to put more into extracting nutrients from bones. This is especially apparent in evidence that reveals Neanderthals attempted to break open even low marrow yield bones, like the small bones of the feet.

Antonio Rosas: Demise - Inbreeding and climactic change

- Antonio Rosas's theory of N Demise: climactic changes induced familial inbreeding with the loss of genetic variability, which is the substrate on which evolution works.

- If genetic variability is lost, in the face of possible environmental changes, the species lacks genetic resources for survival

- At the time of the extinction of the Neanderthals, a great climatic change takes place on the planet: the last glaciation, which entails a cooling of the climate and a destruction of the existing ecosystems at that time.

Antonio Rosas: Demise - multiple factors

- It is possible that the ecosystems to which the Neandertals were more adapted were forested. This cooling and increase in aridity would end up destroying both deciduous and Neanderthal forests in many places.

- So, if we have isolated and scattered Neanderthal groups with low genetic variability, the ecosystems of those that were acclimated and adapted are deteriorating, and a very competitive species also enters, the combination of these factors leads to extinction.

- Problem with theory: Last Glacial Maximum = 33 to 14 Ka, after the N extinction

Climate

- None of the proposed dates for the Neanderthal extinction coincides or immediately precedes a major cooling episode, rejecting the hypothesis that catastrophic climate deterioration was the major cause for the Neanderthal disappearance

- The fact that Neanderthals had successfully survived previous cold phases also makes it difficult to accept climate change as the sole reason for their demise.

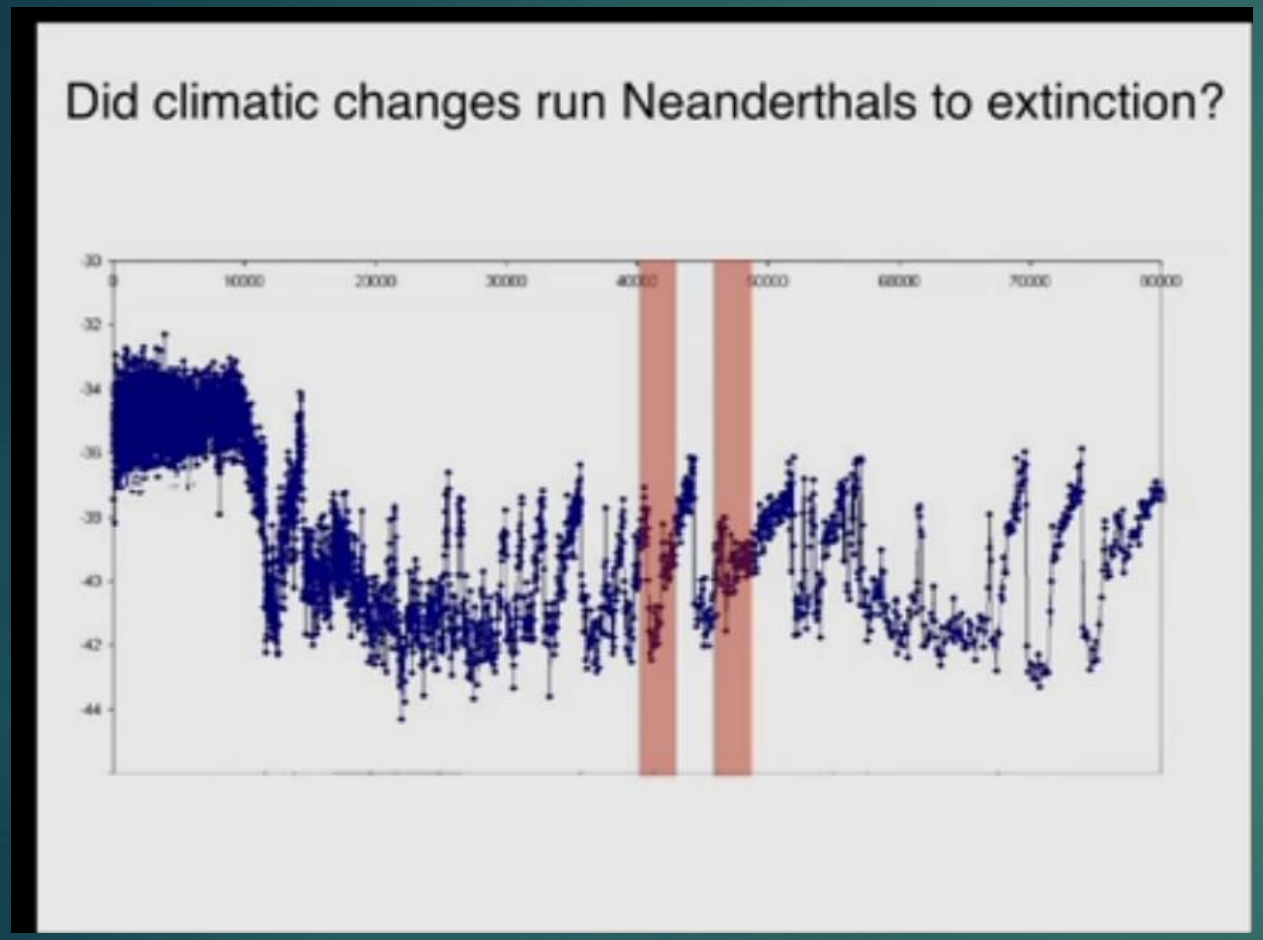
Climactic

- The genome of one female N from the Altai Mountains shows signs of long-term inbreeding in her population, a further indication of low numbers and isolation.

- Regular and sometimes extreme climatic fluctuations continually fragmented Neanderthal groups during their last 100,000 years, preventing them from building up large populations and continuous distributions across their range.

