The Contradictory Diversity of Anthropoid Societies

Evolutionary equilibrium means that a strategy has to be optimal to any changes either sex might inflict, or any deflection from the game theoretic equilibrium the situation might present. In the context of sex this means that societies need to reflect the complementary interplay between the vastly differing reproductive investments females and males make, the one massive and forthright, and the other opportunistic and competitive.

Diverse ape societies derive their complexity and viability through responding to this sexual interplay, without the extensive capacity humans have for imposing 'artificial' cultural structures upon it. The relative clumping or diffuse nature of plant foods, determine, through the female foraging distribution, and the opportunities it provides males, whether ape species are monogamous (very dispersed females), form harems (clumping sufficient for one male to guard several females - e.g. gorillas) or promiscuous (intermediate distributions requiring free movement of individuals, as in the case of our closest relatives, the chimpanzee. Pan troglodite, and the bonobo or pygmy chimpanzee, Pan paniscus. In turn these reproductive patterns determine the shifting hierarchies and coalitions of social structure.

The most promiscuous ape societies are the most complex and versatile. Monogamous gibbons lead a solitary and relatively sterile existence in widely spaced territories with little social interaction. For Gorillas there is a little more dynamic movement. Largely affairs are dominated by a silver back who retains dominance over his harem while struggling endlessly against being toppled and his females robbed by a more powerful male. But females will also mate with a younger male if he is present in the group. However only in chimp and bonobo societies do social complexities and subtleties really come to the fore.

Pan troglodyte: Chimpanzee

Chimps have a narrow muscular penis inviting intentional displays rather than the fat hydrodynamic penis of the human. Females have a large sexual swelling in estrus, usually mate from behind and females grunt at climax in a way suggestive of 'orgasm' (Pusey R581). Chimp societies are complex, dynamically changing 'fission-fusion' societies with shifting sexual relationships between females and males, however here the emphasis is on male hierarchies and coalitions. In de Waal's perceptive words (R162 62) "Male chimpanzees hunt together, engage in fights over territory, and enjoy a half-amicable, half-competitive camaraderie. Their cooperative action-packed existence resembles that of a human male, who in modern society teams up with other males in corporations that compete with other corporations." While males display rituals of dominance, amid blustering aggression and reconciliation, females exert significant reproductive choice by subtlety and charisma, with up to half the offspring coming from secret liaisons outside the troop on safari trysts (Fisher R209, Jolly R346). Females seem to be more concerned with establishing and keeping a set of solid relationships with a small selective circle of friends and a few more clearly defined enemies. De Waal notes: "Over the years. I've gained the impression that each female in the Arnhem colony has one or two absolute enemies with whom reconciliation is absolutely out of the question'. Instances which would have been previously attributed to male aggression on closer examination reveal the action was instigated by a female with a long-standing grudge of her own" (Watson R735 117).

When females have sexual swellings indicating fertility, they are extremely gregarious and range over large areas. Otherwise females usually feed alone or are accompanied only by their dependent offspring in core areas of about 2 square kilometers. In the wild they spend about half their time in each mode. In contrast the adult males are more sociable, spending less than a fifth of their time alone and ranging over an area of 8-15 square kilometers, seeking females and protecting and expanding their range against other males. Female distribution in relation to food resources is only a partial explanation for this

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arrangement because females are also monopolized into seeking the protection of male ranges to avoid aggression against themselves and their infants (Pusey R561 15-17).

Apes, unlike most monkey species, are female exogamous, with half to 90% of chimp females moving to other troops (Hrdy R330 51, Pusey R561 20), while the males remain with the existing group, which thus consists of males related to varying degrees who have a kin altruistic basis for reproductive cooperation. However males only show significant relatedness in some chimp troops (Taï, but not Gombe) (R561 25). Mitochondrial mtDNA testing of hair suggests that mitochondrial genes are shared between chimps several kilometers apart, indicating wide-ranging exogamy (22). Analyzing DNA found in the hair follicles collected from chimpanzee nests has become a method to test chimp paternity in the wild. At Gombe Julie Constable has found about 20% of conceptions come from low-ranking males with a majority from mating inside the group, particularly with males that were alpha at some time. All three mothers with more than one offspring fathered them by different males, emphasizing both female choice and the shifting nature of male hierarchies. (Pusey R561). In the Tai National Forest on the Ivory Coast, Pascal Gagneaux found only 6 out of 13 cases of paternity could be traced to male residents in the community the females frequented (Strier R673, Pusey (R561), linking most to secret liaisons outside.

Incest avoidance and female exogamy in chimps are linked in a way which suggests it is females and not males in humans which should naturally be driving the incest taboo by their exogamy rather than being regarded as mediums of exchange by males, since they have to bear the full reproductive burden of inbreeding. Females coming into adolescence initially mate with most of the males in their own community. However females with older brothers or close relatives cease to travel with them and rarely mate with them. Even if the male shows interest in the female, she will scream and avoid him, presumably as a result of histocompatibility (MHC) odor similarity (p 355) and familiarity during immaturity. Females become fearful of older males in their own community but when they wander with sexual swellings they eagerly meet and mate with males from new communities, either joining the new community permanently or returning pregnant (Pusey R561 19). Sperm competition in utero may allow for selection of sperm with greater viability and genetic fitness. Promiscuity may also aid fertility by promoting histo-complementarity relative to the female's own MHC and immunity type, again through odour (Birkhead R63 204). Mate guarding by an alpha male at the peak of fertility towards the end of the estrus (which ironically means 'gadfly') may also serve to give her access to generally fitter genes, despite her promiscuity.

This pattern of female reproductive choice, despite male mate guarding, is shared among many primate species. Despite living in harems dominated by a 'silver back' male, female gorillas sometimes mate with subordinate younger 'black backs' whom they are present (Hrdy R330 147). Recently a mature captive female has been seen teaching her daughter how to bring up a child after she abandoned her first one, suggesting some matrilineal adaption (Leahy R401). A female savannah baboon in estrus will frequently mate with many different males, despite focusing her favours on a few dominant males who can secure her attentions when in peak. These strategies are all consistent with females applying genetic choice and manipulating such services of protection and resourcing as males have to offer.

