

# Human species and mating systems: *Neandertal–Homo sapiens* reproductive isolation and the archaeological and fossil records

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**Summary** - *The present paper examined the assumption of strong reproductive isolation (RI) between Homo neanderthalensis and Homo sapiens, as well as the question of what form it might have taken, using insights from the parallel case of chimpanzee–bonobo hybridization. RI from hybrid sterility or inviability was thought unlikely based on the short separation-to-introgression timeline. The forms of RI that typically develop in primates have relatively short timelines (especially for partial implementation); they generally preclude mating or influence hybrid survival and reproduction in certain contexts, and they have the potential to skew introgression directionality. These RI barriers are also consistent with some interpretations of the archaeological and fossil records, especially when behavioral, cognitive, morphological, and genetic differences between the two human species are taken into consideration. Differences potentially influencing patterns of survival and reproduction include interspecies violence, Neandertal xenophobia, provisioning behavior, and ontogenetic, morphological, and behavioral differences affecting matters such as kin and mate recognition, infanticide, and sexual selection. These factors may have skewed the occurrence of interbreeding or the survival and reproduction of hybrids in a way that might at least partially explain the pattern of introgression.*

**Keywords** - *Hybridization, Speciation, Introgression.*

## Introduction

Comparison of Neandertal and modern human biparentally inherited nuclear DNA has been interpreted as demonstrating unidirectional gene flow from Neandertals to some modern human populations; this contrasts with data from uniparentally inherited DNA (mitochondrial DNA and Y-chromosome markers), which show no evidence of introgression (Gibbons, 2010; Green *et al.*, 2010; Wall *et al.*, 2009; Yotova *et al.*, 2011). Recent theoretical models, over a range of demographic parameters, have indicated that these genetic patterns are predicted if successful interbreeding events were rare; with evidence of some period of coexistence, this implies that the

RI barriers between them must have been strong (Currat & Excoffier, 2011; Neves & Serva, 2012).

One theoretical model postulating strong reproductive isolation (RI) between *H. neanderthalensis* and *H. sapiens* is that of Currat *et al.* (2008), who noted that introgressive genes typically flow from local to invading species in plants and animals; on this view, gene flow simply followed the general pattern in introgressing from resident Neandertals to early modern humans expanding out of Africa. Even a small introduction of local alleles would have the potential to reach relatively high frequencies because introduction at the inception of the invasion, no matter how small the total period of interspecies contact, would have the potential to proliferate

the alleles widely as a function of demographic change (Currat *et al.*, 2008; Durand *et al.*, 2011; Sankararaman *et al.*, 2012); the *H. sapiens* population was increasing while that of *H. neanderthalensis* was decreasing (Green *et al.*, 2010; Mellars & French, 2011). Other factors may also have intervened. As Bruner (2013) noted, early modern humans and Neandertals may have interbred “to such a negligible degree that evolution and selection did not care” (p. 12); further, the phenomenon of local extinctions could have resulted in some interbreeding events leaving traces in the genome while others did not (Green *et al.*, 2010).

While the population genetics explanation is sufficient to explain the pattern of introgression, Currat *et al.* (2008) acknowledged that their model could not explain all cases, since it was insensitive to complicating factors (e.g., selection functions, preferences and biases, and behaviors) and assumed uniform parameters (e.g., territorial carrying capacities; rates of migration and interbreeding) that might not hold in all cases or across single cases over time. Several plausible alternatives have also been proposed: Eriksson & Manica (2013) interpreted genetic similarities as reflecting ancient population structure rather than hybridization, though Sánchez-Quinto *et al.* (2012) and Yang *et al.* (2009) have argued that a scenario involving distinct African subpopulations was unlikely. Gokcumen *et al.* (2013) suggested that divergent haplogroups mimic the admixture signature, implying that any introgression would have occurred before the two human species diverged. Another hypothesis is that of Pinhasi *et al.* (2011) and Wood *et al.* (2013), who interpreted recent site dating analyses as indicating a minimal contact period; if this is correct, the introgression discussion will need to incorporate a significantly reduced window of opportunity (especially for Europe), which would nonetheless be compatible with the population genetics explanation. Others have noted that the period of coexistence may have been extensive, possibly exceeding 10,000 years (Currat & Excoffier, 2004; Hublin *et al.*, 2012), with the result that the two human species may have been constantly in contact, particularly in

locations such as the Near East (i.e., at the borders of or the overlap between the two ranges).

Assuming that admixture did occur and that the interpretation of unidirectional introgression is correct (matters still under debate), the implication would be that the two human species were reproductively isolated to a significant degree. The implication of strong RI is interesting and warrants further examination; the question of what form RI between the two human species might have taken was therefore examined in light of general primate RI tendencies. Future avenues of research were also suggested for the archaeological and fossil records and contemporary primatology, consistent with the RI tendencies of primates, especially baboons (because of their frequent hybridization) and chimpanzees and bonobos (because of their genetic similarity to Neandertals and modern humans).

