

1 **Sexual behaviour in Neanderthals**

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Abstract

Improved clarity of Neanderthal ways of life brought about by advancements in analysing the fossil and archaeological records, accompanied by increased willingness to accept complex Neanderthal cognition, makes it appropriate to begin to understand their sexual behaviour. In this chapter, we briefly review current understandings about Neanderthals based on anatomy, genetics and behaviour evidenced from the archaeological record. We then integrate this with broad behavioural ecology and evolutionary sexual selection concepts to consider potential selection pressures on Neanderthals' sexual and reproductive behaviours. Large adult brain size, rapid infant brain growth, and protracted offspring development, similar to *Homo sapiens*, were supported by adaptations in social organisation, mating and parental effort. It is likely that male provisioning and investment in offspring strengthened reproductive pair bonds, improved infant survival, and impacted mate choice in both sexes. Systematic collaborative subsistence strategies were probably matched by a heavy reliance on kin and other trusted adults within the cooperative breeding group, reducing the energy burden on reproducing females, and enabling shorter lactation and reduced interbirth intervals. Neanderthals' wide ecological tolerances and behavioural flexibility suggest that they also adjusted their sexual and reproductive behaviour according to environmental circumstances. Small group size, local-to-regional social networks and potentially seasonal breeding enabled populations to adapt to fluctuating energy availability. During harsher climatic phases, limited access to mating opportunities may have favoured social monogamy, with genetic isolation and inbreeding more likely. When conditions were milder (during interglacials, in warmer regions or seasons) with more plentiful resources, group sizes and social networks may have permitted polygyny. Finally, we explore the behavioural implications of genetic evidence that Neanderthals interbred with other hominins including *H. sapiens*. This suggests that differences in physical appearance and social structures did not prevent copulation or raising hybrid infants, although sterility and lower fitness of the latter may have limited the spread of genes between species.

Keywords

Reproduction; life history; lactation; division of labour; hominin evolution; cooperative breeding; brain size.

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58 Introduction

59 Despite a remarkably persistent pop culture image of Neanderthals as semi-upright,
60 hairy, cavemen wielding clubs, science provides us with a different picture. There is no doubt
61 that the evolutionary forces that shaped Neanderthals and *Homo sapiens* differed, but recent
62 evidence of interbreeding tells us that our anatomy and physiology were compatible and
63 differences in physical appearance were not an obstacle to social interaction. Similarities in
64 growth and development indicate that, like us, Neanderthals also gave birth to helpless young,
65 and imply complex social lives necessary to support reproduction and protracted phases of
66 offspring development. Of course, some uncertainty will always surround the behaviours of
67 extinct species, but we can be sure that Neanderthals had sex and successfully reproduced for
68 hundreds of thousands of years, and the archaeological record and DNA evidence can illuminate
69 behaviours that are invisible anatomically. In this chapter, we synthesize diverse data, theories
70 and models to reconsider aspects of Neanderthal sexual and reproductive behaviour and
71 contextualise inferences within our current understanding of their physical characteristics, life-
72 ways and genomics.

73 Who were the Neanderthals?

74 Neanderthals were an archaic hominin species (*Homo neanderthalensis*) first recognised
75 in 1856 from fossils recovered from the Feldhofer Cave in the Neander Valley, Germany
76 (Fuhlrott, 1859; Busk, 1861). From their discovery, perceptions varied in terms of their
77 evolutionary placement, but the notion that Neanderthals lacked intelligence and behavioural
78 sophistication persisted (King, 1864; Chase and Dibble, 1987). However, by the 21st our
79 perceptions of Neanderthals were revolutionised through advancements in archaeological
80 methods and genetics, alongside the discovery of new fossils (Harvati and Harrison, 2008;
81 Roebroeks and Soressi, 2016).

82 Neanderthals occupied western Eurasia from approximately 350 Ka to 40 Ka years ago
83 (Higham *et al.*, 2014; Roebroeks and Soressi, 2016). Neanderthals, as a distinct lineage, began
84 emerging in mosaic form in Europe before 400 Ka, and genetic evidence points to descent from
85 the Sima de los Huesos population, around 430 Ka¹ (Meyer *et al.*, 2016; Roebroeks and Soressi,
86 2016; Galway-Witham *et al.*, 2019). Neanderthals shared a common ancestor with humans
87 approximately 550-770 Ka ago (Meyer *et al.*, 2016; but see Gómez-Robles, 2019), and current
88 theories suggest that neither *Homo antecessor* nor *Homo heidelbergensis* (for which questions
89 also exist around its species status) were ancestral to Neanderthals, but rather represent sister

¹ Many researchers consider the Sima de los Huesos populations to be proto/early Neanderthals, while others contend that these should be grouped within *H. heidelbergensis*.

90 lineages from an earlier common ancestor (Bermúdez de Castro *et al.*, 2019; Galway-Witham *et*
91 *al.*, 2019). While early *H. sapiens* evolved in Africa, the lineage leading to Neanderthals saw
92 further diversification before 600 Ka, leading to the Denisovians (Rogers *et al.*, 2020). This
93 species was initially identified genetically and currently little is known about its anatomy, but it
94 appears to have primarily occupied eastern Eurasia. The Neanderthals' own history is far more
95 complex than once believed, with apparent replacement after 100 Ka of Altai region populations
96 by western Eurasian Neanderthals moving east (Kuhlwilm *et al.* 2016; Slon *et al.*, 2018). The
97 extremely wide geographic range from northwestern Europe through the Middle East, into
98 Central Asia and at least as far east as Southern Siberia (Roebroeks and Soressi, 2016), as well
99 as their survival through multiple cycles of Pleistocene climate change, demonstrates their
100 adaptability as a species.

101 The classification of Neanderthals as a separate species from *H. sapiens* remains
102 contentious (White *et al.*, 2014; Caspari *et al.*, 2017), but what is clear is that despite evidence
103 for multiple phases of contact and interbreeding beginning before 200 Ka, both retained their
104 anatomical distinctiveness (White *et al.*, 2014). The extinction of Neanderthals in phenotypic
105 terms appears to fall between 41-39 Ka (Higham *et al.* 2014; Devière *et al.* 2021), but the cause
106 of their extinction continues to be debated, and likely centres on a number of factors including
107 palaeoclimate and environmental pressure coupled with competition from a later dispersal of *H.*
108 *sapiens* after 80 Ka perhaps bringing with them differences in demography and social
109 connectivity (see Wragg Sykes, 2020 and Vaesen *et al.* 2021 for recent reviews).

110 The extinction of a species, whatever the precipitating factors, is ultimately bound up
111 with a perpetual failure to maintain reproduction rates above replacement levels. While
112 elucidating the demise of the Neanderthals is important, as a long-lived species that successfully
113 reproduced for thousands of generations, understandably their sexual behaviour is also
114 important in its own right. Yet, this does highlight a problem: how to do this for a species that
115 has been extinct for approximately 40 Ka.

116 **Sexual behaviour: A broad concept**

117 The concept of human sexual behaviour refers to “all behaviour motivated by sexual
118 feelings, desires or gratification...[incorporating] non-reproductive genital stimulation and
119 same-sex sexual behaviour” (Kennair *et al.*, 2017). Focusing on psychological drivers makes
120 sense for living, observable subjects, but with fossil organisms the situation is more challenging.
121 When considering extinct hominins on evolutionary timescales, investigating sexual behaviour
122 also forces consideration of mating and reproduction in relation to adaptation. As a foundation
123 for investigating Neanderthal sexual behaviour we combine concepts of behavioural ecology
124 (Emlen and Oring, 1977) with social-ecological niche construction (Sterelny, 2007; Hrdy, 2009;
125 Tomasello *et al.*, 2012; Tomasello and Gonzales-Cabrera, 2017).

126 In general, reproductive mechanisms are associated with brain size (Shultz and Dunbar, 2007;
127 Isler and van Schaik, 2009). Brains are highly metabolic but slow-growing organs that require
128 stable nutritional support. As resources and time are limited, species face trade-offs in energy
129 allocated to 'maintenance' (essential basal requirements and activities of living), and
130 'production' ('growth' and 'reproduction') (Charnov and Berrigan, 1993; Snodgrass and
131 Leonard, 2009). Within 'reproduction' further trade-offs occur between finding and keeping a
132 mate (mating effort), producing and raising offspring (parental effort), and assisting relatives
133 and their offspring (nepotistic effort) (Hawkes *et al.*, 1998; Bribiescas *et al.*, 2012; Hawkes,
134 2014). Within 'growth', reproductive fitness is influenced by an organism's life history phases,
135 which may vary according to selective pressures from the physical and social environment
136 (Harvey and Clutton-Brock, 1985; Kuzawa and Bragg, 2012).

137 Most small-brained mammals living in uncertain environments have a short juvenile
138 phase preceding maturity and a shunt in energy allocation from growth to reproduction
139 (Charnov and Berrigan, 1993). This trade-off prioritises offspring quantity over quality (r and K
140 selection; see Hopkinson *et al.*, 2013). In larger-brained (and bodied) social mammals, such as
141 elephants, social carnivores, and anthropoid primates that occupy more stable environments,
142 lifespan is prolonged and offspring quality is prioritised (Bogin, 2003; Isler and van Schaik,
143 2009). Humans, with relatively large brains and protracted development, exhibit biologically-
144 distinct life history phases: infancy from birth to weaning, childhood from weaning to first
145 permanent molar eruption (M1), juvenile phase from M1 eruption to puberty onset, adolescence
146 occurring from puberty onset to growth cessation, and adulthood including a reproductive
147 phase followed by a post-reproductive period (Nowell and Kurki, 2020). Through human
148 evolution, infancy, childhood, adolescence and the post-reproductive phase all appear to have
149 been targets for adaptation (Hawkes *et al.*, 1998; Hrdy, 2009; Hawkes, 2014; Tomasello and
150 Gonzalez-Cabrera, 2017). While longer development reduces reproductive rate (Charnov and
151 Berrigan, 1993; Isler and van Schaik, 2009), it also increases developmental and behavioural
152 plasticity (Bogin, 2003; Kuzawa and Bragg, 2012; but also see Wells, 2012). Therefore an
153 organism's reproductive strategy is intimately bound to both socio-ecology (e.g., resource
154 availability and mortality risk) and allocation of energy expenditure to life history (Emlen and
155 Oring, 1977; Harvey and Clutton-Brock, 1985).

156 Darwin (1871) first developed the theory of sexual selection to explain differences
157 between males and females of the same species. In most primates, males compete for access to
158 females, whereas females are choosier about mates because they invest more in reproduction
159 (Trivers, 1972). Female reproductive success hinges on improving offspring survival through
160 parental effort by seeking resources and avoiding predators (Wrangham, 1980). In contrast,
161 males tend to maximise their reproductive success by seeking mating opportunities, which

162 increases male reproductive variance and promotes sexually dimorphic characteristics
163 signalling dominance and 'good genes', such as sexually-selected adornments linked to
164 testosterone (e.g., male orangutans' cheek flanges and men's beards) (Dixson, 2009; Puts, 2010).