Chimpanzees enter into "deals" whereby they exchange meat for sex, according to researchers. "By sharing, the males increase the number of times they mate, and the females increase their intake of calories," said Dr Gomes. "What's amazing is that if a male shares with a particular female, he doubles the number of times he copulates with her, which is likely to increase the probability of fertilising that female." Meat is important for the animals' diet because it is so high in protein. Since female chimps do not usually hunt, "they have a hard time getting it on their own," explained Dr Gomes. (Chimpanzees exchange meat for sex BBC Victoria Gill 7 April 2009)

However other research contradicts this idea:

Only one study has found statistically meaningful, if indirect, support for such swaps, showing that male chimpanzees are more likely to hunt for monkeys when oestrus females are around. Yet when Gilby's team examined observations from four chimpanzee communities in Uganda and Tanzania spanning 28 years, they found no evidence that female fertility affected whether males hunted or not. Other evidence also questions the idea of meat for sex, Gilby says. Males with access to meat were no likelier to share it with oestrous females – who can become pregnant – than with non-oestrous females. Nor do they preferentially give meat to older females, who tend to be more likely to conceive than younger females (Exchange meat for sex? No thank you May 2010 New Scientist).

However a negative finding in chimps doesn't imply a negative finding in early humans and some human groups such as the Bushmen do seem to have traded meat for sex.

Both chimps and bonobos share an overt reproductive cycle, and a frankly promiscuous reproductive life, in which the females assume almost all the responsibility for child-rearing. On average a chimpanzee will make love 100 times as often as a gorilla. Rather than a larger body size, the chimp has large testicles which can sustain frequent 'flooding' ejaculates to compete in a promiscuous environment. Copulating with as many males as possible in the vicinity within her immediate troop while she is in oestrus and can pass without harassment, may serve to reduce a variety of risks of infanticide, although females on the periphery of an established group remain vulnerable to attack both from the existing troop and from outside males, particularly of their male of

At least four female mating modes are in play, mating with the dominant alpha male, openly mating promiscuously with all the males in the troop (to protect against infanticide), going 'on safari' in temporary 'monogamous' relationship with a male with whom a female shares an affectionate bond out of sight of other animals, and 'mate guarding' by a small coalition of males (Jolly R346 78). A female on safari will copulate 5 to 10 times a day, but an estrus female travelling with a group of males may copulate 30 to 50 times in a day (Hrdy R329 148). A high ranking chimp female may stay with the troop giving her offspring added survival support of a central position. The onset of menarche in an adolescent female may occur at about the age of eight but it is several years before her sexual swellings are full sized and grown males pay attention and begin mating in earnest. Even then a female may copulate on the order of 3,600 times during successive subfertile cycles before she conceives the first time, around age 14 and gives birth. Hrdy (R330 185) comments "an adolescent's sexual swellings are especially conspicuous. Like bonobos, young females use them as 'diplomatic passports' that permit safe passage through hostile territories. This way a female can check out competitors and local resources in foreign communities while she decides where to settle and breed." Once she becomes fertile she will be more fecund than older females. A female wandering with such a passport may not be attacked by patrolling males but may not so easily be accepted by resident females in unfamiliar

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Female chimps from dominant ranks are known to commit infanticide against lower ranking females (R330 85). A fertile female who conceives will have made love more than 100 times with as many as a dozen or more males during her ovulatory period. Such motivated sex is lustful and in De Waal’s (R164 53) careful words involves ‘orgasm-like experiences’. Along with bonobo sexual ecstacy this provides an evolutionary basis for human female orgasm in our common ape ancestors. Once she delivers her baby she does not return to the group but takes it alone and feeds in a small core range to protect it from attack.

"While males are forming coalitions, females are often by themselves, and compete for exclusive access to fragments of forest where lots of food can be found," says Anne Pusey, who studies chimps in Gombe National Park, Tanzania. Overt aggression is rare, but infants are at risk of being killed by females who aren't their mothers. There is one situation in which competition is inevitable. "Male chimps don’t migrate - they'd simply be killed when found in the forest all by themselves," says Pusey. "Females usually do, and immigrants are under relentless attack by the other females until a male steps in to protect the cute new girl on the block." (Vernimmen T 2015 Gentle sex?’ Females just as feisty as males over reproduction New Scientist 25 Jun). Male chimps often form flexible coalitions to collectively depose a dominant male or to attack other groups. They have even been observed banding together to kill the alpha male of a troop (American J. of Primatology, doi.org/knr4). They share food as tokens of cooperation. As noted (p 59), successful alpha males often display skills of group mediation and conflict resolution as well as aggression to maintain their position. Coalitions of male chimps also stage raiding parties on neighbouring troops, killing or injuring other males and killing infants. Male monkeys and apes tend to commit infanticide on any offspring not sired by themselves (R330 34) sufficiently frequently to cause female chimps strategic reproductive problems. Infanticide both serves to eliminate genetic rivals before they become active adversaries and is a natural extension of interspecies competition. Males play no part in infant care but may form casual affectionate bonds and be followed by adoring young males. Infanticide plagues both old world monkey and the great apes, being responsible for 38% of infant mortality in baboons and 33% in gorillas, constituting a major reduction of overall fitness and is a stark example of male reproductive strategies acting against natural selection.

Chimp societies display many features shared with human gatherer-hunter societies. including a division of labour between meat and plant foods, predominant female exogamy (2/3 of gatherer-hunter societies are male philopatric and less than 1/5 female philopatric), male cooperation in coalitions, reconciliation of aggression within groups, the presence of inter-group violence between males, raiding parties against individuals in other groups, and a similar group size of about 150 to gatherer-hunter bands (Pusey R561).