- Neanderthals did not all become extinct at the same time. Their disappearance may have been staggered, suggesting that they were replaced by early modern humans as a result of local population extinctions, rather than being quickly overrun.

Did climate play role in extinction of N?



- MH emerge in Europe in 2 waves:
  - 1st at 45 Ka,
  - 2nd in Eurasia at 42-43 Ka
- Older theory: climate jerkiness drove N to extinction
- but N had survived this jerkiness before

Stage 3 Project

- Some have argued that the
  - colder and highly variable climate of Oxygen isotope Stage 3 (57 to 24 Ka)
  - resulted in periods of climatic stress
  - which may ultimately have been responsible for the demise of the Neanderthals (Stringer *et al.* 2003)
  - through mechanisms such as the fragmentation of Neanderthal-favored habitats and their inability to adapt to new habitats (Finlayson 2004).

van Andel & Davies 2003, Finlayson & Carrion 2007

Climate

N Demise date

	climate phase	age ka BP
OIS 5a	early glacial warm phase	>74
OIS 4	transitional phase	74-66
OIS 4	first glacial maximum	66-59
OIS 3	stable warm phase	59-44
OIS 3	transitional phase	44-37
OIS 3	early cold phase	37-27
OIS 2	last glacial maximum	27-16

Stage 3 Project: climate between 60 to 24 Ka

- Stage 3 Project Oxygen isotope study: Stage 3 known for its incredible climactic variability, which is itself a stressor
- Temperature varied from warm to cold, at times shifting in 1000 years. 18 shifts during this period.
- At 45 Ka, temp in France was 61 to 72 F ^{o}
- At 41-39 Ka, Ns disappear
- By 33-14 Ka, severe cold: Last Glacial Maximum
- N numbers had decreased before this later cold period. So climate could not have been sole reason for extinction.
- But habitat was changing toward open steppe grasslands.

OIS-3 Climate: inhospitable to all hominins

- New data on the glacial period that occurred from about 65,000 to 25,000 years ago (known as OIS-3) shows that it was a period of rapid, severe and abrupt climate changes with profound environmental impacts.
- Evidence suggests that the severe conditions made the continent inhospitable for all humans living in Europe - and all populations died out about 30-28,000 years ago.
- However, there were other MH populations living in Africa that were able to recolonize Europe at a later date. As there were no Neanderthal populations elsewhere, they became extinct.

N hypoplasia: N teeth = climatic stress and starvation periods

- The teeth of 43 Ka Neanderthals found at El Sidrón cave in Spain showed signs of nutritional stress.

- 40% of all Neanderthal remains have hypoplasia, a condition caused by lack of nutrients in early childhood.

Climate: 60 to 24 K

- Incredibly variable cycle of warmth & cold; a source of stress
- But Northern Europe remained habitable. If look at other animals, most large animals survived this period
- So weather alone was not the cause of N's extinction; their numbers had declined well before climate reached most challenging state
- Toward end of this period, expansion of open steppe grasslands, with gradual cooling

Climate

- Staubwasser: Their study highlighted two cold and dry periods. One began about 44,000 years ago and lasted about 1,000 years. The other began about 40,800 years ago and lasted six centuries.

- The timing of those events matches the periods when artifacts from Neanderthals disappear and signs of H. sapiens appear in sites within the Danube River valley and in France.

Staubwasser et al.

2018: Stalagmite Climate data at 44 and 40 Ka & Ns

- Detailed new natural records from stalagmites in 2 Romanian caves that highlight changes in the European climate more than 40,000 years ago.
- Stalagmite yearly layers preserve a natural archive of climate change
- They found several cold periods that coincide with the timings of a near complete absence of archaeological artefacts from the Neanderthals
- The layers of the stalagmites showed a series of prolonged extreme cold and excessively dry conditions in Europe between 44,000 and 40,000 years ago.
- They highlight a cycle of temperatures gradually cooling, staying very cold for centuries to millennia and then warming again very abruptly.

Climate and Ns

- Climate records and archaeological records of Neanderthal artefacts: correlation between the cold periods and an absence of Neanderthal tools. Indicates the Neanderthal population greatly reduced during the cold periods
- Ecologic stress during these cold period expansion of steppe landscape caused a temporal pattern of depopulation of Neanderthals, which facilitated repopulation by modern humans who appear to have been better adapted to this environment.
- Consecutive depopulation–repopulation cycles during severe cold periods may principally explain the repeated replacement of Europe's population and its genetic composition.

Repetitive climate change

- When temperatures warmed again, Ns smaller populations could not expand as their habitat was also being occupied by modern humans and this facilitated a staggered expansion of modern humans into Europe.

- There was a higher N vulnerability to rapid environmental change and ecologic stress in the more open steppe landscape during cold and arid period of 44-42 Ka in most of the Danube steppe and tundra, modern humans may have been more capable to adapt and habitat track the expanding steppe in Central Europe

Climactic extinction of many megafauna

- Some researchers propose that N extinction can be viewed as one of the many Late Pleistocene megafauna extinctions caused by the loss of an environment with no modern analogue (Stewart et al. 2003; Stewart 2005).

- The contemporary extinction of around 35-40% of co-existing megafaunal species in particular supports the argument of a primary role of environment in Neanderthal decline (Stuart and Lister 2012) with Neanderthal populations eventually dying out in most of Europe between 35-40 Ka and ultimately in Iberia (Finlayson et al. 2006).