## Previous proposals on RI form

### *Hybrid sterility*

Mason & Short (2011) proposed that the pattern of introgression may demonstrate Haldane's rule, in which interspecies genetic interactions yield differential sex ratios and unisexual sterility in hybrid offspring (Haldane, 1922). The syndrome has been observed in insects, birds, and mammals; in some species, female hybrids are not produced at all, are produced infrequently, or are sterile if produced, and in others, the syndrome affects male offspring (Coyne, 1985; Haldane, 1922). Such inviability or infertility of male hybrids may at least partially explain the apparent lack of Y-chromosome introgression the two human species (Mason & Short, 2011). Mason & Short (2011) have also suggested that the only fertile hybrids were female offspring with *H. neanderthalensis* fathers and *H. sapiens* mothers. However, the timeline between *H. neanderthalensis*–*H. sapiens* separation and introgression is relatively short: Their divergence has been estimated to have occurred at a maximum of 500,000 years ago and perhaps as recently as 440,000–270,000 years ago (Green *et al.*, 2006, 2010). The average time for developing hybrid

sterility in mammals is less than 2.0 to 4.0 million years (Fitzpatrick, 2004; Wu, 1992), a period of time at least double that separating the two human species. Mason & Short's (2011) hypothesis would therefore require the onset of hybrid sterility to have been particularly rapid. Thus, hybrid infertility appeared unlikely to have been the form of RI isolating the two human species.

#### *Other hypotheses*

Neves & Serva (2012) suggested that *H. neanderthalensis* and *H. sapiens* were reproductively isolated through cultural or social differences, and Schillachi & Froehlich (2001) proposed that the two human species might have had trouble recognizing each other as suitable mates. Currat & Excoffier (2011) also suggested that the two were reproductively isolated through lower hybrid fitness; the unidirectionality of the introgression suggests that hybrid fitness may have been context-dependent. Together, these analyses suggest examining archaeological and fossil records, as well as hybridization in other primates, for evidence of possible behavioral, cognitive, and morphological differences with the potential to have reproductively isolated the two species.

### **The chimpanzee–bonobo model and its extensibility**

Hybridization between chimpanzees and bonobos was considered on the premise that their case was sufficiently similar to that of *H. neanderthalensis* and *H. sapiens* to illuminate their potential for and form of RI. Chimpanzees and bonobos (*Pan troglodytes* and *P. paniscus*, respectively) are the closest genetic relatives of *H. neanderthalensis* and *H. sapiens* (Green *et al.*, 2010). The small genetic distance between them suggests that they could be considered a single species, as has been suggested for *H. sapiens* and *H. neanderthalensis*, who are also known as *Homo sapiens neanderthalensis* (e.g., Curnoe & Thorne, 2003; Tattersall & Schwartz, 1999; Wegmann & Excoffier, 2010; the debate on this has persisted for well over a century despite the abundance of

Neandertal and early modern human remains available for comparison; see Bruner, 2013). The genetic similarity between the two species pairs suggests that hybridization would have been likely for both, given geographic proximity (see the discussion of *syngameons*, closely related species that hybridize frequently, in Holliday, 2003).

The timelines and reasons for speciation are parallel between the two species pairs. Chimpanzees and bonobos speciated less than a million years ago, a timeline roughly comparable to that separating Neandertals and early modern humans (Green *et al.*, 2006, 2010; Hey, 2009). Both speciation events may have occurred through geographic isolation: Chimpanzees and bonobos are thought to have been separated by the Congo River, which remains impassible today to their relatively poor ability to swim (Matsuzawa, 2006). This is analogous to the circumstances believed to have separated the *H. heidelbergensis* populations ancestral to *H. sapiens* and *H. neanderthalensis*, who were also geographically isolated, perhaps by climate change (e.g., Gippis, 1991).

Chimpanzees and bonobos differ morphologically and behaviorally, and early modern humans and Neandertals might have as well. Morphological differences are subtle, with bonobos being perhaps more paedomorphic (or juvenilized) than chimpanzees; paedomorphy represents the combined effect of heterochronic change in the speed (slowed), onset (late), or duration (shortened) of ontogenetic growth, with the result that descendant adults resemble the ancestral juvenile condition (McKinney, 2000; Schlesinger, 2008; Shea, 1983a,b). *H. sapiens* were similarly paedomorphic relative to *H. neanderthalensis*, who may have matured more quickly and been more robust (Ben-Itzhak *et al.*, 2005; Gunz *et al.*, 2010; Lieberman *et al.*, 2007; Smith *et al.*, 2010). Behavioral distinctions between chimpanzees and bonobos are more overt and include more than three dozen behaviors, such as cooperation, dispersal patterns, dominance, social structures, provisioning, territoriality, tolerance, and mating (Hare *et al.*, 2007; Parish & de Waal, 2006; Prüfer *et al.*, 2012). *H. neanderthalensis* and *H. sapiens* may also have differed in behaviors such as provisioning, diet, tool production, art, and

group size (Kuhn & Stiner, 2006; Lalueza-Fox *et al.*, 2011; Richards *et al.*, 2009; Spikins *et al.*, 2010; Wynn & Coolidge, 2012). The idea that the two human species differed behaviorally is controversial (e.g., Villa & Soriano, 2010; Zilhão *et al.*, 2010), especially since the complexity of the Levallois technique, the use of compound technology, and the very fact of their long-term survival across wide geographic and climatic ranges argue in favor of Neandertal competency (Roebroeks & Villa, 2011; Schlanger, 1996; Stewart, 2005). Nonetheless, comparative cranial morphologies and emerging genetic evidence (discussed below) suggest that the two human species may have differed cognitively, implying that there would have been behavioral differences as well.

There are several limitations to the chimpanzee–bonobo model that constrain its extensibility to the two human species. The first is that the morphological, behavioral, and cognitive differences between chimpanzees and bonobos appear more subtle than those distinguishing Neandertals and early modern humans, possibly because the former inhabit similar subtropical niches, while the latter inhabited divergent environments, with Neandertals becoming cold-adapted (Conard, 2011). A second limitation of the model is that the nonhuman pair is distinct–cognitively, morphologically, and behaviorally–from the human pair, so that the parallels extend only so far. A third limitation in the model arises from the debate on whether *H. sapiens* and *H. neanderthalensis* differed to any significant degree. That is, interpretations of the archaeological record as showing no differences between the two human species argue against RI resulting from morphological, behavioral, or cognitive differences, while interpretations of the archaeological record as demonstrating differences argue in favor of RI.