Chimps at the Whipsnade zoo have been shown to enjoy puzzle solving, and continue puzzle-solving even when they didn’t receive food rewards. Scientists set up a game for six chimps that involved moving red dice through pipes until they fell into a container. The same task was also carried out using brazil nuts instead of dice, so that success led to a treat. "For chimps in the wild, this task is a little bit like foraging for insects or honey inside a tree stump or termite mound, except more challenging because the dice do not stick to the tool." Researchers created higher "levels" of challenge by connecting many pipes together, and making them opaque so the dice or nuts could only be glimpsed through small holes (BBC 2013 Whipsnade Zoo research shows chimpanzees 'solve puzzles for fun' 25 Feb).

Chimpanzees use tools for more purposes than any other non-human species (McGrew), have been seen to make and use spears in the wild in Senegal and 4,300 year old remains have been found of a nut smashing stone in East Africa. Young female chimps learn earlier and faster by watching their mothers than males, who are more involved in wrestling play (Lonsdorf et. al. R424). Females learn earlier and ultimately better how to 'fish' for termites and mirror their mother's techniques in a way which males don’t. These patterns suggest sex differences in human learning go back six million years.

Chimps in captivity also show cultural preferences for conformity with their peers even when they know an alternative tool using strategy is more effective (Nature doi:10.1038/050815-12).

Chimps have also been seen to engage in ‘ritual’ behavior - a dance performed during rainfall and a peculiar slow-motion display in the face of a bush fire in Senegal and more recently young chimps were observed storing stones in a tree and banging rocks against it in what was loosely described as a ‘tree shrine’ (Scientific Reports, doi:10.1038/srep22219). Young chimps have also been seen to use doll-shaped sticks as toys even making nests for them to sleep in (What do chimp ‘temples’ tell us about the evolution of religion? New Scientist 4 March 2016).

Geneic evidence for occasional interbreeding between chimps and bonobos.

Just as there is evidence that there has been genetic exchange between humans and Neanderthals, so there is similar evidence for a small degree of interbreeding between chimps and bonobos between 200,000 and 550,000 years ago contributing about 1% of the current chimp genome (Manuel et al. 2016 Chimpanzee genomic diversity reveals ancient admixture with bonobos Science doi:10.1126/science.aag2602) despite the fact that their current ranges are separated by the Congo and the Lualaba rivers, so they are essentially allopatric - occurring in separate non-overlapping geographical areas.

Pan paniscus: Bonobo

- Bonobo Heaven password="model"

The bonobo or ‘pygmy chimpanzee’ was first discovered only in 1927 from a skull and shortly after recognized as a separate species. It is slightly smaller, darker and more gracile and childlike than the average chimp. This neotenic feature is shared by humans. In 1933 Harold Coolidge (de Waal R164 42) who gave them species status considers them to be anatomically much more generalized than chimps and "may approach more closely to the common ancestor of chimpanzees and man than does..."
any living chimpanzee”. Adrienne Zihlman has found them to be the closest ape to Australopithecus by several quantitative measures. They are often observed to walk bipedally, especially when carrying food. Like humans, bonobos are receptive sexually for most of their ovarian cycle. They regularly make love face to face as humans do, which chimp does only rarely.

Bonobos mating face to face often stare deeply into one another's eyes and French kiss. Here and below centre two females 'mate' in hoka-hoka with the aid of their large clitoris (below left). Right bonobo male giving a penis display (De Waal and Lanting R163, Hrdy R636 ex Amy Parish).

Bonobo societies have become renowned in Franz de Waal's "Good Natured" (R162) as hyper-sexed, promiscuous societies, which use pan-sexuality as a universal social panacea to invite reconciliation for aggression and even at any sight of food, when both males and females will invite sex in a free-for-all. They engage frequent and repetitive apparently orgasmic sex, as much between females (with their especially enlarged clitoris) as between male and female. Males also rub their scrotal areas together in reconciling aggression and occasionally hang upside down in trees rubbing their erect penises together called penis fencing (de Waal R164 54). There are also sexual liaisons between adults and juveniles of both sexes. Frequent sexual encounter has become a contributory phenomenon which generates sufficient cohesion among female coalitions to keep dominant males respectfully deferring to their wishes, trading sex for food in favourable, or indulgent terms, with little molestation of the females. In fact females bond more strongly to one another than to the males and follow them around seven times more. Females having sex together advertise their liaisons to others presumably to enhance their status in the group. Females use sex to solicit food from males. De Waal notes this wryly as "sex as a weapon." They will also claim food possessed by males if necessary by force. Males tend to follow their mothers. By contrast with chimps, male alliances are little developed and ranking males derive key support from their mothers and the alliance between the females. Females are thus regarded as being dominant. However, like other apes and unlike humans, male bonobos appear to make little or no direct parental investment, leaving rearing to the females.

Intriguingly bonobos, like humans, French kiss. Frans de Waal recalls a zookeeper who accepted what he thought would be a friendly kiss from one of the bonobos, until he felt the ape's tongue in his mouth!

However 'loving bonobos' have a carnivorous dark side - they mercilessly hunt and eat monkeys alive (SPNews 1733).

Robert Jay Russel called the bonobos' propensity for males trading food for sex the 'lemur's legacy', as one of our most remote cousins also share the trait (Taylor R683 81). Timothy Taylor demurs that it is simply the males being courteous and offering the females both food and sex. While this is a nice idea, it negates the subtlety of Machiavellian interplay the whole transaction expresses. Neither does it, as he suggests, imply the female sex drive is less, and we know female bonobos have a great deal of sex themselves. He also observes:

"Most shockingly to human eyes, adults and children have a lot of sex. In fact infants are often initiated by their mothers - the only observed taboo on sex is between mothers and any sons over six years of age." (R683 81). Female bonobos in captivity have also been observed acting as 'midwives' assisting the delivery of another female's baby (doi:10.1016/j.evolhumbehav.2018.05.003).