Quaternary Megafaunal Extinction

- The Quaternary Megafaunal Extinction exterminated more than 178 species of the world's largest mammals
- Quaternary Megafauna Extinction claimed two-thirds of mammal genera and one-half of species that weighed >44 kg between ≈50,000 and 3,000 years ago.
- It was Earth's last great extinction event, resulting in extinctions, population number reductions, and range changes due to environmental vegetative impoverishment due to climactic events
- Neanderthals, although they were large mammals (40 Kg); but are rarely mentioned in this megafaunal extinction. It is clear that Neandertals belong in the list of faunal taxa with a body weight greater than 40 Kg that became extinct in this time period

John R. Stewart 2007

N thermoregulation: adaptation to cold?

- N's bodies reflected their long exposure to cold

- The short, heavy stature and short distal limb proportions are thought to follow Bergmann's and Allen's rules for adaption to cold environments (Allen's rule: body better adapted to cold when its surface area is limited by shortened limbs) vs theory that physiology was based on power locomotion for ambush hunting

- Why did they die out in a non-severe cold period?

- Estimation that Ns had just 1 centigrade increased tolerance to cold; mostly depended on good clothing, fire, high fat diet, and shelters to stay warm (Aiello and Wheeler 2003).

VII. Population Dynamics: Ns did it all by themselves

- Charles Darwin observed that large population size is an important hedge against extinction in the presence of predators or other natural enemies
- Population size matters for the survival of a species

- Chris Stringer: "They may have disappeared in different regions for different reasons, but the background cause is clear. They didn't have the numbers."

A demographic marathon

- “When modern humans came," notes Chris Stringer, “there just weren't that many Neanderthals around.“
- For millenniums, some scientists believe, before modern humans poured in from Africa, the climate in Europe was exceptionally unstable. The landscape kept flipping between temperate forest and cold, treeless steppe. The fauna that Neanderthals subsisted on kept migrating away, faster than they could. Though Neanderthals survived this turbulence, they were never able to build up their numbers.
- J. Hawks: “There probably weren't enough of them to fill an N.F.L. stadium."

N demise as a demographic marathon

- Jon Mooallemjan: “Some paleoanthropologists are starting to reimagine the extinction of Neanderthals as something prosaic: not the culmination of some epic clash of civilizations but an aggregate result of a long, ecological muddle. Strictly speaking, extinction is what happens after a species fails to maintain a higher proportion of births to deaths — it's a numbers game. And so the real competition between Neanderthals and early modern humans wasn't localized quarrels for food or territory but a quiet, millenniums-long demographic marathon: each species repopulating itself, until one fell so far behind that it vanished. And we had a big head start.

Jon Mooallemjan, New York Times magazine, January 11, 2017

A demographic marathon

- C. Stringer: With the demographics so skewed even the slightest modern human advantage would be amplified tremendously: a single innovation, something like sewing needles, might protect just enough babies from the elements to lower the infant mortality rate and allow modern humans to conclusively overtake the Neanderthals.
- But Stringer is careful not to conflate innovation with superior intelligence. Innovation, too, can be a function of population size.
- Disappearance of Neanderthals might have resided in the smallness of their populations alone – even if they had been identical to modern humans in their cognitive, social and cultural traits, and even in the absence of competition for the same resources, Neanderthals faced a considerable risk of extinction.

Demographics

Based on current paleogenetic studies which indicate low N genetic diversity, Neandertal populations were small

- Small populations go extinct all the time for stochastic (random) reasons:
  - N had small group sizes
  - Lower birth rates: If low fertility rate, population will crash
  - Higher mortality rates
  - Increased family interbreeding; decline in genetic diversity

Historical pattern of N demographics

- Clear phases of presence and absence of Neandertals in the Late Pleistocene, very probably the result of a process of repeated phases of colonization, regional extinction, and recolonization, during earlier glacial–interglacial cycles.

- This process must have been an important factor in the demography of these populations, including their limited genetic variation:

- Genetic studies show that (late) Neandertal populations had small effective population sizes and were inbred

- They were “Thin on the Ground”

Population Dynamics

- Researchers' simulations suggest that small population sizes and familial inbreeding made Neanderthal populations vulnerable to chance fluctuations in population size.

- Inbreeding, small population sizes, and a pinch of misfortune could have been sufficient to wipe out our hominin cousins around 40,000 years ago.

- MHs were not needed for the Neanderthals to go extinct.

Steven Churchill, 2014: Thin on the Ground

- Ns appear to have lived at relatively low population densities throughout their existence. Their relatively small population size would have impeded technological advancement, while making Ns vulnerable to extinction even before MH appeared.

- The technologically-mediated competitive advantage of MHs may have been an epiphenomenon of population growth. Larger population size correlates with tech innovation; lower size impedes innovation

- Why did Ns live at such low population size, why were they so “thin on the ground.”

- the energetic and ecological factors likely kept Ns at low population density throughout their existence.