## RI and hybridization

RI can be prezygotic or postzygotic (respectively, either before or after a zygote is formed). In prezygotic RI, the formation of hybrid zygotes

is prevented, either before or after mating occurs, because species are isolated geographically (i.e., no proximity), temporally (no synchronization of activity or mating cycles), behaviorally (no recognition of mate suitability), mechanically (no fit between genitalia), or chemically (inability to tolerate another species' reproductive environment) (Nosil, 2012; Wiens, 2004). In comparison, in postzygotic RI, hybrids are formed but have lower fitness, either in any environment or as a function of their ecological circumstance. Lower hybrid fitness in any environment would include cases in which genomic incompatibility precluded successful embryonic development, as well as instances of Haldane's rule (Haldane, 1922). Lower hybrid fitness in certain environments would include cases in which hybrid survival and reproduction were increased or decreased through factors present in their environmental situation.

### *Prezygotic RI*

In primates, speciation through prezygotic isolation requires an average of 1.1 million years (Curnoe *et al.*, 2006). This is slightly longer than the chimpanzee–bonobo speciation timeline and at least double that of *H. neanderthalensis* and *H. sapiens*, suggesting that given the opportunity both species pairs might interbreed, as is indeed the case with captive chimpanzees and bonobos (Curnoe & Thorne, 2003; Vervaecke & Van Elsacker, 1992). Notably, RI through prezygotic isolation may be the norm for primates (Curnoe *et al.*, 2006); the circumstance that chimpanzees and bonobos have not been separated long enough to develop it suggests either that *H. neanderthalensis* and *H. sapiens* were not separated long enough to develop this form of RI, or that their differences (e.g., behavioral, morphological) were significant (and thus might be detectable in the archaeological record).

### *Postzygotic RI*

In mammals, RI from hybrid inviability requires, on average, between 2.0 and 4.0 million years to develop (Fitzpatrick, 2004), at least twice that of prezygotic RI. This average implies that neither species pair would have been

reproductively isolated by hybrid inviability, since both have shorter timelines. In fact, chimpanzees and bonobos produce “apparently normal” hybrids (Curnoe & Thorne, 2003, p. 211), suggesting that Neandertals and early modern humans might have as well. Certainly, other primate species (particularly baboons) produce fertile hybrids (e.g., *Papio hamadryas* and *Theropithecus gelada*; see Dunbar & Dunbar, 1974; Jolly *et al.*, 1997; Markarjan *et al.*, 1974), though the hybrids can also be less successful reproductively, perhaps as the result of subtle morphological or behavioral differences (Jolly, 2009).

RI through hybrid sterility may require less than 2.0 to 4.0 million years to develop in mammals; assessments are complicated by the fact that hybrid sterility falls on a continuum from partial to complete (Wu, 1992). An example is the case of horses and donkeys, whose speciation occurred roughly 3.9 million years ago (based on molecular data; see Vilà *et al.*, 2001). Female horse–donkey offspring, known as mules and hinnys, are usually—but not invariably—sterile (Rong *et al.*, 1988; Rong *et al.*, 1985). This suggests that the development of hybrid sterility in horses and donkeys is nearly complete, in affecting all male and most female hybrids, but nonetheless falls short of being total. This state was reached in four times the amount of time separating bonobos from chimpanzees and eight (or more) times that separating Neandertals and early modern humans. Thus, even if primates developed hybrid sterility at an accelerated rate relative to mammals (which they are not known to do), there may still have been insufficient time for it to have developed in *H. neanderthalensis*–*H. sapiens* hybrids. The idea that the time was insufficient is further reinforced by the circumstance that chimpanzee–bonobo hybrids are probably fertile, something that is difficult to confirm because of legal restrictions on their breeding (Vervaecke, personal communication).

#### *RI variation*

Since RI through hybrid sterility exists on a continuum (Wu, 1992), other forms of RI may as well, possibly accounting for some of the insufficiencies in the speciation timeline. That

is, though it appears there may have been insufficient time for Neandertals and early modern humans to develop different forms of RI in a full and complete manner, there may have been sufficient time for them to develop RI barriers in a partial or incomplete fashion, especially for prezygotic mechanisms requiring shorter development times. Partial RI implementation has a characteristic signature of being skewed since it precludes only some of the possible outcomes of interbreeding while allowing others. Thus, the specific position on the development continuum (from none to complete) might have influenced introgression directionality through some unevenness of effect, an assumption more parsimonious than assuming uniformity across all possible cross-match and circumstantial variations.