De Waal (R162 55) proposes that they avoid incest both by a combination of female exogamy and close familial associations and similar body odours inhibiting sexual attraction, driven principally by females avoiding kin. When a young female reaches adolescence at about seven, she stops having sex with her troop and begins to have her first small swellings. This is a major crisis time for a young female. The swellings act as a passport of 'implied fertility' so she can wander freely from group to group and have sex with strange males in the forest without fear of attack, looking for a group with individuals she can bond with and be safe. She invites sex from the other females. Once accepted, her sexuality flowers. She rapidly gains almost continuous sexual swellings which grow in volume with every cycle till they reach full size at about ten. She can expect her pregnancy at about thirteen or fourteen. This gives the females ample time to find a home troop and become fully integrated into the community before pregnancy ensues. Unlike chimps where females wander alone with small offspring to protect the young from the risk of infanticide, bonobos return to the troop immediately and infanticide is unknown.

Bonobos appear to have a sense of fairness and react differently when they suffer an unprovoked attack which doesn't have a justifiable basis, and in return others gather around to give support indicating a sense of social fairness (Clay Z et al. 2016. Bonobos (Pan paniscus) vocally protest against violations of social expectations Journal of Comparative Psychology 130/1 44-54, doi.org/bcp3). However, unlike humans who from an early age prefer helpful individuals, bonobos appear to prefer hindering 'jerks' in simulated experiments with animals in an African reserve, possibly because favouring dominant individuals is advantageous (Krupenye C, Hare B 2018 Bonobos Prefer Individuals that Hinder Others over Those that Help Current Biology doi:10.1016/j.cub.2017.11.061).
Bonobo (left) and chimpanzee (right) using spears to hunt. Bonobos’ tool-using abilities look a lot like those of early humans, suggesting that observing them could teach anthropologists about how our own ancestors evolved such skills. If so, tool use in great apes may be older than we thought, reaching back at least 5 million years to the common ancestor of chimps, bonobos and humans. Bonobos at a zoo in Germany and a bonobo sanctuary in Iowa were given a series of problems that required tools to solve - for example, showing the bonobos that food was buried under rocks, then leaving a tray of potential aids such as sticks and antlers nearby. Two of eight zoo animals and four of seven in the sanctuary made use of the tools - in some cases almost immediately.

The bonobos used sticks, rocks and antlers to dig, and also used long sticks as levers to move larger rocks out of the way. Some used different tools in sequence. Three of the sanctuary animals used rocks as hammers to smash long bones and expose food in the marrow. Another cracked them neatly open lengthwise, a technique previously thought to be unique to the human lineage. One bonobo even sharpened a stick with her teeth to fashion a spear. (Am. J. of Phys. Anthro. doi: 10.1002/ajpa.22778, doi.org/527). And in 2007, Jill Pruetz from Iowa State University in Ames discovered that chimps in the wild in Fongoli, Senegal, thrust sharpened sticks into nest holes in trees to stab or club small, nocturnal primates called bushbabies. They observed 308 such hunts. Females carried out 61% of them, despite making up only 39% of the chimps in hunting parties. The Fongoli chimps are still the only ones known to use weapons to kill or wound prey, even though chimps elsewhere in Africa - again mainly females - use tools to get at termites and tubers. If female chimpanzees initiated the use of weapons to hunt, the same might have been true of the earliest humans, Pruetz suggests. "Maybe it should cause people to rethink the old premise of man the hunter" (Royal Soc. Open Science doi: 10.1098/rros.140507).

Characteristic of both chimps and bonobos is reconciliation. This is a clear sign of mediation of aggression and implies, despite the relatively peaceful nature of the bonobo that competition, hierarchies and feelings of aggression are still present. In chimps it is the ‘underdog’ who usually initiates reconciliation, whereas in bonobos it is the ‘aggressor’, however reconciliation is so beneficial to a group of chimps that if neither of the warring individuals will initiate it, a third party may step in to broker a deal (Dugatkin R176). Reconciliation in chimps is by kissing and cuddling but in bonobos it is mediated through sex. At the sight of food is an immediate mediation of competition to get enough of a share. Similarly if a male chases another away from a female the males reunite and have a scrotal rub, or if a female hits a juvenile and the mother lunges back they both have sex. Unusually, these types of engagement also occur between troops (de Wael R162 51). The females will groom one another while the males remain tense. Males compete fiercely for rank which is influenced by the rank of mothers, but the female hierarchy, based on age and residency is fairly loose. It is possible the bonobo has been able to engage this strategy because it has access to larger fruiting trees and selects types of abundant terrestrial herbaceous vegetation which can support large groups without conflict. Richard Wrangham has also suggested that the absence of the gorilla in their range opened an evolutionary niche for a less male-dominated social structure. However, missing from both chimp and bonobo societies is any form of pair-bonding or long-term relationship between males and females.

Researchers have suggested that bonobos display signs of early language evolution. Wild bonobos use a specific call type (the “peep”) across a range of contexts that cover the full range positive-neutral-negative in much of their daily activities, including feeding, travel, rest, aggression, alarm, nesting and grooming. Peeps were produced in functionally flexible ways in neutral and positive contexts. Functional flexibility has recently been demonstrated in the vocalisations of pre-linguistic human infants and is the root of context independent language (Clay Z et al. (2015) Functional flexibility in wild bonobo vocal behaviour PeerJ doi:10.7717/peerj.1124).

Deaner et. al. (R156) have found that even rhesus macaques are highly strategically sensitive to socio-sexual images. They found that a male would choose a significant cut in a cherry juice of different tools in sequence. Three of the sanctuary animals used rocks as hammers to smash long bones and expose food in the marrow. Some used dif

Australopithecus: Evolutionary Divergence of the Hominid Line

Our closest evolutionary cousins are the chimpanzee and the bonobo, from which we diverged around 7 million years ago matching the age of the oldest human line fossil Sahelanthropus. The claim that Dryopithecus is a form of gorilla, rather than a precursor (Hecht J 2015 Ape fossils put the origin of humanity at 10 million years ago New Scientist 2 Oct), has pushed the possible date back to 10 million years, with some estimates going back as far as 13 million (Brahic C 2012 Our true dawn: Pinning down human origins New Scientist 21 Nov). The divergence of our common ancestor from gorillas, orangutans and old world monkeys occurred at successively earlier dates. This has led to the idea that we are a species in the same genus as Pan. About 7 million years ago, primate evolution split along two tracks: one leading towards humans, the other towards chimpanzees. One to two million years later, our ancestors adopted an upright gait, and 2-3 million years after that their bodies and brains began to grow and they started making primitive stone tools. Even earlier ‘artifacts’ have been found suggesting primitive tool use in the form of score marks on bones at Dikika in Ethiopia (S. P. McPherron et al. Nature 466, 857-860; 2010) and large stone artifacts, some weighing as much as 15 kilograms from a site west of Kenya’s Lake Turkana whose sediments date to around 3.3 million years ago. One key surface find was a small rock flake, which fitted in a gap in a bed of mud like as a jigsaw puzzle piece, confirming that the tools were made through a flaking process (Galloway E 2015 Nature doi:10.1038/520421a, Harmand et al Nature doi:10.1038/nature14464).