165 When food is seasonal or clumped, and predation is high, females tend to gather
166 together. Large multi-male, multi-female groups form and sexual behaviour is often
167 promiscuous. Females deploy cryptic mate choice, which allows them to bias copulatory
168 outcomes; mating with several males helps to confuse paternity, which reduces infanticide,
169 while increasing protection and male investment. Disguised ovulation and reproductive
170 synchrony in females also reduces the ability of dominant males to monopolise fertile females
171 (Power *et al.*, 2013). Adaptations in anatomy and physiology of the female reproductive tract
172 can also influence the effectiveness of sperm and the evolution of male counter strategies (e.g.,
173 changes in sperm and genital morphology; Dixson, 2009; Pham and Shackelford, 2015).

174 When food patches are smaller, or resources are more evenly distributed, females are
175 dispersed and males bond to fewer females (e.g. female defence polygyny), or breeding pairs
176 form (Emlen and Oring, 1977; Opie *et al.*, 2013). Under these conditions paternity certainty is
177 greater. In monogamous primates, male partners alleviate female energy expenditure by
178 helping to carry the infant, as well as defending the female and infant against infanticidal males.
179 This energy 'saving' enables females to devote more energy to breast milk and shorten lactation,
180 which ultimately increases reproductive rate (Opie *et al.*, 2013).

181 The ability to allocate energy towards infants is important, particularly in primates that produce
182 relatively large-brained neonates (Martin, 1996). Great ape mothers are responsible for raising
183 offspring whose costly brains are paid for by spreading offspring growth over a much longer
184 period, resulting in very slow reproductive rates (Charnov and Berrigan, 1993; Isler and van
185 Schaik, 2009). This strategy produces large infants that are buffered against shortfalls in energy
186 during growth (Isler and van Schaik, 2009), but extended lactation and infant dependency
187 typically means inter-birth intervals of 4-7 years (Hrды, 2009). Rearing such expensive offspring
188 may not be fully compensated by a longer female lifespan, thereby imposing a 'gray ceiling' on
189 brain size evolution in great apes (i.e., a size beyond which a species becomes demographically
190 unviable; Isler and van Schaik, 2012).

191 Humans have overcome these constraints. Adult human brain size is three times that of
192 great apes and we give birth to larger, fatter neonates (DeSilva, 2011; Wells, 2012). Human
193 neonates, however, are less developed at birth (secondary altriciality; Portmann, 1969; also see
194 Dunsworth *et al.*, 2012), with brain size only a third of its adult size (Martin, 1996; Isler and van
195 Schaik, 2012). While this relative immaturity has long been claimed as adaptive in terms of the
196 need to fit bigger heads through bipedally adapted pelvises (Washburn 1960), more recent work
197 suggests 9 month gestations reflect the metabolic limit sustainable for humans (Dunsworth and

198 Eccleston, 2015; Nowell and Kurki, 2020). The ensuing high postnatal brain growth rate is
199 highly unusual and demands around 30% of an infant's energy, making them particularly
200 vulnerable to disruptions in subsistence (Martin, 1996; Ponce de Leon *et al.*, 2008). Increased
201 infant adiposity can be protective against this (Wells, 2012), but supplying the necessary energy
202 through lactation places a huge energetic burden on mothers.

203 Cooperative breeding has enabled humans to break the 'gray ceiling' (Burkart *et al.*,
204 2009; Hrdy, 2009; Isler and van Schaik, 2012; but see Thornton *et al.*, 2016 and references
205 therein). Cooperative breeding reduces mothers' reproductive burdens by enlisting the help of
206 fathers, kin, and other trusted adults, enabling energy and time to be shared (Isler and van
207 Schaik, 2012; Wells, 2012). Fathers often play an integral role by provisioning females and
208 investing in offspring (Kaplan *et al.*, 2000; Bribiescas *et al.*, 2012), although investment quality
209 varies according to paternity certainty, availability of other helpers, and ecological constraints
210 (Hrdy, 2009; Bribiescas *et al.*, 2012). Alloparenting, particularly provisioning of infants through
211 co-nursing or procurement of weaning foods (Hewlett and Winn 2014; Palmquist, 2020),
212 enables females to shorten lactation, return to mating and invest in future offspring, even
213 though they may already have several dependent offspring ('infant-stacking') (Hrdy, 2009;
214 Hawkes, 2014). This strategy decreases interbirth intervals, and allows for higher rates of
215 completed fertility. As a result, reproductive rate is speeded up; humans can reproduce twice as
216 fast as great apes (Walker *et al.*, 2008).

217 Slow development makes offspring more vulnerable over longer periods (Charnov and
218 Berrigan, 1993), but provides a wider range of supervised social situations and learning
219 opportunities (Sterelny, 2007; Tomasello *et al.*, 2012; Tomasello and Gonzalez-Cabrera, 2017).
220 Adolescence, for example, may serve as an 'apprenticeship' for adult life, helping to reduce
221 overall mortality (Kaplan *et al.*, 2000; Bogin, 2003). Niche construction, particularly with regard
222 to the social domain (Sterelny, 2007), is probably critical to human cooperative breeding
223 through the ontogeny of shared intentionality (see Hrdy, 2009; Tomasello *et al.*, 2012;
224 Tomasello and Gonzalez-Cabrera, 2017). By utilising collaborative offspring rearing and
225 spreading the cost of growth over a prolonged period, the relationship between an individual's
226 energy expenditure and reproductive potential has been relaxed (Isler and van Schaik, 2012;
227 Wells, 2012), allowing humans to live fast *and* slow (Hopkinson *et al.*, 2013). Although large
228 brains are not a prerequisite for cooperative breeding in primates (e.g., small brained
229 callitrichids; Burkart *et al.*, 2009), development of large, energy-hungry brains over prolonged
230 periods is dependent on *continued* help from others. Taking into account the above discussion,
231 the obvious similarity in brain size and probably life history between *H. sapiens* and
232 Neanderthals implies both cooperative breeding and a complex social niche for Neanderthals.

233 Before we examine this further, more detailed consideration of Neanderthal anatomy and
234 lifeways is useful.

235 **Neanderthal anatomy**

236 Neanderthals' brains were at least as large as *H. sapiens* (Ponce de León *et al.*, 2008);
237 some studies indicate larger average size (Pearce *et al.*, 2013), but this may be due to
238 overrepresentation of larger individuals in the Neanderthal sample (VanSickle *et al.*, 2020).
239 Differences in brain structure over growth resulted in a relatively long and low (front to back)
240 cranium (Weaver, 2009; Gunz *et al.*, 2010). Their classically distinctive elongated facial
241 architecture, with a projecting midface, double-arched brows, 'swept back' cheekbones, large
242 noses and receding chin (Trinkaus, 1987; Weaver, 2009) has often been associated with cold
243 climate adaptation, but may also reflect genetic drift (Weaver, 2009). The Neanderthal
244 postcranial skeleton is also traditionally described as being 'cold adapted' (Holliday, 1997;
245 Churchill, 2014), but recent research focus has considered morphological traits associated with
246 high levels of activity, for example biomechanical theories focusing on the use of the anterior
247 dentition as a vice, are debated (Trinkaus, 1987; Weaver, 2009), and nasal adaptations may be
248 linked to higher respiratory function related to lifestyle (Froehle *et al.*, 2013; Churchill, 2014,
249 329-30; Gómez-Olivencia *et al.*, 2018). Neanderthals were shorter and heavier than most
250 contemporary humans (Churchill, 2014, 73), with broad bodies, short limbs (relative to their
251 trunk), a deep rib cage (front to back) and thicker cortical bone (Weaver, 2009; Gómez-
252 Olivencia *et al.*, 2018). Their highly active lifestyle is reflected in higher bone density and
253 strength of the skeleton when compared to *H. sapiens* (Churchill, 2014; Kubicka *et al.*, 2018).
254 Body size and shape varied with latitude, with heavier and more robust forms associated with
255 northern regions of Eurasia (Ruff, 2010). Northern populations may have also carried higher
256 proportions of adipose tissue that seasonally fluctuated (Churchill, 2014).

257 Neanderthal neonates were already distinguishable from *H. sapiens* in their facial
258 features, which projected further and lacked chins (Gunz *et al.*, 2010; Zollikofer and Ponce de
259 León, 2010; Hublin *et al.*, 2015). From infancy, Neanderthals developed deeper chests, wider
260 torsos, and robust limbs, making them appear stockier than modern human youngsters (García-
261 Martínez *et al.*, 2020).

262 Whatever the aetiology of these features, and despite the fact that Neanderthal cranio-
263 facial characteristics and other anatomy incorporates variation (Vandermeersch and Garralda,
264 2011), compared to derived early *H. sapiens* with their higher, more globular cranium and
265 smaller, retracted face (Gunz *et al.*, 2010; Schwartz and Tattersall, 2010), Neanderthals would
266 have looked quite different in person.

267 **How did Neanderthals live?**

268 The climate cycles of the Middle and Late Pleistocene shifted between glacial and
269 interglacial periods, dramatically altering the distribution of vegetation and prey available to
270 Neanderthals (Dennell *et al.*, 2011; Hopkinson *et al.*, 2013). Western Eurasia and particularly
271 Europe was probably the Neanderthal heartland, but the archaeological record indicates
272 complex patterns of presence and absence in response to changing climate (Dennell *et al.*, 2011;
273 Roebroeks and Soressi, 2016). Neanderthal diet largely focused on hunting medium and large
274 herbivores (Richards and Trinkaus, 2009), but marine resources, small game and plants were
275 also consumed (Stringer *et al.*, 2008; Blasco, 2008; El Zaatari *et al.*, 2016; Weyrich *et al.*, 2017).
276 Evidence suggests that, at times, Neanderthals cooked their food (Hardy *et al.*, 2012; Blasco *et*
277 *al.*, 2014), which was potentially important for weaning foods (Nowell 2021).

278 Neanderthals were skilled collaborative hunters that successfully competed against
279 large carnivores (Richards and Trinkaus 2009; Churchill, 2014). They utilised strategies that
280 incorporated close-range ambushing techniques, often focussing on groups of prime-age
281 animals that were sometimes killed in large numbers (Adler and Bar-Oz, 2009; White *et al.*,
282 2016). Living sites included organised use of space often centred on hearths, and in open air
283 contexts sizable shelters were built (Bourguignon *et al.*, 2002). Neanderthals had a
284 sophisticated understanding of material technologies, employing diverse stone flaking methods,
285 crafting wooden tools and innovating in adhesive manufacture for composite tools (Wragg
286 Sykes, 2015; Roebroeks and Soressi, 2016) and plant-based thread (Hardy *et al.*, 2020). Animal
287 skins were prepared with stone and bone tools (Soressi *et al.* 2013) and likely used for clothing
288 (Collard *et al.*, 2016), as well as shelters and mats.