#### *Hybridization*

Hybridization is common among primates generally and may have occurred between ancestral chimpanzees and the hominin lineage following speciation from the last common ancestor (Aguilar *et al.*, 2008; Patterson *et al.*, 2006; Zinner *et al.*, 2011). This suggests that the willingness to breed across species might characterize both descendent lineages, a supposition confirmed by the fact that chimpanzees and bonobos will interbreed in captivity (Curnoe & Thorne, 2003; Vervaecke & Van Elsacker, 1992). The morphology of primate hybrids is highly variable but generally intermediate between that of the two parent species; morphs can range from being indistinguishable from either parent species (cryptic), in between the two (intermediate), or outside the range of variation of either (unusual) (Ackerman, 2010; Zinner *et al.*, 2011). In addition to morphological intermediacy, behavioral intermediacy has been observed in mammal hybrids (e.g., Weber *et al.*, 2013). Notably, chimpanzee–bonobo hybrids are characterized by both morphological and behavioral intermediacy (Vervaecke, personal communication). In general, some hybrids are more vigorous, some less, than the two parent species (Ackerman, 2010); chimpanzee–bonobo hybrids have been described as having normal vitality, though this

observation relates to circumstances of captivity (Curnoe & Thorne, 2003). By extension, *H. neanderthalensis*–*H. sapiens* hybrids might have had morphological and behavioral characteristics that were generally intermediate between their two parent species, and while their vitality might have been normal, it could also have been a factor in their ability to respond to specific environmental conditions.

#### *Forms of RI observed in primates*

Prezygotic RI (the primate norm; see Curnoe *et al.*, 2006) and lower hybrid fitness (postzygotic RI) have been observed in primate hybridization (Aguiar *et al.*, 2008). Asymmetric gene flow from postzygotic RI has also been observed in primates (e.g., *Macaca mulatta* and *M. fascicularis*; see Stevison & Kohn, 2009), with behavior (e.g., philopatry; dispersal) and social group structure influencing gene flow and population structure (Tung *et al.*, 2010). These RI barriers and influences, coupled with a timeline that may preclude the development of RI between *H. neanderthalensis* and *H. sapiens* in any form but especially in the forms of hybrid inviability and sterility, suggests that if the two human species were reproductively isolated, the form it might have taken would have followed these primate tendencies. That is, if *H. neanderthalensis* and *H. sapiens* were reproductively isolated, it may have been through behaviors that prevented the occurrence of mating, through lower hybrid fitness if mating did occur, or both.

### **Interbreeding between *H. neanderthalensis* and *H. sapiens***

The question posed by the chimpanzee–bonobo model, in which interbreeding between species is common (at least in captivity) and productive (in terms of hybrid vitality and possibly hybrid fertility as well), is why interbreeding between *H. neanderthalensis* and *H. sapiens* would have been rare once the populations reencountered one another (Currat & Excoffier, 2011; Currat *et al.*, 2008; Neves & Serva, 2012). The assumption of strong RI is curious given that the genetic

distance between the two human species was smaller than that between some modern human populations (Curnoe & Thorne, 2003; Neves & Serva, 2012). Behavioral, cognitive, and morphological differences do not prevent chimpanzees and bonobos from interbreeding, at least under the choice-restricted circumstances of captivity, or from producing hybrids of apparent normality, as assessed against the artificial conditions of captivity (Curnoe & Thorne, 2003; Vervaecke & Van Elsacker, 1992). In addition, the four chimpanzee subspecies – *P. t. schweinfurthii*, *P. t. troglodytes*, *P. t. vellerosus*, and *P. t. verus* – are similarly isolated by geography and differentiated by their behavior and morphology; however, they are known to interbreed both in the wild and in captivity and have been said to do so in all combinations (Becquet & Przeworski, 2007; Fischer *et al.*, 2004; Gagneux *et al.*, 2001; Hey, 2010; Matsuzawa, 2006; Won & Hey, 2010). These circumstances suggest either that the differences between Neandertals and early modern humans were more profound than those distinguishing chimpanzees and bonobos (precluding mating), or that interbreeding between the two human species was common but factors such as higher hybrid morality influenced hybrid survival and reproduction and hence the directionality of the introgression—or both, since the two are not mutually exclusive.

Apparently no barrier to interbreeding, chimpanzee–bonobo behavioral differences nonetheless imply cognitive differences between the two nonhuman species; for example, the greater ‘patience’ of bonobos relative to chimpanzees implies a difference in inhibition, an executive function (Rosati *et al.*, 2007). These cognitive differences are consistent with the endocranial differences between the two species, which result from the divergent ontogenetic trajectories followed by each (Durrleman *et al.*, 2012; Mitteroecker *et al.*, 2005). The assumption that cognition may have similarly distinguished *H. neanderthalensis* and *H. sapiens* may not be unwarranted, given that morphometric differences in their fossil endocasts imply differences in cognitive domains such as language, spatiality, and creativity (e.g., Bruner, 2004, 2010; Bruner *et al.*, 2003; Coolidge &

Wynn, 2013; Gunz *et al.*, 2010; Lieberman *et al.*, 2002; Pearce *et al.*, 2013). The idea that there were differences in cognitive functioning is consistent with archaeological interpretations of behavioral differences (e.g., Coolidge & Wynn, 2001, 2004; Henshilwood & Marean, 2003; Mellars, 2004; Wynn & Coolidge, 2004, 2012).

#### *Anatomic evidence with cognitive implications*

Morphometric comparison of *H. neanderthalensis* and *H. sapiens* endocasts reveals differences in asymmetry, the relative size and shape of the major lobes, and the cerebellum. Greater frontal-temporal encephalization and differential asymmetry patterns in *H. sapiens* suggest a language advantage for that species, enabling more effective communication between individuals (social cooperation) and across time (cultural learning) (Gunz *et al.*, 2010; Lieberman *et al.*, 2002;). Frontal lobe volume appears relatively equal between the two species (Bruner & Holloway, 2010), so differences in executive functioning cannot be determined by morphometric analysis and endocast comparison alone. However, differential executive functioning may reflect differential neural reorganization subsequent to encephalization (both human species) or globularization (*H. sapiens* only) (Coolidge & Wynn, 2001).