Steven Churchill, 2014: Thin on the Ground

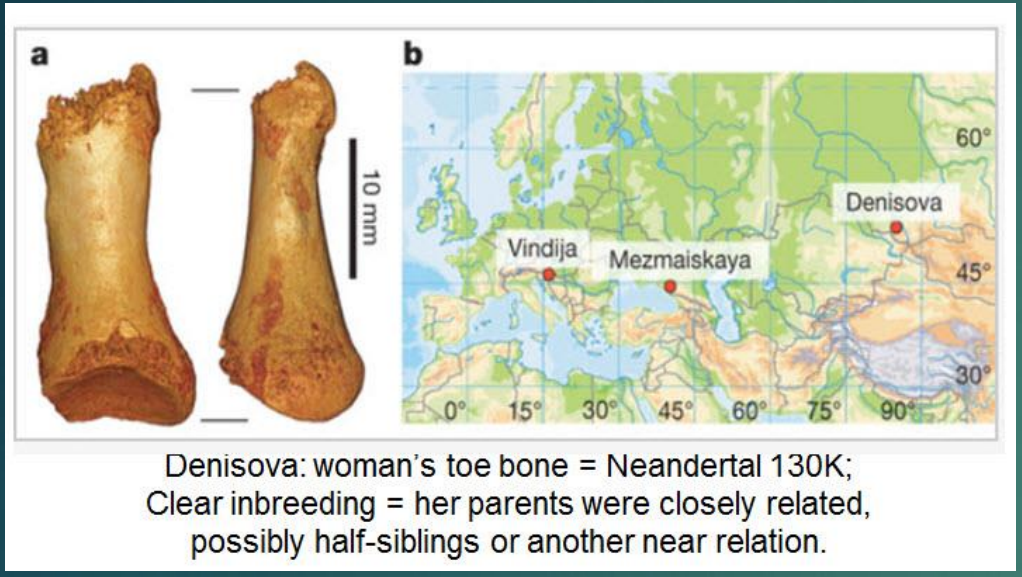
- First, Ns physical adaptations were effective, but energetically costly (body shape produced heat vs cold). He believes high cost of somatic maintenance and foraging resulted in N energy budgets that were vey tight.

- Ns physical adaptations constrained fat storage and reproduction energy.

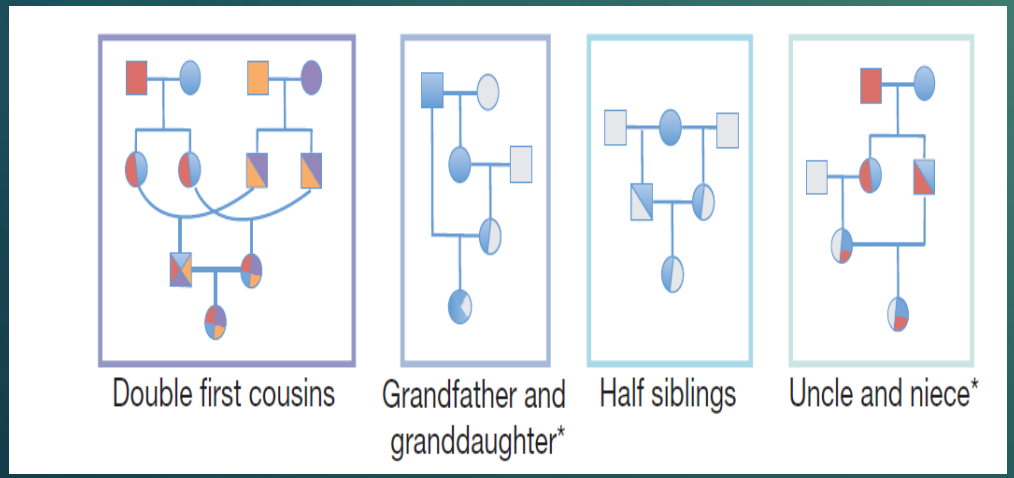
- Ns had more difficult time attaining levels of fertility needed for population growth. Given high adult mortality, even reproduction sufficient for maintenance of stable population may have been a challenge for Ns at some time.

- Second, consideration of carnivore resource competition suggests that N population growth may have been ecologically constrained. N population size may have been constrained by ferocious cast of carnivore competitors.

2014: Reason for Neandertal Demise: Low population number with interbreeding



Denisova: woman's toe bone = Neandertal 130K;
Clear inbreeding = her parents were closely related, possibly half-siblings or another near relation.



Prüfer, 2014: Denisova Neandertal woman toe bones:

Chromosome 21: M & F genetically related (19 Mb base pairs with no difference)

- Half siblings
- Grandfather-granddaughter
- Aunt-nephew
- Double first cousins

Pruefer et al., , Nature, 2014

Allee effect: individual fitness depends on population size

- Species go extinct. A small group of a rare butterfly or of individual of any species, is more prone to extinction.
- Allee effects = population size effects the biological fitness (ability to servive and reproduce) of members of a group;

- Allee effects are a small population phenomenon in which population growth rate is reduced by small group size; Allee effects are strongest in small populations.

- Clyde Allee, a zoologist, noticed that in many species it was *small group size,* not competition, that limited population growth. Having larger group size has positive effects on the survival

Allee effect: individual fitness and population size

- An Allee effect is a positive association between average individual fitness and population size over some finite period.

- Such a positive association may give rise to a critical population size below which the population cannot persist

- Allee effects have two manifestations:

1. Positive association between some fitness component (e.g., viability, juvenile survivorship, fertility) and population size

2. Positive association between population growth and population size.

Allee effect: individual fitness and population size

- A negative relationship between fitness and population size can be caused by a variety of mechanisms that affect reproduction and survival. Examples of Allee effect:
  - Too few people to hunt and provide food , or to raise the group's kids
  - Low availability of mates (Mate limitation reduces reproduction):
  - Low population size = decreased reproductive success or survivorship
  - Increased vulnerability to predators: risk of predation is larger in smaller prey populations than in larger prey populations
  - If population size is small, inbreeding can cause an Allee effect by reducing average fitness as population size declines
- Small populations suffer from reduced average individual fitness.

Just random, bad luck

- Vaesen 2019 study: “Humans were not needed for the Neanderthals to go extinct. It’s certainly possible that it was just bad luck.”

- The Neanderthal population was so small at the time modern humans arrived in Europe and the Near East that inbreeding and natural fluctuations in birth rates, death rates and sex ratios could have finished them off.

- With small N population size, the models implement three factors that conservation biology identifies as critical for a small population’s persistence,
  - Inbreeding,
  - Allee effects and
  - Random natural fluctuations.