289 As hunter-gatherers in temperate northern latitudes, Neanderthals needed to move
290 frequently and probably employed a fission-fusion resource exploitation strategy (Grove *et al.*,
291 2012; Machado *et al.*, 2013; Wragg Sykes, 2020: 187, 212–3). There is no evidence that locales
292 were settled for more than a few weeks (Churchill, 2014, 290), even though particular locations
293 were re-used over decades and centuries, probably by the same groups (Vallverdú *et al.*, 2012),
294 indicating some level of seasonal or annual scheduling (Roebroeks and Soressi, 2016). There are
295 also indications that migratory prey was regularly intercepted at the same time of year (Adler
296 and Bar-Oz, 2009). Neanderthals' behavioural flexibility enabled them to adjust to local
297 conditions (Nowell, 2013; El Zaatari *et al.*, 2016), although stochastic environments made life
298 difficult and risky. Their need to fuel metabolically expensive bodies would be even more
299 intense when caring for growing offspring over extended periods (Snodgrass and Leonard,
300 2009). The investment required for living such an energy-expensive and socially intense
301 lifestyle means that choices about who to mate with were also decisions about survival.

302 **The evolution of Neanderthal sexual behaviour**

303 Non-human primates exhibit primary mating systems that are stable over time (Dixon,
304 2009), and close, enduring bonds between individuals are a fundamental part of primate social
305 behaviour (Shultz and Dunbar, 2007). Among great apes, human sexual behaviour appears to be
306 the most flexible arising from the interplay between psychology, biology, and socio-cultural
307 factors (Gray, 2013; Curra, 2020). A pair-bonded core underpins variation in sexual selection
308 that often differs across environments (Low, 2006; Kramer *et al.*, 2017; Schacht and Kramer,
309 2019). This flexibility in mating strategies may be a prerequisite of cooperative breeding in
310 humans (Hrdy, 2009). However, it is unclear when flexible mating evolved in *Homo* because
311 (fragmentary) skeletal indicators of sexual selection, such as body size dimorphism, appear
312 variable in Early Pleistocene populations (Ruff, 2010), complicating estimates of mating systems
313 and male parenting effort (Bribiescas *et al.*, 2012; Plavcan, 2012).

314 A proposed shift in social behaviour with the evolution of cooperative breeding in *H.*
315 *erectus* (Aiello and Kay, 2002) may have overcome the 'gray ceiling' on brain size (Isler and van
316 Schaik, 2012; Shultz *et al.*, 2012). Evidence for an emerging collaborative hunter-gatherer niche
317 exploiting energy-rich foods led to interdependence (Tomasello *et al.*, 2012; Tomasello and
318 Gonzalez-Cabrera, 2017). As males shifted from promiscuous mating opportunities in favour of
319 parental effort through food sharing, increasing energy available to females and infants, sexual
320 bonding behaviour likely intensified (Aiello and Kay 2002; Isler and van Schaik, 2012). Help
321 from other kin would have also facilitated larger, slower developing young (Hawkes *et al.*, 1998;
322 Hrdy, 2009; DeSilva, 2011; Thompson and Nelson, 2011) and increased fertility through
323 shortened lactation and reduced interbirth intervals (Hawkes *et al.*, 1998; Aiello and Kay, 2002).

324 Between the Early and Middle Pleistocene in Europe various predecessors of the
325 Neanderthals evolved including *H. antecessor* and *H. heidelbergensis*, with body sizes similar to
326 *H. sapiens* (Ruff, 2002; Arsuaga *et al.*, 2015) and brains approaching, or exceeding 1000 cc,
327 signalling a shift towards more prolonged development (Smith, 1991). Dental remains express a
328 mixture of characteristics, some overlapping with *H. sapiens* (Ramirez Rozzi and Bermúdez de
329 Castro, 2004; García-Campos *et al.*, 2020), and overall evidence points to prolonged growth with
330 extended childhood and adolescent phases (Bermúdez de Castro *et al.*, 2010). Predictions of
331 female maturity and age of first reproduction also overlap with *H. sapiens* (Kennedy, 2003).
332 There is no evidence of significant sexual dimorphism in *H. heidelbergensis* (Plavcan, 2012;
333 Arsuaga *et al.*, 2015), suggesting low male-male competition (contra Wrangham, 2019).

334 Neanderthals followed similar patterns, with brain and body sizes implying life history
335 variables similar to *H. sapiens* (Ponce de León *et al.*, 2008; Thompson and Nelson, 2011), and
336 low sexual dimorphism pointing to reduced male-male competition (Trinkaus, 1980; Churchill,
337 2014), mating effort and increased parental effort (Bribiescas *et al.*, 2012). However, these
338 interpretations are complicated by the difficulty of using size to identify males and females,

339 particularly in a wide-ranging species (see VanSickle *et al.*, 2020). Regarding infants, similar
340 neonatal brain size to *H. sapiens* suggests secondary altriciality in Neanderthals (Hublin *et al.*,
341 2015), with helpless babies. While postnatal brain growth was faster compared to *H. sapiens*,
342 resulting in absolutely larger brains, it was not larger relative to body mass (Hublin *et al.*, 2015)
343 and the time taken to reach adult brain size was not significantly different (Zollikofer and Ponce
344 de León, 2010). Infants with large, fast-growing brains imply late maturing Neanderthal
345 mothers with sufficient energy stores to support gestation (Ponce de León *et al.*, 2008).
346 However, increased neonatal size has consequences for maternal and infant mortality, and
347 models of birth mechanisms indicate some obstetric constraints for Neanderthals (Ponce de
348 León *et al.*, 2008; Weaver and Hublin, 2009; also see Nowell and Kurki, 2020).

349 While Neanderthals show broadly human-like somatic growth patterns indicating a
350 prolonged childhood and juvenile phases, subtle differences have been highlighted in dental and
351 skeletal aspects (Guatelli-Steinberg 2009; Martín-González *et al.*, 2012; Rosas *et al.*, 2017). Early
352 attainment of skeletal robusticity might indicate faster growth (Arsuaga *et al.* 2007), though
353 other skeletal-based measures suggest slower development (Martín-González *et al.*, 2012; also
354 see Mateos *et al.*, 2014). Dental evidence indicates some Neanderthals developed more rapidly
355 and ceased growth earlier than recent humans and early *H. sapiens* (Ramirez Rozzi and
356 Bermúdez de Castro, 2004; Smith *et al.*, 2007). Additionally, while Neanderthals had an
357 adolescent growth spurt, it may have been shorter (Zollikofer and Ponce de León, 2010;
358 Thompson and Nelson, 2011). These contradictory patterns may be associated with modularity
359 and decoupling of somatic and dental growth rates (Churchill, 2014; Mateos *et al.*, 2014; Rosas
360 *et al.*, 2017) as a response to local ecological conditions (i.e., nutrition and mortality). Patterns
361 of life history are species-specific and are targets for developmental plasticity and epigenetic
362 changes (Kuzawa and Bragg, 2012; Wells, 2012); consequently growth and development of
363 Neanderthals will not mirror modern human patterns (Smith *et al.*, 2007).

364 **Sociological aspects of Neanderthal sexual behaviour**

365 In primates, larger brain size, particularly neocortex size, is associated with the number
366 and quality of social relationships (Aiello and Dunbar, 1993). On this basis Neanderthals would
367 be expected to have rich emotional lives, with recent estimates of social network size of around
368 115 individuals (Pearce *et al.* 2013). Archaeological and genetic data indicate Neanderthals
369 lived within 'family/kin' groups varying from 8 to 30 adults (Vallverdú *et al.*, 2010; Hayden,
370 2012). Regional population densities were low and effective breeding populations in some cases
371 very small (<60 individuals), resulting in genetic and physical indicators of inbreeding (Prüfer *et*
372 *al.*, 2014; 2017; Harris and Nielsen, 2016; Kuhlwilm *et al.*, 2016; Ríos *et al.*, 2019; Kolobova *et*
373 *al.*, 2020). That Neanderthals did not all live in tiny isolated groups, however, is indicated by
374 genetic diversity in some populations that was within the range of contemporary hunter-

375 gatherers (Prüfer *et al.*, 2017), and is also hinted at by very long distance stone artefact
376 transfers (Hayden, 2012; Pearce and Moutsiou, 2014). Where expanded social networks existed,
377 Neanderthals would have benefitted from a social ‘safety net’, crucial in heterogeneous
378 environments (Whallon, 2006) for buffering against inbreeding and resource scarcity (Kaplan *et*
379 *al.*, 2000; Wells, 2012; Chang and Nowell, 2020).

380 Exogamy (exchange of mates within social networks and beyond; Hoffeecker and
381 Cleghorn, 2000; Hayden, 2012) is especially important for organisms, including hominins, living
382 at low population densities (see Kramer *et al.*, 2017). It avoids mating with close kin (Wilson,
383 2020), which can result in low genetic variability and impact fertility (Fareed and Afzal, 2017;
384 Ríos *et al.*, 2019). Despite very different social structures, both chimpanzees and bonobos show
385 patrilocality, with females migrating to other groups (Koenig and Borries, 2012). For
386 Neanderthals, there is one instance from the Denisova Cave, Altai, of inbreeding close enough to
387 be classed as incest (Prüfer *et al.*, 2014), however, inbreeding to this extent is not present in all
388 genetic samples, so some level of exogamy must have been present (Hayden, 2012; Pearce and
389 Moutsiou, 2014). Claims that mtDNA profiles from Neanderthals at El Sidrón indicate
390 patrilocality (Lalueza-Fox *et al.*, 2011) are hard to support because while those individuals were
391 closely related and relatively inbred, their original association as a contemporaneous ‘group’ is
392 uncertain (Vigilant and Langergraber, 2011). More broadly, there is no direct evidence for
393 formal kin-bonds with transfer of family members between groups (Hoffeecker and Cleghorn,
394 2000) or formalised large gatherings (Hayden, 2012). Exogamy would then be more likely when
395 resource competition was lower and antagonism was reduced (Hayden, 2012; Wragg Sykes,
396 2020: 215), as such seasonal prey aggregations would have offered opportunities for gatherings
397 and movement of individuals between groups, the former being noted in bonobos (Sakamaki *et*
398 *al.* 2018). However, these instances are extremely difficult to trace archaeologically (Davies and
399 Underdown, 2006).

400 How might Neanderthal intra-group relations have worked? For non-human primates
401 and hunter-gatherers, relationships between adult females within the same group increase
402 reproductive success, as they become helpers when females start reproducing (Hawkes *et al.*,
403 1997; Hrdy, 2009; Silk *et al.*, 2009; Kramer, 2014). Strong intra-group friendships and
404 provisioning by others would be especially important for Neanderthal females as they began to
405 sexually mature, enabling them to gain practice in sexual experience (during the anovulatory
406 phase), and provide energy for future pregnancy and infant care (Bogin, 2003; Ponce de León *et*
407 *al.*, 2008). Similarly, assuming males were playing a key role in provisioning the group, and
408 there is abundant evidence for meat being systematically brought back to living sites (Adler and
409 Bar Oz, 2009; Hayden, 2012), adolescence would also be crucial stage for male socialisation and
410 the development of skills necessary to become a collaborative hunter. If the timing of the

411 growth spurt was late in adolescence, as it is in male *H. sapiens*, learning (including mating
412 skills) would have occurred without young males being perceived as direct competitors by adult
413 males (Bogin, 2003).