Bruner and colleagues (Bruner, 2004, 2010; Bruner *et al.*, 2003) have suggested that parietal change may be the characteristic that truly distinguishes the two human species: The parietal region of early modern humans has an expansion (probably in the intraparietal sulcus, medial region, or upper cortex) not found in Neandertals. Parietal expansion has been associated with globularization, neural reorganization, and enhanced parietal functioning, including multimodal processing, visuospatial and sensory integration, planning and manipulation of motor sequences, control of fingers, spatial analysis, and the creation of 'inner space' representations of external space (Bruner, 2004, 2010; Bruner *et al.*, 2003). Thus, parietal change may have contributed to the adaptive success of *H. sapiens* through improved multimodal integration, visuospatial integration, and social functioning (Holloway, 1996) or by contributing

to higher-level capabilities for symbolism (Coolidge & Overmann, 2012).

The *H. sapiens* cerebellum may also have differed. Weaver (2005) found mean cerebellum volume to be absolutely and relatively higher in modern *H. sapiens* than in *H. neanderthalensis*, and further, a derived cerebellar quotient (cerebellum/overall brain volume) was also larger in *H. sapiens* than in *H. neanderthalensis* (however, a caveat is in order: Weaver's study involved small samples, limited metrics, and straightforward statistical analyses). Every major lobe of the cortex projects through the pons to the cerebellum, and the cerebellum through the thalamus reciprocally connects to at least 14 neocortical sites. While early theories of cerebellar function proposed that motor learning and fine motor control were key attributes, recent research has clearly established that the cerebellum has an important role in non-motor cognitive functions as well, particularly with its interconnections to the prefrontal cortices and to the parietal lobes. Balsters *et al.* (2013) demonstrated that cerebellar lobules (Crus I & II) have prefrontal-projecting connections activated when processing first- and second-order cognitive (non-motor) instructions. Weaver (2005) further argued that cerebellar development in *H. sapiens* may have provided greater computational efficiency and adaptive ability. Koziol *et al.* (2010) attributed greater speed of adaptation and behavioral mastery and refinement to cerebellar development, and Vandervert (2009, 2011) attributed creativity, giftedness, and the neural basis for child prodigies to the efficiency and nature of the cerebrum-cerebellar loops. The smaller Neandertal cerebellum may therefore imply a difference in creativity, which would be consistent with archaeological interpretations suggesting behavioral differences between the two human species (e.g., Coolidge & Wynn, 2001, 2004, 2005; Wynn & Coolidge, 2002, 2004, 2012).

Pearce *et al.* (2013) also noted that the larger portion of the Neandertal brain dedicated to vision implied both a visual difference at higher latitudes and a corresponding reduction in the size of other brain regions; the relative resizing of non-occipital regions of the Neandertal brain implies

concomitant differences in their cognitive functionality because of the relationship between brain region size and functionality (Striedter, 2005).

#### *Genetic evidence with cognitive implications*

Emerging genetic evidence suggests there were at least subtle differences in the cognitive abilities of *H. neanderthalensis* and *H. sapiens*: Paixão-Côrtes *et al.* (2013) found nine non-synonymous substitutions (i.e., substitutions resulting in biological change and therefore subject to natural selection) in genes implicated in various forms of learning and memory; these imply that the two human species may have differed in these cognitive domains, as has been suggested by Wynn & Coolidge (2004). The nine non-synonymous substitutions were 10% of 93 alleles examined in the study; Neandertal data for another 27% were missing, admitting the possibility that additional genetic changes with cognitive implications may be found. While the 10% difference presently identified would not decrease, were the missing data to vary at the same rate, the difference would show a minor increase (12%) but could increase to as much as 37% in the unlikely case that all 25 cases of missing data differed. In view of studies showing that a single gene can significantly alter the brain (e.g., Bakircioglu *et al.*, 2011), the study by Paixão-Côrtes *et al.* (2013) suggested that the genetic differences identified (plus any additional instances identified once the missing Neandertal data have been established) should be investigated for their impact on cognition, learning, and memory, especially short-term and visual memory, cognitive abilities potentially affected by the contribution and interaction of seven or more non-synonymous substitutions.

### **Behaviors in the archaeological record and other primates**

Anatomic and genetic evidence of potential cognitive differences between Neandertals and early modern humans are consistent with archaeological interpretations of behavioral differences between

the two human species, differences with the potential to contribute to RI. Behaviors and behavioral differences that possibly acted to reduce or preclude interbreeding are suggested by evidence of intergroup violence, Neandertal xenophobia, and differential provisioning and dispersal. As shown in Table 1, intergroup violence and Neandertal xenophobia might have reduced the likelihood of interbreeding across the board, and differences in provisioning behavior might have increased the likelihood of interbreeding between *H. neanderthalensis* males and *H. sapiens* females. The effect of dispersal pattern differences was uncertain.

#### *Intergroup violence*

As “many kinds of primates are intolerant of strangers,” a factor in the formation of breeding groups (Erwin, 1986, p. 297), interspecies violence related to territoriality might have discouraged contact between groups, thereby reducing mating opportunities. While baboons do not appear to be particularly territorial (Cowlshaw, 1995; Howell & Bourlière, 2008), wild chimpanzees have been known to engage in cooperative defense and even patrol their territories, influencing female reproductive behavior (Mitani & Watts, 2005; Mitani *et al.*, 2010; Williams *et al.*, 2004; Williams *et al.*, 2004; Wilson *et al.*, 2001). Violent contact between the two human species is suggested by Shanidar-3, the Neandertal skeleton from Shanidar, Iraq whose ninth rib is lesioned in a way that would be consistent with the projectile weapons of early modern humans (Churchill *et al.*, 2009; Santamaria *et al.*, 2010); actuarial support for weapons producing similar wounds cannot, however, be taken as proof that Neandertals and early modern humans were in contact, let alone in conflict. However, some interpretations of the archaeological evidence have suggested that whatever contact limitations were in place at the beginning of the coexistence period may have improved toward its end, based on Neandertal techno-cultural changes that imply prolonged, amiable contact with early modern humans (Green *et al.*, 2006; Hublin *et al.*, 1996; but also see Higham *et al.*, 2010, who highlight the challenges of establishing clear associations between artifacts and their makers).