Krist Vaesen, et al., 2019

Alee effects: female reproduction

- Modeled the effects of inbreeding, Allee effects and random yearly changes in the numbers of births and deaths, as well as gender ratios.
- Could these factors alone have caused extinction over a period of 10,000 years – findings:
  - while inbreeding by itself was unlikely to have led to the decline of Neanderthals,
  - it could have had an impact when combined with a sudden decline in birth rates.
- Reproduction-related Allee effects: if N females giving birth within a year dropped to 25 % or less, as is commonly seen in modern-day hunter-gatherer groups, result would have caused extinctions in Neanderthal groups as large as 1,000.

Living on the edge: Was demographic weakness the cause of Neanderthal demise?

- 2019 Degioanni modeling study of demographic factors:
- Investigate the disappearance of Neanderthals by examining the extent of demographic changes needed over a period of 10,000 years (yrs) to lead to their extinction.
- A slight (<4%) but continuous decrease in the fertility rate of younger Neanderthal women could have had a significant impact on these dynamics, and could have precipitated their demise.
- Our results open the way to non-catastrophic events as plausible explanations for Neanderthal extinction.

Anna Degioanni, et al., 2019

Demographic Weakness: conclusions

- In the long run, a slight change in the fertility rate of younger females could have had a dramatic impact on the growth rate of the Neanderthal metapopulation and thus on its long-term survival, in agreement with the observed extinction of Neanderthals within a 10,000, 6,000 or a 4,000 years period.
- Our modelling suggests that it is not necessary to explain the decrease in size of the Neanderthal population on the basis of catastrophic causes (diseases, extreme climatic events, and disasters such as volcanic eruptions. . . .) or even of the direct or indirect intervention of *sapiens*.
- It only takes a slight decrease in food resources over a period of some years to cause a decrease in fertility.

Ns = 40% less fit

- Computational geneticists Kelley Harris of Stanford Univ. and Rasmus Nielsen of UCB propose a simple answer to N's demise:

- Due to their smaller population size, Neanderthals were less evolutionary fit than modern humans, for the same reason that small, inbred groups today are less healthy.
- In small populations, mildly harmful mutations are more likely to persist and rise in frequency, while in larger populations they are weeded out by natural selection.

- Average Neanderthal would have had at least 40 % lower evolutionary fitness than the average modern human at the time they met.

40% less fit

- This would result in Ns having had fewer surviving offspring than modern humans when the groups were in the same place, at the same time — fewer offspring = lower evolutionary fitness.

- The hybrid offspring of N and MHs would also have been less fit, and those small bits of Neanderthal DNA in present-day humans may reduce our fitness by 0.5 percent.

Neanderthal Demographic Estimates: Population Size

- Hypothesis: demography of the Neanderthal metapopulation, living under conditions where extreme environmental instability over short periods was the norm, stayed small, with frequent bottlenecks and episodes of decline.
- Hublin: Their winters were brutal and long. It's likely that many of their small groups simply died out in long phases of starvation and were replaced by new members. Even in times of their widest distribution, there were probably no more than an estimated 10,000 'Neanderthal Europeans'. 'The Stone Age was an empty world,' Hublin says.

JP Bocquet-Appel & A. Degioanni- 2013

Demographic reason for N demise: Gradual replacement

- Another study: computer modeling to show that the continuous migration of modern humans from Africa into Eurasia meant that they were always going to eventually replace Neanderthals
- Recurring migration from Africa into the Levant and Europe — even at a low rate — was sufficient to result in the Neanderthals' replacement even if neither species had a selective advantage over the other, and regardless of possible differences in population size between the two species
- Even when the migration rates of humans were low, Neanderthals in the model died out within 12,000 years. This, Kolodny and Feldman write, proposes a scenario of "gradual replacement." This model raises questions as to whether modern humans really were all that superior to their stocky, heavy-browed peers

VIII: Genetic Assimilation/Hybridization

- Fred Smith: First to propose theory of N extinction by hybridization or genetic assimilation
- What if our species -- arriving in waves from Africa -- overwhelmed Neanderthals, and perhaps Denisovans, with affection rather than aggression?
- "Part of the story of these groups is that they may simply have been absorbed by modern populations," said Svante Pääbo. "The modern humans were more numerous, and the other species might have been incorporated."
- Nielsen et al. (2017) raise the possibility that Neanderthal extinction is due to interbreeding and absorption into Homo sapiens groups, rather than an inability to out compete them or to adapt to climate change.

Fred Smith, et al., 2005

"Extinction by Hybridization"

- Genetic swamping is a well-known extinction cause among plant and animal species.
- A smallish group of native, localized trout, for example, may lose their genetic identity after a large influx of a different species with which the native fish are able to breed.
- "When local populations are specialized, and for some reason there is a change in their interaction with adjacent populations, and that interaction level goes up, they tend to go extinct—especially if one population is much smaller than the other. In conservation biology this is called extinction by hybridization."
- Over generations of genetic mixing, the Neanderthal genome would have dissolved, absorbed into the *Homo sapiens* population, which was much larger.

Genetic Assimilation/Hybridization

- As MHs entered Europe ~ 45 Ka, only those Neanderthals that rejected MH contact would be able to sustain a distinct gene pool.
- Most modern hunter/gatherers positively engage new people, because their wealth is measured in social relations, encouraging interbreeding (oldest human law) or 'marrying out'.
- Over time, the two populations would blend and the group with the fewest members, would have the least impact on descendant genetic makeup.
- Since modern humans had babies earlier and more often, Neanderthal populations were eventually subsumed into the modern population.

Interbreeding: MHs have 1-2% N genes

- In 2010 a draft sequence of the Neandertal nuclear DNA provided clear evidence of interbreeding between Neandertals and modern humans.
- Originally noted as 1-4%; a revised estimate now suggests 1.5–2.1%.
- In sum, interbreeding and assimilation are now supported by genetic data
- Gene flow from Ns to modern humans occurred, ~50 Ka.