414 The highly mobile, risky lives of Neanderthals, especially among adolescent and young
415 adult males (Trinkaus, 1995; 2011) may have meant that social adaptations would have also
416 extended to caring responsibilities. As with many hunter-gatherers, Neanderthals experienced
417 fairly high rates of injuries and diseases (Trinkaus and Villotte, 2017; Trinkaus, 2018; Spikins *et*
418 *al.*, 2019). Among adult skeletal remains, there are relatively few elderly individuals, but
419 demonstrating age beyond 40 years is difficult in archaeological contexts (Trinkaus, 1995;
420 Caspari and Lee, 2006) and bias in the record must also be considered (e.g., a scarcity of
421 complete female skeletons; Churchill, 2014, 77-78; also see Trinkaus, 2011; VanSickle *et al.*,
422 2020). Healed injuries, including bone fractures and infections, suggest social provisioning went
423 beyond food, to some kind of ‘nursing’ (Spikins *et al.*, 2019). Evidence from dental calculi
424 indicate some Neanderthals ingested plants with medicinal qualities (Hardy *et al.*, 2012;
425 Weyrich *et al.*, 2017), but demonstrating self-medication is difficult. Given the close emotional
426 bonds necessary to raise slow-developing offspring, a level of care and altruistic compassion
427 should be expected, as is seen in apes. Equally, however, primate evidence shows caution is
428 required since chimpanzees can survive with surprising levels of injury and age-related tooth
429 loss (Trinkaus and Villotte, 2017). Nevertheless, for Neanderthals there are several cases
430 implying some assistance, in particular the Shanidar 1 male who suffered a severe injury leaving
431 him with a limp, probably partially sighted, perhaps deaf and without one lower arm. That he
432 survived well into late adulthood implies not only food provisioning, but also some kind of
433 physical care (Trinkaus and Villotte, 2017; Spikins *et al.*, 2019).

434 How Neanderthal females experienced birth has been explored largely via analysis of
435 their pelvic skeletal anatomy. While their transversely-wide birth canals suggest that infants
436 may not have made the complex triple twist that characterises birth in *H. sapiens* (Weaver and
437 Hublin, 2009), their large skulls still made it a tight fit and probably as physically taxing, if not as
438 dangerous (Ponce de León *et al.*, 2008). Birthing assistance is close to being a universal feature
439 in humans (Rosenberg and Trevathan, 1995; Trevathan, 2015), and has been observed in other
440 primates (Demuru *et al.* 2018; Li *et al.*, 2020). While we cannot prove this occurred in
441 Neanderthals, it would have minimised risks and birth trauma (Spikins *et al.*, 2019; Nowell and
442 Kurki, 2020). After birth, the obvious high investment needed for helpless, slow-developing
443 infants implies not just an extended parenting phase, but also alloparenting (Kaplan *et al.*,
444 2000). Certainly the mother-infant dyad in Neanderthals would be expected to involve very
445 strong emotional attachments supported by neuroendocrine responses (Pearce *et al.*, 2017),
446 perhaps evidenced by deposited infant skeletons (Wragg Sykes 2020, 290–292).

447 Whether Neanderthals practiced division of labour by sex and age as seen in all hunter-
448 gatherer cultures is debated (Estalrrich and Rosas, 2015), and some contend it only emerged in
449 *H. sapiens* after 50 Ka (Kuhn and Stiner, 2006). This food sharing system allows groups to
450 balance local resource availability with individual contributions that vary according to physical
451 ability, reproduction and other factors. This kind of flexibility in provisioning is a core aspect of
452 cooperative breeding in humans (Hrdy, 2009). Gathered food is significant because it buffers the
453 unpredictability of hunting (Wrangham *et al.*, 1999; Hrdy, 2009). While in many hunter-
454 gatherer societies males are responsible for most large game hunting, providing the majority of
455 calories (Kaplan *et al.*, 2000), this is not always the case (Marlowe, 2005; Hrdy, 2009).
456 Sometimes gathered foods and small game hunting by women and children are the primary
457 source of subsistence, and in other cases women will hunt large game alone or in mixed-sex
458 groups. In the latter case, proximity of prey is important in tandem with available childcare, and
459 being pregnant or carrying nursing infants is not necessarily a barrier to women's hunting
460 (Goodman *et al.*, 1985; Haas *et al.*, 2020). Beyond the fact that breastfeeding and probably most
461 infant carrying was done by women, given the range of environments they occupied, we should
462 expect Neanderthal females at some times and places hunted large game, as well as being
463 heavily involved in sourcing small game and gathering foods (Kuhn and Stiner, 2006; Haas *et al.*,
464 2020). Evidence from limb development and dental wear patterns; however, indicate the sexes
465 were using their bodies differently (Estalrrich and Rosas, 2015). Females were more often using
466 their arms in symmetric motions (Sparacello *et al.*, 2017), which may have been related to skin-
467 working (Estalrrich and Rosas, 2015); this is supported by their more heavily worn teeth,
468 similar to patterns in hide-working cultures from ethnographic samples.

469 **Cognitive aspects of Neanderthal sexual behaviour**

470 Perhaps the clearest demonstration of advanced cognition in Neanderthals comes from
471 their manufacture of composite tools and adhesives (Mazza *et al.*, 2006; Wragg Sykes, 2015),
472 some involving sophisticated control of fire and experimental recipes (Degano *et al.* 2019;
473 Niekus *et al.*, 2019). In addition, aesthetic and symbolic behaviour including use of pigments and
474 potentially parietal art (Hoffmann *et al.*, 2018), no longer appear limited to early *H. sapiens*
475 contexts (Finlayson *et al.*, 2012; Peresani *et al.* 2013; Radovčić *et al.*, 2020). Evidence for burial
476 and funerary practices is also accumulating (Balzeau *et al.*, 2020; Pomeroy *et al.*, 2020).
477 However, unlike for *H. sapiens*, there is reluctance to link symbolic behaviour in Neanderthals
478 with complex language abilities (Miyagawa *et al.*, 2018).

479 Chimpanzees and bonobos use gestures and vocalizations (Hobaiter and Byrne, 2014),
480 and based on varied evidence it would appear Neanderthals' vocal communication systems
481 were *at least* as complex (Mithen, 2007). Their hyoid bone appears virtually identical to that of
482 *H. sapiens* (Dediu and Levinson, 2018), and their middle ear anatomy was similarly tuned to the

483 frequencies of speech necessary to support complex and efficient vocal communication (Conde-
484 Valverde *et al.*, 2021). Furthermore, expanded thoracic vertebral canals suggest the fine control
485 of breathing necessary for speech (Maclarnon and Hewitt, 2004). However, while the *FOXP2*
486 gene is found in *H. sapiens* and Neanderthals (Krause *et al.*, 2007), it is not identical in protein
487 expression; moreover, multiple genes are involved in language development (Atkinson *et al.*,
488 2018). Even so, taken together the evidence implies some form of speech in Neanderthals,
489 though the level of hierarchical and symbolic complexity is uncertain (Davies and Underdown,
490 2006). With relevance to sexual behaviour, it has been argued that admixture between
491 Neanderthals and *H. sapiens* may be evidence for a broadly compatible verbal capacity
492 (Johansson, 2015); the successful raising of hybrid infants also suggests this.

493 The quality of male vocal signals to attract females corresponds with mating success
494 (Hagen and Hammerstein, 2009), and human language has been implicated in mating
495 behaviour, particularly in males during adolescence (Locke and Bogin, 2006). Speech and
496 singing abilities share activation patterns and processing components within the brain (Peretz,
497 2009), and psychological experiments show that musical sounds induce emotional and
498 behavioural changes (Launay *et al.*, 2016; Nowell, 2018), for example, the singsong quality of
499 'musical speech' and 'motherese' strengthens bonds between infants and mothers (Falk, 2004).
500 It has been claimed that music emerged early amongst ancestral hominins (Mithen, 2007),
501 potentially in relation to sexual selection and gaining higher quality mates (Miller, 1998), and
502 that synchronised chorusing by male hominins to attract females might be an origin of human
503 music (Hagen and Hammerstein, 2009; also see Miller, 1998; Launay *et al.*, 2016). Evidence
504 supporting these hypotheses, however, is scarce and unconvincing (Fitch, 2006). Nevertheless,
505 this does not exclude the fact that, within Neanderthal groups, it is likely that vocal
506 communication in some form played a key part of everyday interactions, and a singing
507 component would likely have increased endorphins implicated in social bonding and group
508 stability (Launay *et al.*, 2016; Pearce *et al.*, 2017).

509 **Biological aspects of Neanderthal sexual behaviour**

510 **a) The reproductive system and copulation**

511 As Neanderthals and modern humans were able to interbreed and produce fertile
512 offspring (Fu *et al.*, 2015; Slon *et al.*, 2018), there must have been compatibility between their
513 reproductive systems and copulatory behaviour. Human reproductive anatomy more closely
514 resembles primate species that copulate less frequently (i.e., less intense sexual selection) than
515 promiscuous species, such as chimpanzees (details in Dixson, 2009). Simplified penile
516 morphology, including loss of spines and baculum, occurred in *Homo* prior to the divergence of
517 *H. sapiens* and Neanderthals (McLean *et al.*, 2011; Brindle and Opie, 2016), suggesting extended
518 copulation duration between pair-bonded, cooperatively breeding individuals (McLean *et al.*,

519 2011; but see Dixson, 2009). Vaginal size coevolves with penile size in primates (Dixson, 2009)
520 and while a coarse measure, Neanderthal pelvic anatomy suggests vaginal dimensions similar to
521 *H. sapiens*; the clitoris was likely also involved in female sexual pleasure (Wragg Sykes, 2020).
522 In chimpanzees, copulations occur mainly in the morning and late afternoon rather than during
523 fission events for subsistence (Gray, 2013). *H. sapiens* vary widely in the timing and location of
524 sexual activity, but are also constrained to some extent by the patterns of daily life (Refinetti,
525 2005; Gray, 2013), and Neanderthal copulation was probably as variable and context-
526 dependent. A variety of positions for sexual intercourse (ventro-ventral, female superior, dorso-
527 ventral), female orgasm, and masturbation in both sexes are reported in many primate species
528 (Dixson, 2009; Thomsen and Sommer, 2017), including *H. sapiens*, and similar diversity
529 probably characterised Neanderthal sexual activity. In a context of resource sharing and strong
530 emotional bonds perhaps in particular between females, bonobo-like homosexual (and more
531 diverse) behaviours may also have been normal.