### *Neandertal xenophobia*

An aspect of group-level intolerance of strangers is that of possible Neandertal reluctance to approach strangers (xenophobia), which might have reduced the likelihood of their approaching human individuals for any reason, including mating. The characterization of Neandertals as shy is based on archaeological evidence of their living in small groups and generally lacking exotic raw materials at their sites, factors interpreted by some scholars as suggesting that Neandertals may have had difficulty managing numerous face-to-face contacts and relatively restricted territorial mobility that imply possible cognitive constraints on sociality and spatiality, respectively (Fernández-Laso *et al.*, 2011; Gamble, 2011; Gamble *et al.*, 2011; García-Antón *et al.*, 2011; Lalueza-Fox *et al.*, 2011; Wynn & Coolidge, 2004, 2012). However, this possible influence on interbreeding must be tempered by the insight that Neandertals may not have been as territorially restricted as once thought; for example, recent evidence of diet and raw material exploitation suggests that they may have exploited larger territories and had less restricted diets than previously believed (Richards *et al.*, 2008, 2009; Spinapolice, 2012).

### *Provisioning behaviors*

Communal hunting by Neandertals, with gathering plus gendered division of labor by early modern humans (Kuhn & Stiner, 2006; Richards *et al.*, 2009), imply differential opportunities for mating and conspecific interference, factors that could have reduced or prevented interbreeding. That is, the inclusion of both Neandertal males and females in hunting groups suggests that both sexes were less likely to be unaccompanied and thus less likely to be in situations in which mating could occur, whether opportunistic or coercive (Buss, 2007). By comparison, human males engaged in hunting may have been more likely unaccompanied or have had group dominance advantages that would facilitate mating, while human females engaged in gathering would more likely have been unaccompanied or in female-only situations in which conspecific male

**Tab. 1 - Influence of differential behavior and morphology.**

POTENTIAL INFLUENCE ON RI	F: <i>Hn</i> ; M: <i>Hs</i>	F: <i>Hs</i> ; M: <i>Hn</i>
Behavior		
Intergroup Violence	Reduce	Reduce
Neandertal Xenophobia	Reduce	Reduce
Provisioning	Increase	Reduce
Dispersal	Uncertain	Uncertain
Morphology		
Ontogenetic Differences	Increase	Uncertain
Sexual Selection	Increase	Reduce

Note - Key: F = Father; M = Mother; *Hn* = *H. neanderthalensis*; *Hs* = *H. sapiens*. The overall pattern suggested an increased likelihood of interbreeding between *H. neanderthalensis* males and *H. sapiens* females and a reduced likelihood of interbreeding between *H. neanderthalensis* females and *H. sapiens* males.

interference and protection would have been less likely, as remains the case in modern situations (e.g., Koshen, 2007). Conspecific interference is certainly a behavior observed in wild chimpanzees (e.g., Williams *et al.*, 2004). However, the inclusion of gathering as a provisioning strategy by Neandertals (Hardy *et al.*, 2012) and the phenomenon of *H. sapiens* female hunting in modern hunter-gatherer societies (Kuhn & Stiner, 2006) suggest that there may have been a significant amount of commonality in the provisioning behaviors of both human species, with the result that the contribution of behavioral differences in provisioning to RI requires further examination.

### *Dispersal patterns*

Differences in age- or sex- based dispersal patterns may have affected the occurrence of interbreeding. For age, dispersal-pattern differences have been noted in baboon hybrids (*P. anubis* and *P. cynocephalus*; see Alberts & Altmann, 2001), suggesting that *H. neanderthalensis*-*H.*

*sapiens* hybrids may have dispersed at a different age than non-hybrids. Regarding sex-based differences, Neandertals may have been male philopatric, a primate social system in which males remain in their natal range while females reaching sexual maturity emigrate to new groups (Lalueza-Fox *et al.*, 2011). Genetic evidence supporting this hypothesis derives from 12 Neandertal remains at El Sidrón, Asturias, Spain, which show three different maternal lineages for all 12 individuals but the same mitochondrial DNA for the three adult males (but also see Vigilant & Langergraber, 2011, who argue that this evidence is inconclusive at best). In comparison, 70% of all modern human societies are patrilocal (a related and fairly synonymous term for a social system in which married females reside with their husband's family; the terms may be differentiated along lines of humans [patrilocal] and nonhumans [male philopatry]; see Chapais, 2008). The rate for *H. sapiens* has been estimated by some researchers as greater than that of modern chimpanzees, which are strongly biased toward male philopatry and female dispersal (Hashimoto *et al.*, 2008; Langergraber *et al.*, 2007; Matsuzawa, 2006). However, Parish & de Waal (2006) have reported lower estimates of patrilocal for humans and have suggested that there is no typical pattern of female dispersal for hunter-gatherers. Differences in the degree of philopatry between the two human species might therefore have had the potential to skew the pattern of interbreeding.