Stone artifacts from Lake Turkana dating back 3.3 million years consistent with Australopithecus tool use (Harmand s et al 2015 Nature doi:10.1038/nature14464).
The first modern-looking humans appear in the fossil record about 130,000 years ago. By 50,000 years ago, there is evidence for humans who appear to have distinctly modern bodies and life-styles. They created complex tools and jewelry, built shelters, buried their dead in graves and probably had similar language skills to us.

Analysis of early human-like A. africanus populations in southern Africa suggests females left their childhood homes, while males stayed at home. An international team examined tooth samples for metallic traces which can be linked to the geological areas in which individuals grew up. The conclusion was that while most the males lived and died around the same river valley, the females moved on. Similar patterns of female exogamy have been observed in chimpanzees, bonobos and modern humans (Ancient cave women ‘left childhood homes’ BBC 1 June 2011).

Sellen-Tulberg and Moller researching the family tree of living primate species by mating type, come to conclusions consistent with the idea that monogamy is a latecomer to the human line (Diamond R166). They suggest that monogamy has not been a trait of our primate evolutionary history, but rather promiscuity in lower primates followed by a common harem-building ancestor, as the gorilla is today. Since recent evolutionary trees place chimps closer to humans than gorillas, the ancestor probably then passed through a promiscuous phase. This missing link probably had the slight evidence of ovulation we find in both primitive primates and gorillas and evolved in opposite directions in humans and chimps, the chimp and bonobo forms of promiscuity emphasizing overt ovulation accompanied by estrus behavior and human monogamy with moderate polygyny favouring concealed ovulation. The overt estrus seen in chimps and bonobos is rare in primates and constitutes a specific adaption (Hrdy R330, 217).

Exciting stone tool find in Kenya 2011

Sexual dimorphism varies by different measures from little or none in monogamous gibbons. Slight to moderate differences in bonobos and chimps (various measures range from 6-30% (Reno et. al. R573, Pusey R561 35 Wrangham R765 35). Pair-bonding but moderately polygynous human populations vary from 6 to 23% with an average around through 15%. Harem-forming gorillas, and orangutans and bonobos, have a difference of 100% characteristic of species where sexual choice is strongly related to male competition. Matt Ridley (R580 19) comments “Better to be only a little larger than a female and use cunning as well as strength to rise to the top of the hierarchy”.

Relative body, penis and testicle size viewed by an ape female and relative body, breast and ovulation signals as viewed by an ape male (redrawn from Jolly R346 180). Humans have intermediate testicles size between promiscuous chimps and lone harem-forming male gorillas, indicating sperm competition and moderate polygyny.

By contrast with savannah baboons, hamadryas are female exogamous. They live in fission-fusion groups, within which exclusive mating units interact with one another through alliances of adult males, leaving females largely powerless (Wrangham R765). Females are abducted as juveniles and taught firm rules of obedience necessary for survival in their harsher environment, supported by biting on the scruff of the neck if they protest. Despite the paternalism, the sexes are coevolved. The investment of the male is substantial over time, chastising, educating, helping feed, and even carrying his much smaller charges. They will rescue neonates at risk during delivery. Within each large herd, males do not so much as look at females in another alpha male’s harem (Hrdy R329 75, 101).
Mammals give birth to live young and lactate. This has caused the reproductive investment of the two sexes to become highly skewed, with males investing primarily in fertilization, while females are investing primarily in parenting. This has a variety of consequences. For example only around 3% of mammal species are socially monogamous, with the rest being either polygynous with harems, or having promiscuous females. This again skews the reproductive strategies further, because there are secondary consequences. Females are less likely to go in heat and become pregnant while they are lactating a brood, and offspring of other males will compete with his own, so there is a double investment in species with competing males, to kill the offspring of competitors - male infanticide. Around half of mammalian species, including the ancestors of the great apes and humans, are inveterate infanticiders, as promiscuous chimps and harem forming gorillas are, and the trait appears to have evolved multiple times. In turn, the females adapt to promiscuous mating, often with an advertised estrus to make it as difficult as possible for males to determine paternity (Lucas & Huchard 2014). Finally the males adapt by forming larger testes to deal with the issues of sperm competition involved in promiscuity.

When Raymond Dart in 1925 announced the discovery of Australopithecus africanus, he speculated on flimsy evidence that it had been a bloodthirsty carnivore. With it we inherited a pessimistic ‘killer-ape’ notion consistent with ‘man the hunter’ (R729, R486), based on the connection between hunting and warfare that aggressiveness drives cultural progress. Konrad Lorenz (R426) in “On Aggression” amplified this claiming our species had not had enough evolutionary time to develop the inhibitions against our own kind, as do full carnivores. With the discovery of violent aggression, murder and raiding parties among wild chimps (Wrangham and Peterson R764) our common origin “suggests that chimpanzee-like violence preceded and paved the way for human war, making modern humans dazed survivors of a continuous 5-million year habit of lethal aggression.” However there is continuing debate between the ‘hominid the hunter notion’ and brain and Binford’s notion of the humble scavenger (Adovasio et. al. R792 43).