532 **b) Neanderthal reproductive effort**

533 **i) Mating effort**

534 As noted above larger male body size in primates is associated with higher male-male
535 competition (e.g., gorillas), while size similarity in the sexes is typically associated with low
536 male-male competition, increased male parental effort and monogamy (e.g., gibbons) (Plavcan
537 and van Schaik, 1997; Opie et al., 2013). In chimpanzees, despite clear dominance hierarchies,
538 sexual promiscuity, and high levels of sexual selection, male coalitionary behaviour appears to
539 lessen sexual dimorphism (Dixson, 2009; Plavcan, 2012). However, it is noteworthy that,
540 despite similarities in sexual size dimorphism between chimpanzees and bonobos, their social
541 behaviour is very different, and it is increasingly recognised that *Pan* species are probably
542 derived compared to the common ancestor shared with hominins (White *et al.*, 2015; also see
543 Hare, 2017). Human sexual size dimorphism falls between largely monogamous gibbons and
544 promiscuous chimpanzees and bonobos (Plavcan, 2012), and general estimates for
545 Neanderthals fall within the same range (Churchill, 2014). Interestingly, though sample sizes
546 are small especially for (what we perceive to be) females, when Neanderthals are considered
547 within their eco-geographic sub-populations (based on latitude), stature dimorphism appears
548 reduced, though difference in mass increases, with males heavier than females (Churchill, 2014,
549 75). However, these estimates hinge on abilities to correctly attribute sex to often fragmentary
550 specimens (see above).

551 **Males:** Regardless of sex, Neanderthal muscle mass is predicted to have been absolutely
552 higher than recent hunter-gatherers (Churchill and Rhodes, 2006; Churchill, 2014), and the
553 effect of androgens (e.g., testosterone) probably contributed to the higher proportion of muscle
554 mass in males. Puts (2010) estimates lean muscle mass in contemporary male *H. sapiens* as 60%

555 higher than females. While some have argued that this, along with other masculinised
556 characteristics, supports evolutionary pressures towards male contests and higher reproductive
557 effort in humans (see Dixson, 2009), in Neanderthals, the effects on muscle mass associated
558 with evolving in higher latitudes (Snodgrass and Leonard, 2009), as well as biomechanical
559 adaptations from high activity levels (Churchill, 2014), must also be considered. Sex differences
560 in Neanderthal limb size and skeletal robusticity, however, show similar levels to recent *H.*
561 *sapiens* (Ruff, 2002), prompting Trinkaus (1980) to propose they ranged between monogamous
562 and 'mildly' polygynous with some male-male competition, as in contemporary humans (Low,
563 2006).

564 Adult male reproduction and sexual behaviour is dependent on androgens for building
565 metabolically costly muscle and developing secondary sexual traits and masculine behaviours
566 (Churchill and Rhodes, 2006; Gray *et al.*, 2019). Various anatomical traits have been interpreted
567 as signalling high androgenisation in Neanderthals. Digit length ratios suggest increased
568 prenatal sensitivity to androgens (Zheng and Cohn, 2011; Manning, 2001), including characters
569 associated with higher male-male competition, aggression, and polygyny (Roney *et al.*, 2010;
570 Nelson *et al.*, 2011; Butovskaya *et al.*, 2015). Similarly, features of higher androgenisation seen
571 in Neanderthal cranial morphology have been perceived to indicate the absence of self-
572 domestication (Hare, 2017; Theofanopoulou *et al.*, 2017). Self-domestication occurs within
573 species (e.g., bonobos, *H. sapiens*) when females express a preference for less aggressive, more
574 prosocial males, which leads to the feminisation of some anatomical characters, but also
575 increases communicative and cooperative flexibility (Hare, 2017; but also see Wrangham,
576 2019).

577 Male craniofacial development is sensitive to androgens reflecting masculinity
578 (Bribiescas *et al.*, 2012) and is taken to signal 'good genes' (i.e., genetic quality; see Buss, 2016,
579 33) and variation in parental effort; important traits for female mate selection (Roney *et al.*,
580 2006). Faces likely played a similarly key role in Neanderthals, however, studies of sexual
581 dimorphism in this anatomical region are lacking. For Neanderthals in small, tightly-knit kin
582 groups, social cohesion would have depended on low levels of male aggression and reduced
583 alpha-male dominance hierarchies, whether or not monogamy was dominant. This may be
584 visible in shared goals, such as collaborative hunting (Tomasello *et al.*, 2012).

585 In male *H. sapiens*, adolescence marks the transition from growth to reproduction, and
586 coincides with resource independence in hunter-gatherers (Hrdy, 2009). It is also a time of
587 integration into adult male society (Bogin, 2003; Hopkinson *et al.*, 2013). Life history is a target
588 for developmental plasticity (Kuzawa and Bragg, 2012), evolutionary change (Tomasello and
589 Gonzales-Cabrera, 2017) and the timing of maturation is a trade-off in energy between growth
590 and reproduction in response to environmental factors (Charnov and Berrigan, 1993). If

591 Neanderthal demographics based on skeletal samples are taken at face value, and there was
592 high prime and young adult male mortality (Trinkaus, 1995), then earlier maturation is
593 predicted (see Charnov and Berrigan, 1993). Depending on the estimate, the Le Moustier 1 male
594 fossil was aged 11-15 years old, and may indicate earlier puberty and faster adolescent growth
595 rates compared to *H. sapiens* males (Thompson and Nelson, 2011; Hublin *et al.*, 2015). However,
596 age estimates for development in the El Sidrón juvenile male suggest maturation within *H.*
597 *sapiens* values (Rosas *et al.*, 2017).

598 In human males a high mortality environment can promote early adolescence and
599 termination of growth leading to lower sexual dimorphism in stature, while insufficient early
600 nutrition can delay and dampen the growth spurt, again reducing sexual dimorphism (Kuzawa
601 and Bragg, 2012). These disruptions can also interfere with the development of the endocrine
602 system and the production of adult male sex hormones, potentially impacting reproduction
603 (Bribiescas, 2001). However, since developmental stress, indicated most clearly by enamel
604 hypoplasia (indicating systemic disease, infection, or severe lack of nutrition), is not more
605 common in Neanderthals compared to archaeological and contemporary foraging populations
606 (Trinkaus, 2018; McGrath *et al.*, 2021), it is unlikely to have affected their reproductive success.
607 However, there is a clear link with hypoplasias and potential weaning age (4th year) and
608 adolescence (12th year) in the El Sidrón sample (Rosas *et al.*, 2006). The impact of this, together
609 with the possibility that earlier or shorter male puberty may have increased mortality in young
610 males (Trinkaus, 1995; Hublin *et al.*, 2015), is not clear.

611 **Females:** While small, the apparent sexual dimorphism in Neanderthals may reflect
612 higher proportions of lean muscle in males versus adipose tissue in females (Churchill and
613 Rhodes, 2006; Churchill, 2014, 75). To successfully produce and raise a large-bodied infant,
614 Neanderthal mothers needed sufficient energy reserves (Ponce de León *et al.*, 2008; Wells,
615 2012). Neanderthals systematically targeted animal fat, offal, marrow, as well as meat (Adler
616 and Bar-Oz, 2009), with protein and fats important for thermic protection and buffering against
617 nutritional fluctuations (Snodgrass and Leonard, 2009), with the latter also crucial for female
618 adolescent development, fertility, and lactation (Snodgrass and Leonard, 2009; Wells, 2012), as
619 was nutritional input from plants (Hockett, 2012).

620 Preceding menarche, signs of female fertility are often signalled by fat deposits emerging
621 under the influence of oestrogens (see Bogin, 2003). Menarche onset is affected by factors such
622 as environmental uncertainty and high mortality (Kuzawa and Bragg, 2012); as such,
623 considerable variation exists in small-scale human societies (Kramer *et al.*, 2017, Săffa *et al.*,
624 2019). Genomic data suggests menarche in Neanderthals may have occurred at the earlier end
625 of the human range (Kuhlwilm and Boeckx, 2019).

626 Menarche initiates a phase of anovulatory menstrual cycles (1-3 years in humans
627 (Bogin, 2003; Gray, 2013), and since a 'pre-fertile' phase is also present in female chimpanzees
628 (Pussey, 2001), this may be an ancestral condition shared by Neanderthals (Bogin, 2003).
629 Anovulatory cycles allow adolescent females to continue to invest energy in pelvic and somatic
630 development, while providing time to build social relationships and consolidate childcare skills
631 (Hrdy, 2009; Kramer, 2014) before the huge burden of pregnancy (Bogin, 2003). Theories
632 around advertising, concealing, or confusing ovulation to optimise fertility in hominins exist
633 (Power *et al.*, 2013), and it seems parsimonious to assume that (human-like) concealed
634 ovulation probably occurred in Neanderthals. As with males, if adolescent females experienced
635 early maturation and low nutrition, it may have adversely affected development. The pelvis
636 appears particularly sensitive to adverse conditions, leading to increased risk of birth
637 complications (Shirley *et al.*, 2019). Reconstruction of birth mechanisms based on the Tabun 1
638 (Israel) Neanderthal female pelvis and predictions of neonatal head size based on the infant
639 Mezmaiskaya 1 (Russia) and other very young Neanderthal specimens suggest human-like (i.e.,
640 tight) cephalo-pelvic relationships during birth (Ponce de Leon *et al.*, 2008; also see Weaver and
641 Hublin 2009). However, these models are likely to accommodate error as they are built upon
642 fragmentary remains, and a composite mother-infant dyad based on regionally and temporally
643 dispersed specimens.

644 Mortality rates similar to (or potentially greater than) recent hunter-gatherers would
645 necessitate high fertility rates to maintain Neanderthal population levels (Trinkaus, 1995).
646 Speaking broadly, within humans high waist-to-hip ratios (WHR) in women present a dual
647 signal. Greater adiposity is often considered healthier and associated with fertility in societies
648 vulnerable to food shortages (Marlowe and Wetsman, 2000; Swami and Tovée, 2007), while
649 central body fat also indicates a hormonal profile high in adrenal androgens and cortisol that
650 helps support female resource-gathering behaviours (e.g., stamina and competitive aggression),
651 but can also reduce fertility and shorten lifespan (Cashdan, 2008). As hunter-gatherers often
652 living in challenging environments, Neanderthal groups likely suffered seasonal food shortages,
653 and high-energy animal fat was a focus, but there is no direct evidence that males preferred
654 females with higher body fat. Nor, in the absence of any soft-tissue preserved corpses, do we
655 know if fat deposition patterns in Neanderthals differed those in *H. sapiens*. Certainly if fatter
656 females had increased fitness their adipose deposits would have added to their already
657 (genetically) wide body shape (Ruff, 2010).