(Green *et al*., 2006; Prüfer *et al*., 2014).

Interbreeding

- 20-30 percent of all Neanderthal DNA survived in modern humans
- Early MHs exhibited a larger percentage of N genes than the current 1-2% in MHs
- Ns and MHs share 99.7% of our nuclear DNA (1 M basepair difference); we share 202 MtDNA basepairs with N; me and you share 99.9% nDNA
- 23andMe tests 7,462 N variants; CJV has 223 N variants (in lowest 25%tile)

Interbreeding

- Interbreeding of Ns and MHs
  - helped modern humans to immunologically adapt to non-African environments
  - also introduced alleles that were not tolerated and contributed to N male hybrid sterility

- Much of N DNA appears to haven been deleterious in humans, and natural selection acted to remove it.

The Neandertal fate: assimilation or replacement?

- Wynn and Coolidge: Proponents of the Neandertal indistinguishability claim (e.g., Villa & Roebroeks, 2014; Zilhão, 2014) have adopted it to support the idea of Neandertal assimilation, a wholesale incorporation and integration into the AMH population.

- However, the assimilation hypothesis is challenged by the low percentage of Neandertal DNA in the human genome: only 1.5 to 2.1% of the genomes of Europeans and Asians

- The low introgression rate, along with a skew in its directionality (i.e., from Neandertals to AMH but not the reverse), [CJV: ????] argues that interbreeding was rare, non-productive, or both

Evidence of hybrid sterility

- Modern humans show an absence of Neanderthal-derived
  - patrilineal Y-chromosome (Neandertal Y-chromosome genes are gone in current MHs)
  - matrilineal mitochondrial DNA (mtDNA), along with
  - underrepresentation of Neanderthal X chromosome DNA,
- These could imply reduced fertility or frequent sterility of some male hybrid crosses, representing a partial biological reproductive barrier between the groups, and therefore species distinction.

- Svante Pääbo prefers term “human metapopulation”, not different species

Like feral cats today

- Trinkaus compares it to how European wildcats are currently disappearing, absorbed into much larger populations of house cats gone feral. It wasn't a flattering analogy — we are the house cats — but that was Trinkaus's point: "I think a lot of this is basically banal"

- Finlayson on Gibraltar Ns: Likened the population there to critically endangered species today, like snow leopards or imperiled butterflies: living relics carrying on in small, fragmented populations long after they've passed a genetic point of no return. "They became a ghost species."

Interbreeding: fossil evidence of hybrids: N features in MHs

- The most vocal proponent of the hybridization hypothesis has been Erik Trinkaus.

- Trinkaus claims various fossils were N-MH hybrid individuals, including the 24,000-year-old skeleton of a modern human boy from Lagar Velho in Portugal, argue that although the pelvis and facial morphology are sapiens-like, the robusticity and limb proportions are more Neanderthal-like.

- Also the fossils found in 1952 in the cave of Peștera Muierilor, Romania, at ~37–42 Ka, are likewise claimed as hybrids, as are those of Peștera cu Oase find.

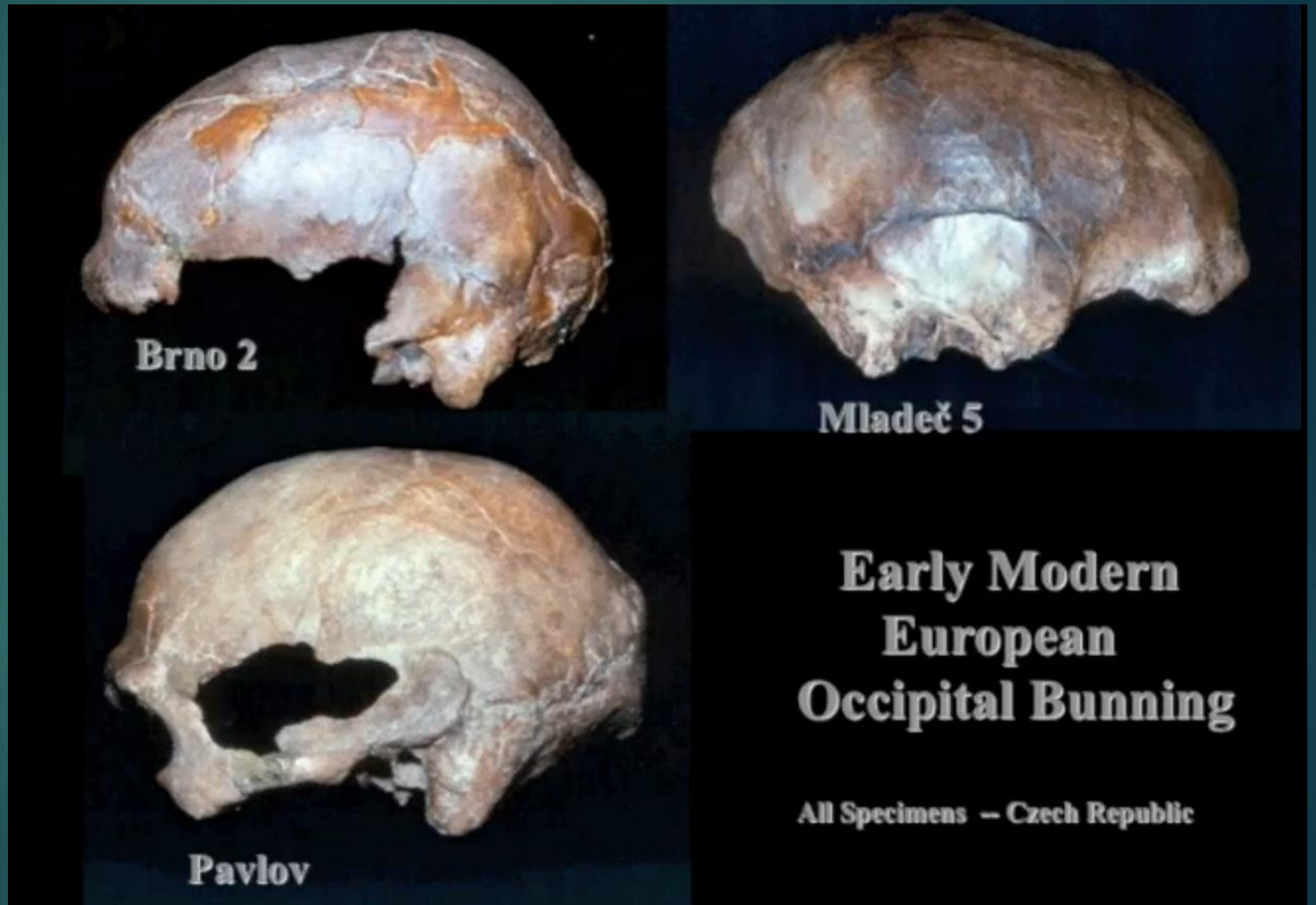
Fossil evidence of Interbreeding: N features in MHs