Research suggests that, despite the versatility of the human hand with its opposed thumb and index finger, it may represent a more primitive form of the hand dating from before the divergence of humans and chimps, implying that its evolution in early humans came not as a result of tool use but diverse forms of dexterity for example involving food gathering (Almecija S et al. 2015 The evolution of human and ape hand proportions Nature Comm 6 7717 doi:10.1038/ncomms8717).

This position has again been modified with the discovery of the more peaceful bonobo and the idea that aggression is an option, depending on environmental correlates and not a fixed drive. Many authors have drawn conclusions about general trends in evolution from apes to humans based on the greater size differences between males and females believed to have existed in early Australopithecines of about 100% compared with modern human differences of only 5-16% across cultures. These conclusions have applied both to Australopithecus, which might be assumed to have been a harem-forming species on this basis, and changes presumed to have accompanied the reduction of these differences later in Homo erectus, for example the rise of pair-bonding. If the sexual dimorphism of Australopithecus is less overall it is as likely to indicate a promiscuous origin.

Owen Lovejoy's group (Reno et. al. R573, Larsen R399) contradict previous findings of extreme size dimorphism in Australopithecus afarensis, our 500cc brained ancestor of some three and a half million years ago. They suggest a sexual dimorphism less than that of humans, consistent with pair-bonding monogamy or promiscuity rather than harems with strong male competition like gorillas as previous studies implied. Canine dimorphism is greater in chimps, leading them to further suggest a monogamous phase. It should also be noted that the female status of the small ‘Lucy’ skeleton is also open to debate (Adovasio et al. R792 38, 84).

However an intriguing find in 2016 is the group of footprints left in volcanic ash that rapidly hardened 3.66 million years ago oranso–Mille study area, central Afar Regional State, Ethiopia (Haile-Selassie 2014). Below: 2.8 million-year-old specimen found in the Ledi-Geraru research area, Afar Regional State, Ethiopia, is 400,000 years older than researchers thought that our kind first emerged. The discovery in Ethiopia suggests climate change spurred the transition from tree dweller to upright walker. Below: Teeth and jaw of Australopithecus deyiremeda from 3.3-3.5-million-year-old deposits in the Woranso–Mille study area, central Afar, Ethiopia (Haile-Selassie Y e et al. Nature doi:10.1038/nature14448). The age of the remains means that this was potentially one of four different species of early humans that were all alive at the same time. The most famous of these is Australopithecus afarensis - known as Lucy in 1974 - who lived between 2.9-3.8m years ago, and was...
Initially thought to be our direct ancestor. However, the discovery of another species called Kenyanthropus platyops in Kenya in 2001, and of Australopithecus bahrelghazali in Chad, and now Australopithecus deyiremeda, suggests that there were several species co-existing. Most ancient hominins ate a broad diet, but one species Australopithecus bahrelghazali specialised on sedges, which might have led to its downfall. Unlike East Africa, and the Rift Valley, it migrated further west to an area of Chad which was rich in sedges and largely predator-free, allowing for a quiet life and a lot of time for eating. Yet such a restricted diet would have left it more vulnerable to extinction when the habitat changed. as the climate dried out (Journal of Human Evolution, doi: 10.1016/j.jhevol.2015.06.009).

However skeletal research suggests bipedalism evolved six-million years ago long before we can expect social patterns characteristic of humanity (Galik et. al. R232). Lovejoy's argument implies monogamy even before we came out of the trees, explaining bipedalism in terms of bringing roots back to a monogamous partner, males' wider ranging avoiding direct competition with closer ranging females based on the claim that human child rearing must have changed very early on to increase survival and shorten birth intervals, given a more slowly maturing infant and the five to eight year interval between births of apes. Jolly laconically notes "meanwhile the females progressively concealed her ovulation so as not to inflame all available males ... but ready to mate with her own man whenever he came home. Both female and male acquired permanent attractiveness, big breasts, big penis which continually advertised both sexiness displays and reassurance to the mate, as in mated birds that engage 'triumph displays'. Feminists were outraged. The idea of hulking polygynous males was horrid, but this kind of monogamy seemed even worse. ... on behavioral grounds, I would opt for big males, small females and a medium level of promiscuity, rather than Lovejoy's monogamy. " Adrienne Zihlman (R782) also has bipedalism evolving from gathering but males learning from their mothers to gather and share with the immediate group in a polygamous rather than monogamous environment.

There is no evidence for Lovejoy's notion of monogamy ever having evolved in a species-wide sense among humans but rather pair bonding with a degree of polygyny in a majority of individual societies worldwide. There is a major problem here with the definition of monogamy as an intentional cultural trait defining relationships as one on one in the sense of marriage, with all its trappings of punishments for infidelity. Human societies clearly show they have a large majority of woman-man partnerships with a minority equilibrium of polygynous extended families as male resources permit. This is a complex and flexible form of social system which can provide optimal resourcing to females despite the tensions between co-wives. The idea that archaic humans would have defined a narrow prohibitive monogamous marriage code is contradicted by almost all societies outside Christianity.

Neither do the relative lack of male canines indicate monogamy since even early hominins before the archaeological advent of tool use could have come to depend more on stones than teeth is dominance displays, as noted in Chris Knüsel's theory of bipedalism in which throwing was the key advantage gained (Taylor R683 36). Arguments in which human emergence is driven by tool use have palled with the discovery that wild gorillas use tools (Public Library of Science Biology Oct 2005) as well as chimps (p 66). Sarah Hrdy (R329 175) also notes that the reduced canines is a weak point in the argument since it does not seem necessary that early man used his teeth in fighting as other primates do. Richard Wrangham (R765) also find the arguments unconvincing: "The anatomist Owen Lovejoy once suggested that bipedalism evolved in order to allow males to bring food to their mates but his much publicized idea of monogamy among the woodland apes now seems farfetched. One of several difficulties is the question of sexual dimorphism in body size. ... Other obstacles to Lovejoy's scheme include scepticism that a male who left his mate to find food for her could guard her from rival males. The absence of any evidence of home bases, the matter of why females became bipedal and evidence that Australopiths life histories resemble those of apes, not of humans as Lovejoy's scheme implied they should. In addition, no living non-human primates exhibit monogamy within social communities. Part of the explanation is that any female who mates exclusively with a low-ranking male within a social group can expect to find her offspring the target of infanticide attempts by more dominant males. " The difficulty with arguments based on changes in infant care in Australopithecines is the chicken and egg problem of brain size and what caused it. Australopithecus has a small brain and major child-rearing changes requiring additional partner resourcing are naturally responses to pressures created by delayed development caused by increasing brain size and the need for birth to take place before the brain puts on its spurt of growth. It is thus difficult to place such child-rearing changes before our large brain evolved. When we move to Homo erectus with an increasing brain size, we still find sexual dimorphisms suggested to be a little larger than humans in the range of 20% larger in males, consistent with Jolly's position and with social monogamy emerging later.