### **Morphology in the fossil record and other primates**

The morphological differences between the two human species seen in fossils may have influenced mate recognition through factors of ontogenetic development and sexual selection; this is distinct from the idea of trying to recognize hybrid morphology in fossils (Holliday, 2003). As shown in Table 1, ontogenetic differences and sexual selection may have provided possible advantages for *H. neanderthalensis* males.

### *Mate recognition and ontogenetic differences*

Neandertals may have matured faster (and thus earlier), based on evidence showing that they had shorter periods of dental development than was typical for early modern humans (Smith *et al.*, 2010; but also see Guatelli-Steinberg *et al.*, 2005, who note that Neandertal dental growth rates fall within the human range). Cranial development may have differed as well, with *H. sapiens* developing a more globular brain shape postnatally that implies a longer period of neural reorganization than would have been the case for *H. neanderthalensis*, who lacked postnatal globularization (Gunz *et al.*, 2010). This suggested that brain development (and thus immaturity) would have been prolonged in *H. sapiens* relative to *H. neanderthalensis* (however, also see Ponce de León *et al.*, 2008, who suggest that brain growth rates were similar in both human species). These potential differences in maturity, if substantiated by future studies, might have been a factor in dispersal patterns and mate recognition, enhanced for the earlier-maturing Neandertals and degraded for later-maturing early modern humans. Such is the case for hybrid baboons, with hybrids of both sexes maturing and dispersing earlier, resulting in a selective advantage for hybrid males (advantages for female hybrids are offset by other social and environmental factors; see Alberts & Altmann, 2001; Charpentier *et al.*, 2008; Tung *et al.*, 2008).

### *Mate recognition and sexual selection*

As previously noted, *H. sapiens* were paedomorphic relative to *H. neanderthalensis*, who were characterized by greater muscle mass and bone strength (Ben-Itzhak *et al.*, 2005; Gunz *et al.*, 2010; Lieberman *et al.*, 2007; Smith *et al.*, 2010). These physiological differences might have influenced mate recognition, especially in female choice: *H. neanderthalensis* females might have interpreted paedomorphic *H. sapiens* males as having unsuitable youthfulness or lower fitness, thereby reducing their recognition as suitable mates. It is also possible that *H. sapiens* females might have interpreted the earlier maturing,

more robust *H. neanderthalensis* male form as indicating suitability for mating and higher fitness. A similar pattern might be predicted for chimpanzees and bonobos (i.e., that there would be female selection differences depending on the particular combination of paedomorphic vs. robust species); however, the literature on chimpanzee–bonobo hybridization does not address whether this has been observed, and in any case the influence of captivity on opportunity and choice would have to be considered as well. The effect has been observed in macaques, however, with introgression “biased strongly” toward *M. mulatta* males (the larger species) and *M. fascicularis* females (the smaller species), either because the females prefer the larger males or because the larger males can more easily coerce sex (Stevison & Kohn, 2009, p. 2470), biases that might also have also characterized Neandertal males and early modern human females (see Mason & Short, 2011, who note the strength differential). The tendency is also found in baboon hybrids: *P. hamadryas* and *P. Anubis* hybrid males have a phenotype that is apparently more attractive to females (Nystrom, 1992).

### Hybrid fitness mediated by context

Morphological and behavioral intermediacy for *H. neanderthalensis*–*H. sapiens* hybrids may have influenced the directionality of introgression by reducing their fitness or by reducing mate or kin recognition. As shown in Table 2, intermediacy in hybrid morphology possibly provided an advantage to hybrids among early modern humans but a disadvantage for hybrids among the Neandertals. In addition, uncertain paternity, hybrid behavioral intermediacy, or weakened kin recognition might have reduced hybrid survival in either situation.

#### *Lower survival outcomes from intermediate hybrid morphology*

Fossil trauma patterns suggest that the Neandertal led an arduous, dangerous lifestyle that included close-in hunting of large animals

**Tab. 2 - Influence on hybrid fitness.**

POTENTIAL INFLUENCE ON RI	HYBRIDS AMONG <i>H. sapiens</i>	HYBRIDS AMONG <i>H. neanderthalensis</i>
Survival (Morphology)	Increase	Reduce
Infanticide	Reduce	Reduce
Survival (Behavior)	Reduce	Reduce
Kin Recognition	Reduce	Reduce

Note - The overall pattern suggested that hybrids might have had a slightly better chance of surviving among *H. sapiens* than among *H. neanderthalensis*.

and megaherbivores (e.g., mammoth, woolly rhinoceros); the combination caused severe, often fatal injuries (Berger & Trinkaus, 1995; Bocherens, 2011; Gaudzinski-Windheuser & Roebroeks, 2011). The trauma patterns are consistent with other fossil evidence of young–old differentials suggestive of early mortality for Neandertal adults and a generally high rate of mortality for Neandertal infants (Pettitt, 2000; Richter, 2001; Trinkaus, 1995, 2011). Given the intermediate morphology of chimpanzee–bonobo hybrids, it is likely that *H. neanderthalensis*–*H. sapiens* hybrids would also have taken an intermediate form as well (consistent with the variability noted by Ackerman, 2010). In general, hybrids might have been less robust in terms of muscle mass and bone strength than was typical for Neandertals but stronger and more robust than usual for early modern humans (Ben-Itzhak *et al.*, 2005), a potential disadvantage for hybrids among the Neandertals but a potential advantage among early modern humans, possibly influencing the direction of introgression.