- Evidence of Neanderthal features in some Cro-Magnon (*Homo sapiens*) populations.

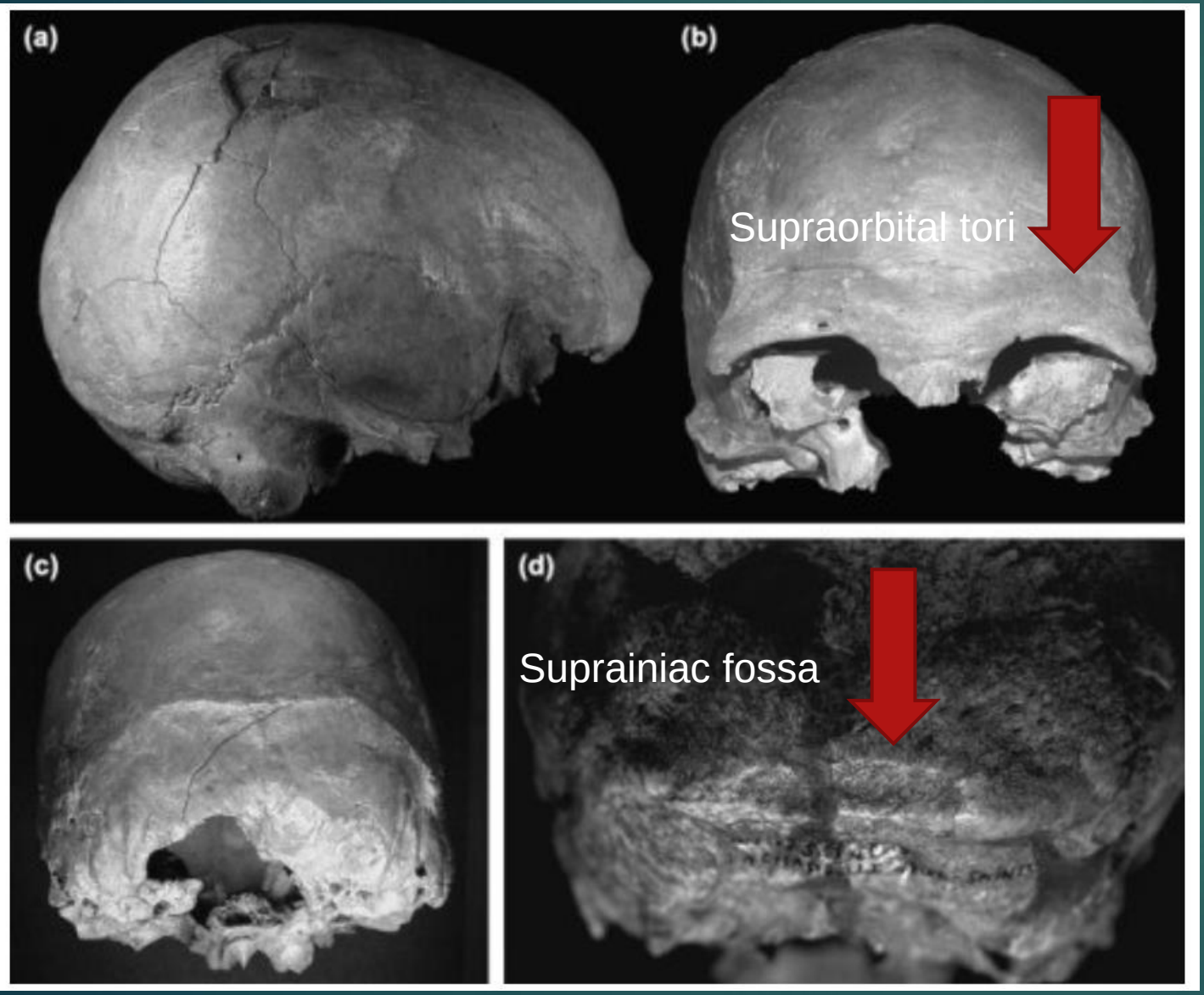
- As the age of the skeleton is later than the time of the last known Neanderthal, these features must represent significant interbreeding and transmission of DNA between modern humans and Neanderthals.

- Cro-Magnon remains from Vogelherd in Germany and Mladec in the Czech Republic also exhibit a Neanderthal-like projection of the occipital bun at the back of the skull, more so than in later *Homo sapiens*.