Timothy Taylor suggests that breasts and genital hair of the human female are an evolutionary response to bipedal walking:

Stated in brief, I believe that upright walking hid females' engorgable estrus skin between their legs; walking itself both required buttock muscles and hid the female genital opening - an important focus of sexual signaling in primates; the new buttock area became denuded of hair to compensate for the lost sexual signal; and the bare buttocks were mimicked around the front, in the form of bare breasts, [and a pubic triangle of hair against a bare background]. That is, nakedness developed as a form of sexual signaling to compensate for the disappearance of estrus skin, which had formerly performed that function. The emergence of nakedness was thus not a question of losing hair but of extending areas of sexual skin. This process culminated through sexual selection within a cultural environment-clothes and cosmetics enhanced and selectively covered the areas from which hair was lost, and encouraged it to be lost over yet wider areas. In my view, therefore, we have never been truly naked apes (R683 34).

Although acknowledging fatness and fecundity as a genuine indicator of reproductive fitness to carry a baby to term under fluctuating fortunes, and inviting the reader into a sensual notion of nakedness through sexual selection, Taylor cites a simple deterministic environmental selection theory the loss of overt estrus signals, for what is a creative product of sexual choice. The critical flaw in such 'external factor' theories is that they attempt to explain the genesis of the most complex system we know of - human culture - in terms of the external advent of a single, generally simplistic, causal factor. The same applies to theories of human emergence based on bipedalism, tool use, hunting, monogamy and even language, each of which is a product of complexification, rather than the cause, although each can facilitate a qualitative leap forward. What is centrally at stake is the complexity of human sexual selection and how it has carried us forward into culture at the edge of chaos (p.306). Central to this idea is understanding how the sociobiology of sex becomes the cultural phenomena which surround us today, not just the social varieties of sexuality itself but all the creative and coercive phenomena of culture, which like our hairlessness and language appear to have been driven by sexual rather than natural selection. To this end Taylor does acknowledge the advent of clothing invites 'gender' - the cultural interpretation of social sex roles.

A similar argument for the human penis holds marginally better, i.e. that a large penis signals an attractive sexual feature, but this is far short of the heady race between the penis and clitoris for insatiable sexual satisfaction Geoffrey Miller conjures up. Timothy Taylor also acknowledges that penis envy is as much a phenomenon of the locker room (R683 24) and male pride among one's comrades as it is to impress the highly elastic vaginas of the girls, just as has been found for risk-taking games like Chicken (p.24). The idea that a bigger penis has direct advantages in fertilization also looks shaky, particularly given that promiscuous chimps have a small penis but large testicles.

In an interesting twist to the origin of bipedalism associated with the loss of forest and the spreading of savannah around the rift valley, the idea is that there may have been large areas of swamp land created during the same epoch. Chimpanzees are much more prepared to walk bipedally when partially immersed and need to do so to breathe. Such a scenario is not inconsistent with the 'aquatic ape' hypothesis (Morgan R482), explaining our hairlessness and other gracile features including a dependency of 98% of the population on eicosanoid (a 20 carbon oil) found in fish on the basis of an association with margins of water.

However Elaine Morgan's aquatic ape theory is based on a constellation of unverified assumptions, which don't stand up to closer scrutiny, including 'creative' use of a whole nexus of advantages, from the 'aquatic' hairlessness itself, through the curious vestigial webbing between our digits not seen in apes, to fatty breasts doubling as swimming floats for the kids, long hair to grab mum by in the water etc. Neither do seals lack fur. Nevertheless it is true that chimps walk upright much more readily when buoyed by water, while foraging in swampland.

The 2.5-million-year-old Taung Child skull shows gaps between frontal skull bones at an age of 3 or 4 indicating similar skull development to modern humans allowing for increasing brain size (PNAS DOI: 10.1073/pnas.1119752109).

In 2010 a skeleton was found of a species Australopithecus sediba dating back 1.9 million years, which bears many of the hallmarks of Homo sapiens, features seen in the brain, feet, hands and pelvis, making it a possibly more plausible ancestor of humans and Homo erectus, than Homo habilis or Homo rudolfensis. A. sediba's brain appears to have been about 440 cubic centimetres in volume, or about the size of a medium grapefruit. This is smaller than much older fossils in the record such as the famous "Lucy" specimen, Australopithecus afarensis (3.2 million years), but, intriguingly, the shape is more human-like, especially at the front (African fossils put new spin on human origins story, BBC Sep 2011).

The humanity switch: How one gene made us brainier

Although we may look for historical evidence of evolutionary emergence of Homo in an 'environment of evolutionary adaptedness' in the Pleistocene (Hrdy R330 97), modern humans are an overlapping of many evolutionary processes on vastly different time scales. The molecule prolactin central to human maternal behavior and mammalian lactation generally has an evolutionary history running back to controlling water balance in fresh water fish and metamorphosis in amphibians (R330 130). By contrast changes in allele frequency as a result of sexual selection occur extremely rapidly and could change from a 2% incidence to 98% within 10,000 years (R330 106). Thus although humans have been molded by characteristics emerging over four million or so years, some are much longer and some are subject to extremely rapid selection and variation in modern human societies.