#### *Infanticide*

Intermediate and unusual (but possibly not cryptic) hybrids on both sides might have been subjected to infanticide, a consequence of the greater likelihood of their being recognized as

having uncertain paternity (a significant cause of infanticide across primate species; see Hiraiwa-Hasegawa, 1988) or to reduce the competition for resources (Hrdy, 1979). The latter may have been particularly true for non-cryptic hybrids among the Neandertals, given the range of potential factors contributing to the species' demographic decline and eventual extinction. Infanticide has been practiced by many human groups, including contemporary ones, and has been observed in modern chimpanzees, where it has been interpreted as the result of male aggression, pathological female cannibalism for the sake of nutritional advantage, or the selection of particularly vulnerable targets during inter-group violence (Sherrow & Amsler, 2007; Townsend *et al.*, 2007). Male aggression against infants has also been observed in baboons (Cowlishaw, 1995). The greater likelihood of being subject to infanticide might have reduced hybrid survival in both groups, especially among the Neandertals.

#### *Lower survival outcomes from intermediate hybrid behavior*

Hybrid males, assuming they survived past infancy, might have been more aggressive than the norm (hybrid behavioral intermediacy) or less able to inhibit aggressive impulses (hybrid cognitive intermediacy), creating situations of early mortality through risky behavior, or exile or attack from an inability of the group to tolerate abnormal levels of behaviors such as aggression. Such behaviors and consequences are known among modern chimpanzees and humans (e.g., Nishida, 2004; Nishida *et al.*, 1995; Townsend *et al.*, 2007; Wrangham & Peterson, 1996), implying that they might also have characterized the Neandertals as well. Behavioral comparisons of chimpanzees and bonobos suggests that bonobos, the more paedomorphic species, are less aggressive and display greater inhibition (an executive function) than chimpanzees (Hare *et al.*, 2007; Parish & de Waal, 2006; Prüfer *et al.*, 2012; Rosati *et al.*, 2007). A comparison of the cognitive capabilities of Neandertals and early modern humans suggests that the latter may have had similar advantages

in executive functioning, including inhibition (Coolidge & Wynn, 2001, 2004, 2005; Wynn & Coolidge, 2002, 2004, 2012), a possible factor in hybrid survival. However, while cognitive differences can be inferred from the morphological comparison of fossils, similar inferences of behavioral differences from archaeological remains are open to interpretation. Nonetheless, the greater rate of traumatic injury in Neandertals might be consistent with higher levels of risk-taking, suggesting that hybrid behavioral variability could have been a survival factor.

#### *Reduced mate and kin recognition*

Another potential outcome of hybrid intermediacy might have been reduced mate and kin recognition, which has been observed in primate hybrids (e.g., Bradley & Mundy, 2008; Jolly, 2009). For example, *P. hamadryas* interbreeds with *M. mulatta*, but the resultant hybrids are less reproductively successful, either because they are not recognized as suitable mates or they are infertile (Jolly, 2001, 2009; Markarjan *et al.*, 1997). Across primate species, mechanisms used for mate and kin recognition include phenotypic matching and behavioral cues (Silk, 2005; Strier, 2004), mechanisms potentially weakened by hybrid morphological and behavioral variability and possibly exacerbated by Neandertal xenophobia. The likelihood of survival might have been decreased further by the demands of the Neandertal lifestyle, especially given the lack of older individuals available to assist with provisioning and infant care (Trinkaus, 1995, 2011); among *H. sapiens*, these conditions were perhaps not as severe, with the result that the likelihood of survival may have been marginally better.

## Conclusions

The pattern of introgression detected in comparison of the *H. neanderthalensis* and *H. sapiens* genomes (Green *et al.*, 2010) may not have been the result of hybrid sterility (Mason & Short, 2011) because of the insufficient amount of time between the separation and reunion of the two

human species, nor of hybrid inviability, which requires at least as much time (if not more) to instantiate. However, introgression directionality could have been influenced by forms of RI that are typical for primates—specifically, prezygotic (pre mating) isolation and postzygotic survival and reproduction differentials—given two assumptions: first, that behavioral, morphological, and cognitive differences (which are consistent with emerging genetic evidence) were sufficient to influence matters such as mate recognition and sexual selection; second, that hybrid intermediacy was sufficient to influence survival and reproduction outcomes. While these RI mechanisms may have skewed the pattern of interbreeding and hybrid survival and reproduction, all of them require a more in-depth examination of the archaeological and fossil records, as well as comparisons with modern primate species that hybridize (especially baboons, chimpanzees, and bonobos). If interbreeding between the two human species was more likely to have involved *H. neanderthalensis* males and *H. sapiens* females, and survival and reproduction outcomes were better for hybrids among early modern humans but lower for hybrids among the Neandertals, these factors may be apparent from the archaeological and fossil records, as well as tendencies observed in contemporary primate species.

A limitation of the present review was that it assumed that hybrids would remain with their natal groups to interbreed with the species raising them if they survived to sexual maturity and were recognized as suitable mates. It is of course possible that hybrids might not have remained with their natal groups, instead moving between groups of different species, perhaps with greater ease and acceptance than might have been the case for non-hybrids. However, this possibility reflects a level of granularity seldom reached in fossil analysis, since hybrid phenotypes are difficult to disambiguate from inter-individual variation (Ackerman, 2010). Observational data from nonhuman primates might determine whether hybrid acceptance varies across primate groups generally, though the reduced reproductive success of hybrids (Jolly, 2009) suggests a decreased

acceptance within natal groups that might extend to non-natal groups as well. A second limitation of the review was that the effect of hybrid gender on survival and reproduction was not considered in detail, something future studies might address.

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