Some Early MHs had Occipital Bunning from N admixture: Czech Republic



Cioclovina 1, Pestera Cioclovina Uscata, Romania, MHs, 33 Ka



- 1942 Discovery: result of a modest level of admixture with Neanderthals
- The area above the neck muscles contains a distinctly Neanderthal feature, a suprainiac fossa –This feature implies some level of Neanderthal ancestry in this otherwise modern human fossil,
- Joins other early modern European fossils, from the sites of Oase and Muierii in Romania, Mlasdec in the Czech Republic, and Les Rois in France in indicating some degree of Neanderthal admixture occurred when modern humans spread across Europe starting around 40,000 years ago.

Andrei Soficaru, et al., 2007

Neanderthal DNA in MHs fossils: 23 examples from 37 to 8 Ka (with 39 to 974 SNPS)

	Upper Paleolithic Shared DNA				Vindija Cave (38.000-45.000BP)		
		Sample ID	Y-DNA // mtDNA	SNP Counts	Neanderthal Vi33.16	Neanderthal Vi33.25	Neanderthal
Upper Paleolithic Europe	Peștera cu Oase (37,800BP)	Oase-1	K* // N*	77.160	2.29%	2.12%	3.64
	Troisième caverne(34.800BP)	Goyet-Q116	C1a // M*	369.322	0.48%	0.32%	0.53
	Dolni Vestonice (30.000BP)	Vestonice16	C1a2 // U5	340.093	0.06%	0.15%	0.15
	Agnano Cave (27.600BP)	Ostuni1	// M*	125.371	0%	0.61%	0.39
	El Mirón Cave (18.700BP)	ElMiron	// U5b*	281.701	0.11%	0.07%	0.12
Mesolithic Europe	Loschbour Cave (8.000BP)	Loschbour	I2a // U5b1a	973.528	1.85%	2.44%	2.57
	Stora Karlso (7.500BP)	Storaforvar11	I* // U5a1f1a	81.607	0%	0%	0%
	Yuzhnyy Oleni Ostrov (7.250BP)	I0211	J1* // U4a	58.976	0.13%	0.98%	1.76
	Motala (7.000BP)	Motala-12	I2a1b // U2e1	743.781	0.24%	0.23%	0.27
	La Braña-Arintero Cave (7.000BP)	La Braña-1	C1a2 // U5b2c1	572.118	0.29%	0.58%	0.3
	Ajvide. Gotland (5.000BP)	Ajvide58	I2a1 // U4d	481.336	0%	0.02%	0.01
Early Neolithic Europe	Gökherm (5.000BP)	Gök2	// H1c	495.113	0.04%	0.04%	0.09
	Karsdorf (7.100BP)	I0795	T1a1 // H1au1b	48.289	1.71%	2.13%	3.81
		I0797	T1a // H46b	39.612	0%	1.79%	1.08
	Halberstadt (7.000BP)	I0659	G2a // N1a1a1a2	256.796	0.02%	0.33%	0.20
		I0048	G2a // U8bK1a	174.543	0.17%	0.49%	0.23
		I0056	G2a // T2b	132.023	0.2%	0.11%	1.12
		I0057	// N1a1a1	59.326	0.64%	1.13%	0.98
	Alsónyék-Bátaszék (7.600BP)	I0174	H2 // N1a1a1b	88.802	0.16%	0.76%	1.25
	Tiszaszőlős-Domaháza (7.650BP)	KO1	I2a // R3	511.431	0.27%	0.29%	0.59
Neolithic Anatolia	Barcin (8.350BP)	I0745	H2 // U8b1	532.874	0.48´%	0.42%	0.47
		I1099	G2a // T2b	240.476	0.07%	0.24%	0.01
		I1100	// U8bK1a6	127.024	0%	0.42%	0.09

Fossil Evidence of Interbreeding: MH features in Ns

- There are MH features in later Neanderthal populations.

- The Vindija Neanderthals look more modern than do other Neanderthals, which suggests that they may have interbred with incoming *Homo sapiens*.

- There are features of Neanderthals in modern Europeans.

- Some Europeans living today have a similar shaped mandibular foramen (nerve canal in lower jaw) to the Neanderthals and the distinct retromolar gap (typical of Neanderthals) appears in isolated modern European populations, as well as less globular skulls.

Reason for N demise

- The extinction of Ns was multifactorial in causation.

- While they had survived for 400+ K years, ultimately a variety of factors were the likely culprits:
  - Last 10 K years of their existence was characterized by repeated, often swift, climatic variability
  - Ns had history of population crashes due to ecological changes
  - Ns had small population sizes
  - Ns had low genetic diversity
  - Ns were prone to significant inbreeding with resultant congenital anomalies
  - Ns may have had lower fertility rates due to repetitively lower food resources
  - And possibly genetic assimilation into the modern human metapopulation, with N male hybrid sterility

- Given that 20-30% of the N genome is still currently present in humans, can we actually say that Ns are extinct?

- This presentation contains some copyrighted material from journals the use of which has not always been authorized by the copyright owner. Such material is made available in an effort to advance understanding of the topics discussed in this presentation. This constitutes 'fair use' of any such copyrighted material as provided for in section 107 of the US Copyright Law. In accordance with Title 17 U.S.C. Section 107, the material on this site is distributed without profit, and is used for nonprofit educational purposes. If you wish to use copyrighted material from this site for purposes of your own that go beyond 'fair use', you must obtain permission from the copyright owner. If you are the copyright owner and would like this content removed from this site, please contact me.

Contact Info

- Charles J. Vella, PhD
- www.charlesjvellaphd.com
- charlesvella@comcast.net
- 415-939-6175