658 **Mate choice:** As mobile hunter-gatherers, Neanderthals probably had few material
659 possessions (Roebroeks and Soressi, 2016), therefore, physical and behavioural characteristics
660 were likely especially important for females choosing mates (Marlowe, 2004). More muscular
661 bodies may have better equipped male Neanderthals to compete for resources and protect the

662 group, improving status and attractiveness (Puts, 2010). Masculine qualities associated with
663 higher androgens may also have signalled greater fitness and 'good genes' (Roney *et al.*, 2006;
664 Puts, 2010). In *H. sapiens*, female mate preferences vary according to environmental conditions,
665 with more masculinised males tending to be preferred in regions with lower life expectancy,
666 higher mortality, and higher disease prevalence (DeBruine *et al.*, 2010). This is interpreted as a
667 trade-off between healthy offspring with 'good genes' versus dealing with potentially
668 undesirable masculine behaviours such as reduced paternal investment, higher aggression, and
669 coercive behaviour (Roney *et al.*, 2006; DeBruine *et al.*, 2010; Gray, 2013), which can
670 compromise female and offspring survival. Inferred higher androgens in Neanderthals (Nelson
671 *et al.*, 2011; Theofanopoulou *et al.*, 2017) might suggest that selection for prosociality,
672 associated with low androgens and feminisation of some anatomical characters, was not a
673 driver of female mate choice as it seems to have been in *H. sapiens* (and in bonobos and dogs;
674 Hare, 2017). It is worth noting, however, that monogamous cooperatively breeding wolves also
675 show high levels of tolerance, prosociality, and social communication as these traits are critical
676 for successfully exploiting their ecological niche (Marshall-Pescini *et al.*, 2017). In other words,
677 selection for characteristics associated with high androgens in Neanderthals may not
678 necessarily equate to females tolerating undesirable behaviours, or a general lack of social
679 sensitivity. If males matured later than females, as in *H. sapiens* (Bogin, 2003; Gray, 2013), then
680 female Neanderthals may have preferred older males (Buss, 2016), with demonstrated
681 provisioning abilities. However, female mate choice likely involved trade-offs between many
682 factors including her own hunting ability, or continued access to kin (i.e., local exogamy
683 patterns).

684 In terms of male choice, coercive abductions do occur in some modern hunter-gatherer
685 cultures, but this has the disadvantage of cutting-off relationships to the female's kin (Hrdy,
686 2009), and there is no evidence for this in Neanderthals. Neanderthal males are likely to have
687 sought females with characteristics that signal high fertility and, depending on the social
688 structure, high fidelity (Buss, 2016; Marlowe, 2004). Cues to females' robustness and stamina
689 were also likely desirable (see Cashdan, 2008), and though competitiveness may be sought
690 after, low aggression is beneficial for long-term mating partnerships (Marlow, 2004). In
691 contexts where females are able to garner significant resources to feed offspring, and sufficient
692 helpers are available, polygyny is predicted to arise, freeing males to dedicate more effort to
693 seeking other mates (Low, 2006). In less productive environments monogamy is more likely
694 (Low, 2006). Additionally, in resource-poor or unpredictable environments Neanderthals' high
695 energetic requirements may have meant females engaged more heavily in hunting (Kuhn and
696 Stiner, 2006; Wragg Sykes, 2020). When male investment is necessary for offspring survival,
697 and help from female kin unavailable, reproductive strategies become more aligned and male

698 parental effort takes precedence over mating effort (Gray, 2013; see Hrdy, 2009). Although
699 sexual division of labour can theoretically increase energy costs in very small groups (Kuhn and
700 Stiner, 2006; Churchill, 2014), independent sex-based activities through the day could also have
701 increased Neanderthals' chances of encountering individuals from other groups, providing
702 opportunities for extra-pair copulations.

703 **Energy and seasonality:** In non-human primates and contemporary *H. sapiens* shifts in
704 energy intake impact reproductive physiology, which modulates mating and parental effort, and
705 contributes to birth seasonality (Ellison *et al.*, 2005; Snodgrass and Leonard, 2009). The high
706 metabolic demands of fuelling larger bodies, gestating and feeding large-brained infants in high
707 and mid-latitudes, makes birth seasonality more likely in Neanderthals (Mussi, 2007; Snodgrass
708 and Leonard, 2009). At present there is no clear evidence for food storage (Hayden, 2012), so
709 the ability to store body fat was probably important when entering late autumn and winter
710 months (Snodgrass and Leonard, 2009; Wells, 2012). As body fat decreased, ovarian and
711 gonadal function would have declined, as energy allocation shifts from mating effort towards
712 'maintenance' (Snodgrass and Leonard, 2009; Santi *et al.*, 2020). Increased sedentism in winter
713 may also have reduced any energetic buffering normally available through extended social
714 networks (Whallon, 2006; Snodgrass and Leonard, 2009).

715 Seasonality and climate variability may also have impacted mating systems (Power *et*
716 *al.*, 2013; Smith *et al.*, 2018). Based on primates, it has been proposed that Neanderthal females
717 may have exhibited reproductive synchrony and desynchrony during glacial and interglacial
718 periods, respectively (Power *et al.*, 2013), which would have been superimposed on seasonal
719 breeding patterns. Hypothetically, reproductive synchrony may be expected during glacial
720 periods (Power *et al.*, 2013), but at the same time, a harsher climate would encourage social
721 monogamy (Low, 2006), mitigating the need for paternity confusion (contra Power *et al.*, 2013).
722 When more food became available (i.e., during spring and interglacials), reproductive function
723 would be restored. Where resources were less seasonally dependent, mating season was likely
724 longer and female reproductive cycles may have become desynchronised (Power *et al.*, 2013).

725 Tooth histology suggests the Payre 6 (France) Neanderthal was born in the spring,
726 indicating summer conception (Smith *et al.*, 2018). This accords with Mussi's (2007) proposal
727 that Palaeolithic populations were more likely to have mated in late summer and early autumn
728 when prey was fatter and more available. Isotopic data from northern Italy found some
729 Neanderthal mothers residing locally around the time of birth and for the first few weeks
730 postpartum (Nava *et al.* 2020), probably facilitating physical recovery and initiation of
731 breastfeeding. If Smith and coworkers' (2018) findings reflect a wider pattern this could
732 indicate over-wintering when substantially reduced mobility helped balance energetic demands
733 of late-term gestation, birth, and lactation (Nowell, 2021). Claims for species-wide physiological

734 hibernation (Bartsiokas and Arsuaga, 2020) however, are hard to reconcile with evidence of
735 some winter hunting and movement.

736 **Finding a mate:** It is not clear if Neanderthals had restricted exogamy patterns (e.g.,
737 patrilocal/matrilocal; see Lalueza-Fox *et al.*, 2011) or if dispersal patterns were more flexible, as
738 in contemporary *H. sapiens* (Chapais, 2013; Vigilant and Langergraber, 2011). In *H. sapiens*
739 hunter-gatherers living at similar population densities to Neanderthals, most mates are found
740 within extended dialect networks (200-800 or more people), composed of many small bands
741 (Hayden, 2012; Pearce and Moutsiou, 2016). Assuming Neanderthals groups were widely
742 dispersed, they would have likely needed to travel significant distances to locate mates..
743 Combined with potential seasonal mating, this highlights that predictable resource
744 agglomerations in the form of herd migrations may have provided opportunities for
745 Neanderthals to find mates outside their natal groups (Sakamaki *et al.* 2018).

746 As with other hunter-gatherers, the death of a reproductive partner was probably not
747 uncommon for Neanderthals and re-entering the mating arena may have been a periodic
748 pressure for females and males. Low population density and small group size probably also
749 made Neanderthal groups vulnerable to sudden shifts in sex and age ratios, which can impact
750 mating behaviour (Hopkinson *et al.*, 2013; Kramer *et al.*, 2017; Maner and Ackerman, 2020). *H.*
751 *sapiens* foraging societies reproductive solve sex ratio imbalances through migration into other
752 groups (Kramer *et al.*, 2017). Given low population densities in Neanderthals, flexible exogamy
753 (i.e., both males and females) would have been adaptive, possibly with movement between
754 paternal and maternal kin-groups to accommodate fluctuations in infant care and maternal
755 support (Hrdy, 2009).

756 Entering an unfamiliar (non-local) group would have incurred costs (Hopkinson *et al.*,
757 2013), although information stored in social networks may have served to ameliorate risks
758 (Whallon, 2006; see also Chang and Nowell, 2020). However, failing to be accepted by a new
759 group, at worst, might lead to violence or death (Hopkinson *et al.*, 2013). If migration was
760 deemed too risky, groups may have altered their typical mating practices (e.g.,
761 polygyny/monogamy), relaxed social norms against mating with close relatives or young
762 adolescents (Kramer *et al.*, 2017), or even neighbouring hominin populations (i.e., Neanderthals
763 with Denisovans). Genetic and anatomical evidence indicating low effective population size and
764 varied inbreeding suggests some Neanderthal groups had restricted mating options (Harris and
765 Nielsen, 2016), although effects on wellbeing and reproduction fitness are unclear (Ríos *et al.*,
766 2019).

767 **ii) Parental effort and nepotistic effort**

768 Ontogenetic studies indicate that similar to *H. sapiens* infants, Neanderthal offspring
769 followed long and extensive postnatal growth periods (Thompson and Nelson, 2011; Ponce de

770 León *et al.*, 2016), requiring dedicated parental effort and help from others. Modelling
771 (Degioanni *et al.*, 2019, 10) demonstrates how risky infant and juvenile mortality could have
772 been for Neanderthals, as, “a decline of less than 1.5% in survival for the youngest children [<1.0
773 year old] leads to rapid extinction (less than 2,000 years)” (see Nowell 2021). However
774 cooperative breeding could have reduced infant mortality through shared responsibility across
775 the group, enabling mothers to ‘stack’ infants and maintain high fertility rates (Hrdy, 2009;
776 Hawkes, 2014), although there is no direct evidence of this in Neanderthals (Power *et al.*, 2013).

777 Parenting is crucial for the health and well-being of offspring (Hrdy, 2009; Ziegler and
778 Crockford, 2017), and in most primates this responsibility mainly falls on the mother. For
779 Neanderthals, as large brained hominins, the social and physical development of offspring
780 would be dependent on relationships with others over long periods of time (Hrdy, 2009; Wells,
781 2012). However, if inferences of high mortality or shorter lifespans in Neanderthals are correct
782 (Trinkaus, 1995; 2011; Caspari and Lee, 2006) and not a reflection of cultural choice (Balzeau *et*
783 *al.*, 2020), these factors would reduce the number of adults and increase the dependency ratio of
784 a Neanderthal social group (number of consumers divided by number of producers) (Binford,
785 2001). Adults may have formed opportunistic coalitions across kin-groups, extending the
786 benefits of collaboration and cooperative breeding, helping increase reproductive success and
787 inclusive fitness (Hrdy, 2009; Tomasello *et al.*, 2012). However, this would have depended on
788 energy available after adult siblings (and other helpers) had provisioned their own offspring,
789 unless children were recognised and treated as a communal responsibility, as in some *H. sapiens*
790 societies (Konner, 2010).

791 Since at least some Neanderthals survived >40 years, provisioning and care of children
792 by grandparents should be considered (Hawkes *et al.*, 1998) in addition to support from less-
793 dependent juveniles, whose assistance could have been important in facilitating mothers’
794 reproduction rates (Hrdy, 2009; Kramer, 2014). The cooperative skills juveniles developed at
795 this time may have also boosted their own fitness through increased competency in parental
796 effort later in life (Hrdy, 2009; Kramer, 2014). Lacking such support, however, would have
797 increased a Neanderthal mother’s energy costs, slowing reproduction through prolonged
798 lactation periods and delaying her return to fertility (Snodgrass and Leonard, 2009). At times
799 infanticide may have been necessary to control the number of dependants (Hrdy, 2009;
800 Harpending and Bertam, 1975).

801 As noted above, male provisioning and possibly direct care of offspring strongly impacts
802 females’ energy budgets, shortening birth intervals, and increasing fertility, but includes a trade-
803 off with seeking more mating opportunities (Bribiescas *et al.*, 2012; Power *et al.*, 2013). Being a
804 successful hunter in a system of food sharing may have provided a Neanderthal male with
805 increased status and mates (mating effort) (see Kuhn and Stiner, 2006), but successful hunters

806 can also preferentially provision their mates and offspring (parental effort). Levels of male
807 investment may be more dependent on paternity certainty (Bribiescas *et al.*, 2012), although
808 provisioning the offspring of other males may have benefits in providing extra mating
809 opportunities with mothers (Gray, 2013; see Hrdy, 2009). Indeed, in some *H. sapiens* foraging
810 societies husbands encourage wives to take on an extra husband to help provision the family
811 (Hrdy, 2009). Risky lives for Neanderthals may have resulted in adults regularly caring for
812 another's offspring, particularly when gaining a mate after the death of a previous reproductive
813 partner, although this could also result in reduced resources to step-children, potentially
814 increasing mortality (Sear and Mace, 2008; Bribiescas *et al.*, 2012). However, altruistic adoption
815 of extra-group orphan infants in bonobos should also be borne in mind when considering the
816 complexity of motivations for parenting decisions in Neanderthals (Tokuyama *et al.*, 2021).

817 In *H. sapiens*, paternity uncertainty can reduce provisioning to females and offspring
818 (Bribiescas *et al.*, 2012), although this is often only one of many factors governing male input in
819 forager societies (Hrdy, 2009). High-energy costs of parenting in Neanderthals would have
820 made long-term pair bonds adaptive, as paternity certainty would have increased provisioning
821 and investment in offspring. Pair bonding aligns male and female reproductive strategies, and
822 also increases tolerance and reduces aggression (Emlen and Oring, 1977; Shultz and Dunbar,
823 2007), clearly important in a cooperative breeding context. Monogamy would have focussed
824 males' efforts and investment on a single breeding female, providing direct and indirect care
825 (e.g., protection, food sharing) that reduced the mother's energetic burden, accelerating
826 weaning and a return to mating (Bribiescas *et al.*, 2012). Neanderthal paternal investment may
827 have relaxed during warm phases (interglacials) potentially due to reproductive desynchrony
828 (Power *et al.*, 2013) or population expansion due to increased resource availability.

829 Despite variation in mating patterns, the inclusive fitness advantages of cooperative
830 breeding would increase selection for motivations and qualities enhancing collaboration
831 (Tomasello *et al.*, 2012), especially close ties between female kin (Hawkes *et al.*, 1997; 1998),
832 which may have been crucial in ameliorating the costs of polygyny and uncertainties around
833 facultative male parental care (Sear and Mace, 2008; Hrdy, 2009; Kramer *et al.*, 2017).

834 **Weaning patterns.** *H. sapiens* foragers fully wean around the age of 2.65-3.00 years,
835 with average interbirth intervals at 3.9 years (Marlowe, 2005; Churchill, 2014, 344), though
836 with considerable variability. Weaning occurs on average later in hunter-gatherer populations
837 occupying cold climates (Kennedy, 2005). Early weaning alleviates maternal energy burdens,
838 enabling mothers to return to provisioning activity (since caregivers can feed the infant), and
839 subsequent hormone changes permit the return of full fertility, meaning greater investment in
840 future offspring (Power *et al.*, 2013). However, very early weaning can be detrimental to infants
841 by reducing energy and access to milk's immune properties, slowing growth and potentially

842 impacting long-term fitness (Kuzawa and Bragg, 2012; Lee, 2012). Extended breastfeeding
843 beyond one or two years improves infant health and survival due to continued immune benefits
844 (Jackson and Nazar, 2006), and while it implies an increased maternal energy burden this may
845 be low and not prevent return of ovulation and mating.

846 Dental isotopic data provide some information on age and even seasonality of both birth
847 and weaning (both onset of non-milk foods and cessation of breastfeeding) in Neanderthals,
848 though samples are very small. In one study comparing three individuals from the same region
849 of Italy (c. 80-50 Ka), weaning onset occurs between 3.8-→ 5 months (Nava *et al.* 2021). Only
850 one of these showed a subsequent signal implying significantly reduced milk intake, which came
851 after 7 months. Data on full weaning ranges from 1.2 years of age at Scladina (Belgium),
852 following initiation around 7.5 months (Austin *et al.*, 2013), to 2.5 years for the Payre 6 (France)
853 child (Smith *et al.*, 2018). However, the Scladina cessation appears sudden and may point to
854 maternal absence or death. Isotopic analysis of bone on the Engis 2 child (Belgium) indicates full
855 weaning by 4 years, rather late compared to modern *H. sapiens* (Bocherens *et al.*, 2001; also see
856 Rosas *et al.*, 2006). While not conclusive, dental enamel hypoplasias between 3 to 5 years of age
857 in other samples may be the result of nutritional/immune stress from shifting fully to solid food
858 (Rosas *et al.*, 2006; Churchill, 2014, 344).

859 Overall, the evidence for weaning in Neanderthals is mixed, with similarity in onset to *H.*
860 *sapiens* foragers and therefore with potential for short birth intervals, but with some variability
861 (Churchill, 2014, 345). It is likely that Neanderthal weaning practices were diverse and flexible,
862 as in *H. sapiens* occupying different environments and socio-economic contexts (Kennedy, 2005;
863 Marlowe, 2005). The limited seasonality data for birth and weaning are spring and autumn,
864 respectively (Smith *et al.*, 2018), but how far this data reflects wider patterns is unclear.

865 Considering the similarities in brain and infant development to *H. sapiens* (Ponce de
866 León *et al.*, 2016) and evidence of complex cognition in the archaeological record, Neanderthals
867 are likely to have also sustained long periods of parental investment. Emotional attachments
868 underpinned by endocrine responses would have supported the behaviours necessary for
869 rearing expensive young within a cooperative breeding system (Pearce *et al.*, 2017; Ziegler and
870 Crockford, 2017). Strong attachments may be revealed in evidence for deposition of the dead,
871 including neonates and young children (Balzeau *et al.*, 2020; Pomeroy *et al.*, 2020; Wragg Sykes,
872 2020; Nowell, 2021), extending thanatological behaviour observed in apes (Lonsdorf *et al.*,
873 2014). Enduring, strong bonds between individuals would maintain group cohesion, although
874 the quality of attachment between males and offspring may have been contingent on
875 perceptions of paternity. Testosterone levels are reduced in fathers, which likely reduces
876 aggression, but also improves regulation of metabolic function and prevents excessive weight
877 loss during additional energetic requirements (Ziegler and Crockford, 2017). If Neanderthal

878 fathers were mostly monogamous, rather than polygynous, their testosterone may have been
879 low (Alvergne *et al.*, 2009), facilitating greater infant care and protection. Down-regulation of
880 androgens in males during the winter may have also been important in reducing aggression
881 when groups (including pregnant females) may have been sedentary for long periods (Churchill,
882 2014). Neanderthal males that invested more in parental care would increase offspring survival
883 and shorten birth intervals, increasing their own reproductive success and inclusive fitness.
884 However, shifts in prioritising mating effort or parental effort may have varied with context
885 (Sear and Mace, 2008; Hrdy, 2009; Bribiescas *et al.*, 2012).

886 **Interbreeding**

887 Interbreeding between evolutionarily close (<1 Ma separation) species is not
888 uncommon (Holliday, 2008; Zinner *et al.*, 2011). For example, *P. troglodytes* and *P. paniscus*
889 diverged approximately 930,000 Ka (Hey, 2009) and interbreed in captivity, producing
890 seemingly healthy, likely fertile offspring (Curnoe and Thorne, 2003; Overmann and Coolidge,
891 2013). Ancient DNA research has confirmed that interbreeding between individuals from
892 different *Homo* species is a fact and potentially played an important role in the evolutionary
893 process (Ackermann, 2010). As the earliest estimate for the Neanderthal and *H. sapiens* lineage
894 divergence is around the same as that in the *Pan* case, (Gómez-Robles, 2019), fertile offspring
895 should be expected (Kuhlwilm *et al.*, 2016; Rogers *et al.*, 2020). Interbreeding was first
896 demonstrated through the draft Neanderthal genome (Green *et al.* 2010), highlighting that most
897 living people have a small percentage (1.5-2.1%) of Neanderthal ancestry. Further samples and
898 recent studies now point to admixture having occurred in multiple phases extending from c. 40
899 Ka to before c. 200 Ka, involving all combinations of male-female pairings between both
900 lineages (Enard and Petrov 2018; Petr *et al.*, 2020). One phase, c. 55 Ka, appears to be the source
901 of the DNA found in living people (Green *et al.*, 2010; Prüfer *et al.*, 2014); later interbreeding
902 also took place, but with *H. sapiens* lineages that have no living descendants. Since Neanderthals
903 also hybridised with the closely related Denisovans (Slon *et al.*, 2018).

904 Research into the history of sexually transmitted diseases provides another line of
905 evidence for the timing and nature of interbreeding. Different strains of the human papilloma
906 virus (HPV) account for more than 99% of all cervical cancers, and the global distribution of
907 variants of HPV 16, one of the deadliest strains, closely matches the prevalence of Neanderthal
908 DNA in modern populations (Pimenoff *et al.* 2016). While Type A is the most common form of
909 HPV 16, Types B and C are found only in sub-saharan Africa where Neanderthal DNA in living
910 populations is extremely low. Furthermore, Type A is more recent and estimated to have
911 emerged c. 60-120 Ka, when the interbreeding source phase in living people took place. By
912 contrast, based on the history of diseases such as herpes simplex 2 (the variant responsible for
913 genital herpes), tuberculosis and *Helicobacter pylori* (a virus that causes stomach ulcers), *H.*

914 *sapiens* may have introduced these viruses into the Neanderthal populations they encountered
915 (Houldcroft and Underdown, 2016). If this is correct, given the low genetic diversity of some of
916 these populations, Neanderthals may have been disproportionately impacted by exchanges of
917 pathogens (Sullivan *et al.*, 2017); potential factors in localised extinction events (Shea, 2008;
918 Wolf and Greenwood, 2010; Houldcroft and Underdown 2016; Sullivan *et al.*, 2017). By contrast,
919 Neanderthal DNA introgressed into *H. sapiens* populations is argued to be a key factor in the
920 human ability to clear RNA viral infections, particularly among living Europeans (Enard and
921 Petrov 2018). One recent study using a Japanese biobank found associations between
922 Neanderthal DNA and population-specific variants of autoimmune diseases, prostate cancer,
923 and type 2 diabetes, underscoring the importance of studying non-European cohorts to address
924 the scale, nature, and impact of interbreeding events (Dannemann, 2020).

925 Further evidence for interbreeding, or at least close contact, between Neanderthals and
926 *H. sapiens* derives from research into the oral microbiome of these species. Five Neanderthal
927 dental plaque (calculus) samples not only provided information on diet, overall health, and
928 likely plant use, but also resulted in the discovery of a mostly complete genome of
929 *Methanobrevibacter oralis* (Weyrich *et al.*, 2017). Dating to 48 Ka, this is the oldest microbial
930 genome ever sequenced and by comparing it with that found in living *H. sapiens*, it is clear that
931 the variants diverged between 110-140 Ka, coinciding with an early phase of interbreeding
932 (Weyrich *et al.*, 2017). While the most obvious mode of transmission is kissing, it may have also
933 occurred through the sharing of food or water.

934 As noted above, despite repeated interbreeding, general reproductive isolation (RI) was
935 maintained, since the phenotypes and genotypes remain distinct through to the disappearance
936 of Neanderthals from the fossil record c. 40 Ka (White *et al.*, 2014). Mechanisms include
937 behaviours or psychological adaptations that prevent other individuals being recognised as
938 suitable mates, non-synchronised reproductive cycles, physiological differences from the
939 reproductive organs to the internal reproductive environment (Nosil, 2012), and geographic
940 separation. In the latter case, which operates over longer timescales (Wilson *et al.*, 1974), RI
941 often leads to lower hybrid fitness, for example one or the other sex is not produced, or is
942 produced rarely and is sterile (Haldan's Rule; Haldane, 1922). On the other hand, some hybrids
943 have higher reproductive fitness and survival (Overmann and Coolidge, 2013). The frequency,
944 vitality, and fertility of Neanderthal hybrids is currently unknown.

945 The recent discovery of bone from a first generation female hybrid with a Neanderthal
946 mother and a Denisovan father is striking, as her DNA contained further evidence for
947 interbreeding in ancestors thousands of years earlier (Slon *et al.*, 2018). In addition, a genetic
948 study of an early *H. sapiens* mandible dating to c. 40 Ka with putative Neanderthal-like anatomy
949 (Trinkaus *et al.*, 2003) was shown to have had a Neanderthal ancestor within just 4–6

950 generations (Fu *et al.*, 2015). Taken together, these and the other DNA evidence implies that
951 while mixing between Late Pleistocene hominin populations was probably not *frequent* due in
952 part to low population density, it may have been *common*, in the sense of a likely possible
953 outcome of contact between groups (Slon *et al.*, 2018). Certainly some differences in behaviour,
954 potentially in cognitive functioning and perhaps reproductive cycles and sperm function existed
955 between Neanderthals, Denisovans, and *H. sapiens* populations that affected the likelihood of
956 encounters and hybridization (Overmann and Coolidge, 2013; Kuhlwilm and Boeckx, 2019),
957 probably varying according to local contexts. While Neanderthals and early *H. sapiens* had an
958 extremely similar ecological niche, potentially leading to competitive exclusion, that fact also
959 increases the likelihood of encounters and hybridization (Garrigan and Kingan, 2007).
960 In terms of the social contexts of sex between Neanderthals and other hominins, there is no *a*
961 *priori* reason to favour a *P. troglodytes*-like tendency to xenophobia and intergroup violence as
962 the most likely scenario. Indeed, while forced copulation is common *within* chimpanzee groups,
963 killing rather than ‘rape’ is the usual response to encountering foreign females (contra
964 Overmann and Coolidge, 2013). On the other hand, ‘raiding’ other groups for women is known
965 among recent hunter-gatherers (Hrdy, 2009). Certainly whether the social context was conflict
966 or consensual, it is likely that Neanderthals recognised Denisovans and early *H. sapiens* as
967 similar enough to attack or be attracted to. In particular, whatever the circumstances of
968 conception and whichever population they were born into, at least some of the hybrid infants
969 must have experienced close maternal attachment and care for them to survive to adulthood.
970 Moreover, to then reproduce in turn, they must have been accepted by their peers as sexual
971 partners (Wragg Sykes, 2020). Together these facts hint that beyond biology, Neanderthal and
972 *H. sapiens* cannot have had wildly differing social structures, behaviour, language facility or
973 culture.

974 **Discussion and Conclusion**

975 Perception of Neanderthals has dramatically altered over time thanks to advances in
976 archaeology and, recently, ancient genetics. These hominins were highly intelligent with socio-
977 economic lives that appear very similar to a human hunter-gatherer ecological and cultural
978 niche, adapted to environments varying from arid woodlands to steppe tundra. Yet despite
979 being the most studied ancient hominin species, with a relatively abundant fossil record, many
980 questions about Neanderthal biology, societies, and cultures remain. In particular, without any
981 soft tissue preservation thus far, their reproductive anatomy and sexual behaviour can only be
982 reconstructed based on skeletal, genetic, and archaeological data. Despite that, by synthesising
983 the available evidence and integrating it with *H. sapiens* biological anthropological and
984 primatological data and models, this chapter demonstrates the surprising amount that can be
985 discerned.

986 *Ethnography, biological anthropology, and primatology*: Menarche may have occurred
987 slightly earlier in Neanderthals than in humans and males probably regarded fat deposits in
988 females as sexually desirable. Exogamy and mating systems were probably flexible and varied
989 with ecological conditions. However, monogamy is likely to have been the prevalent mating
990 strategy, especially in harsher environments, and is associated with higher social tolerance and
991 reduced aggression. In richer environments, such as during interglacials or in the
992 Mediterranean and Near East, polygyny may have also been likely. Parental effort by females
993 and males was likely significant and help from kin probably also played an important role.

994 *Palaeoanthropology (i.e. skeletal evidence)*: Female pelvic anatomy suggests that birth
995 was difficult due to a tight cephalo-pelvic relationship. Assistance from others, probably
996 females, is therefore likely, on the assumption of a tolerant society based around food sharing
997 and cooperative breeding. Birth sometimes took place in spring, and weaning in autumn.
998 Weaning initiation and cessation varied, but broadly matches *H. sapiens* foraging populations.
999 Even with high risks of mortality during prime adulthood, elders (>40 years old) were present,
1000 meaning that intergenerational alloparenting may have been available, not only from older
1001 siblings, but also from grandparents. The availability of maternal grandmothers may have been
1002 particularly beneficial in feeding, caring for, and teaching young grandchildren, which together
1003 with *H. sapiens*-like early weaning initiation, would free women to take part in resource
1004 provisioning, including active hunting. Even so, Neanderthal children sometimes experienced
1005 periods of developmental stress similar to some hunter-gatherer populations, potentially
1006 associated with weaning initiation and breastfeeding cessation.

1007 *Genetics*: Neanderthals lived in smaller effective breeding populations than early *H.*
1008 *sapiens*, but not all were inbred. They interbred with at least two other hominin populations
1009 (Denisovans and *H. sapiens*) in multiple phases over more than 150,000 years, an outcome of
1010 probable infrequent contact. Hybrid infants were able to survive and adapt to being raised in
1011 both Neanderthal and *H. sapiens* social settings. While Neanderthals and *H. sapiens* maintained
1012 their phenotypic distinctiveness, these sexual encounters occurred with sufficient frequency to
1013 allow for the widespread exchange of pathogens.

1014 *Archaeology*: A top-trophic-level, yet flexible hunter-gatherer ecological niche is amply
1015 demonstrated, with group size probably less than 25 and often smaller. Fission-fusion was
1016 probably occurring during normal subsistence practice, which may have provided a mechanism
1017 for exogamy. High-resolution sites indicate hearth-centred social spaces, with evidence of intra-
1018 group social divisions, potentially 'family' units. Low material cultural wealth indicators imply
1019 mate value may have been focused on skill, knowledge and physical appearance (possibly also
1020 kin/alliances). Systematic processing and transport of food back to central living places implies
1021 resource-sharing was important. Close social bonds are indicated by instances where severely

1022 injured individuals were provisioned and survived. The intentional deposition of bodies took
1023 place, including infants and neonates.

1024 In conclusion, drawing on a vast array of sources of data we are able to construct a
1025 surprisingly detailed and richly layered picture of the sexual lives of Neanderthals. Nonetheless,
1026 while some aspects are confidently asserted, others are built up necessarily from probabilities
1027 and inferences. Many questions remain, some of which may be answerable with future
1028 development of analytical techniques and new discoveries. First, can we reconstruct missing
1029 phases of the Neanderthal life course? For example, we have no archaeologically visible
1030 measure of male contributions to reproduction. Similarly, there are no known reliable skeletal
1031 markers associated with either parity or menopause in females, and while we can infer aspects
1032 of the birthing process from the female pelvis and neonate cranial circumference, we cannot
1033 gauge the impact soft tissues had on this process or estimate with any reliability whether or
1034 how often a particular Neanderthal woman gave birth. Second, how much variation existed
1035 between Neanderthal populations in terms of inbreeding, exogamy, weaning times, and other
1036 aspects of sexuality, reproduction and infant care? How do these differences relate to variations
1037 in ecology and cultural traditions? This requires us to take a historically-situated, ethnographic
1038 approach to the data rather than a strictly ethological one. Thirdly, what was the nature of the
1039 sexual encounters between Neanderthals, Denisovans and *H. sapiens*? Is it significant that we
1040 have yet to find any evidence of the co-habitation of members of these different populations?
1041 We should also finally consider how much we could learn about the non-reproductive aspects of
1042 sex and sexuality among Neanderthals.

1043 We acknowledge that much of the data drawn on here privileges a binary division of sex
1044 and gender, yet it is clear that well into prehistoric times *H. sapiens* have comprised a spectrum
1045 of variation in biology and gender construction, expression and identification; moreover
1046 homosexual behaviour is widespread in animals, particularly bonobos, therefore we must
1047 assume Neanderthals had potential for similar diversity. Finally, of necessity, our
1048 reconstructions are fundamentally essentialist, with some of the anthropological questions in
1049 which we have the greatest interest proving to be the most difficult to explore scientifically.
1050 Nonetheless, as has been demonstrated in this chapter, while some questions will remain
1051 elusive, new discoveries and scientific advances are bringing us closer than we ever thought
1052 possible to the intimate lives of Neanderthals.

1053

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1057

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