A: Left: The evolution of SRGAP2 (Geshwind and Konopka Nature doi:10.1038/nature11380), showing the four human genes and the counterposed effects one maturing dendritic spines and another encouraging the formation of more immature spines resulting in a more complex expression. B: Splice variant duplication ARHGAP11B (Florio et al. 2016 below) with unique tail enhancing basal progenitor mitosis and neocortical expansion (green) Right: Evolution of NOTCH2NL and its affect on neurogenesis.

An indication of a key "brain switch" (The humanity switch: How one gene made us brainier New Scientist 9 May 2012 Sara Reardon) which may have led to the increasing brain size of the Homo line has come from investigation of the gene family SRGAP2a,b,c, (Dennis, M. Y. et al. Cell 149 912-922 (2012) doi:10.1016/j.cell.2012.03.033) involved in neocortex maturation,
A human-specific gene may be responsible for human neocortex expansion due to a single nucleotide change which introduces a new splice variant. Neocortical neurogenesis involves two main classes of neural progenitor cells, apical progenitors (APs) and basal progenitors which are better suited for maximizing neuron production. Accordingly, the evolutionary expansion of the neocortex is associated with an increase in the generation of BPs. The gene ARHGAP11B, which promotes basal progenitor amplification and is implicated in neocortex expansion, arose on the human evolutionary lineage by partial duplication of ARHGAP11A, which encodes a Rho guanine triphosphatase-activating protein (RhoGAP). However, the lack of 55 nucleotides in ARHGAP11B mRNA, which leads to loss of RhoGAP activity by GAP domain truncation also results in addition of a human-specific carboxy-terminal amino acid sequence. The 55 nucleotides are deleted by mRNA splicing due to a single C>G substitution that creates a novel splice donor site. Hence, a single nucleotide substitution underlies the specific properties of ARHGAP11B that likely contributed to the evolutionary expansion of the human neocortex (Florio et al. 2016 A single splice site mutation in human-specific ARHGAP11B causes basal progenitor amplification Sci. Adv. 2 e1601941).

A set of three nearly identical genes found only in humans, NOTCH2NL, appears to play a critical role in the development of our large brains (Fiddes et al. 2018 Cell 173, 1356-69 doi:10.1016/j.cell.2018.03.051). The NOTCH2NL genes are found exclusively in humans and appeared between 3 and 4 million years ago, just before the period when fossils show a dramatic increase in the brain sizes of human ancestors. These genes belong to an ancient family of genes known as NOTCH genes, first discovered in fruit flies and named for a genetic defect causing notched wings. The human-specific genes were derived from NOTCH2, one of four mammalian NOTCH genes, through a duplication event that inserted an extra partial copy of NOTCH2 into the genome in an ancient ape species that was a common ancestor of humans, chimpanzees, and gorillas. The partial duplicate was a nonfunctional pseudogene, versions of which are still found in chimpanzee and gorilla genomes. In the human lineage, this pseudogene was revived when additional NOTCH2 DNA was copied into its place, creating a functional gene. Reconstructing the evolutionary history of NOTCH2NL genes revealed that gene conversion was likely responsible for repairing a non-functional version of NOTCH2NL after it was repaired, but before we diverged from our common ancestor with Neanderthals, NOTCH2NL was duplicated several times, resulting in four genes. Three of the four are active genes that direct the production of truncated versions of the original NOTCH2 protein. A complementary team Suzuki et al. 2018 Cell 173, 1370-84 doi:10.1016/j.cell.2018.03.067() also focused on NOTCH2NL because of the importance of its ancestral gene, NOTCH2, in signaling processes that control whether cortical stem cells produce neurons or regenerate more stem cells. And they found that artificially expressing NOTCH2NL in mouse embryos increased the number of progenitor stem cells in the mouse cortex. They found that NOTCH2NL can substantially expand the population of cortical stem cells, which in turn then generate more neurons, a feature expected to distinguish between human and non-human cortical neurogenesis.

The role of micro RNAs which bind to mRNAs and thus are able to initiate a coordinated array of regulatory changes have been implicated in the differences in evolutionary rates of change between humans and chimps. Constitutive gene expression divergence is comparable between humans and chimpanzees. However, humans display a 3–5 times faster evolutionary rate in divergence of developmental patterns. Such accelerated evolution of human brain developmental patterns is twice as pronounced in the prefrontal cortex than the cerebellum, preferentially affects neuron-related genes, and does not depend on cis-regulatory changes, but might be driven by human-specific changes in expression of trans-acting regulators. Developmental profiles of miRNAs, as well as their target genes, show the fastest rates of human-specific evolutionary change. miR-92a, miR-454, and miR-320b are possible regulators of human-specific neural development (Somez M. et al. 2011 MicroRNA-Driven Developmental Remodeling in the Brain Distinguishes Humans from Other Primates PLoS Biology 9/12 e1001214).

Goodman (R248) compared sequences in 97 genes from both human and ape species. When non-synonymous DNA regions are compared, where there are strong selection constraints for unique function we have 99.4% identity to chimps and bonobos. When synonymous sequences are compared we are 98.4% identity. Figures are around 98.7% when general point mutations are considered (Ebersberger et. al. R180) and significantly lower at 94.6% when changes from insertions and
deletions are taken into account (Britten R78). These appear to be important for regulatory changes in existing genes. When differences in gene expression, particularly in the brain are taken into account chimps and humans have a 10% difference of expression of such genes according to Svante Paabo.

A detailed study of comparable chromosomes, human 21 and chimp 22, (R733, R501) has exposed a complex evolutionary process during and since human-chimp speciation, with transposable elements playing a significant and possibly crucial role in the divergence between the species. The 1.44% divergence in single base substitutions is consistent with previous studies, but these changes are widely dispersed across genes, so that 83% of the 231 coding sequences, including functionally important genes, show differences at the amino acid sequence level. In addition there are 68,000 insertions and deletions causing significant changes to 20% of the proteins. The insertions are driven primarily by insertion of Alu and LINE L1 elements (p 331), occurring more commonly in the human line, as well as LTR (long terminal repeat) and endogenous retroviral elements (p 332). Random deletion events also occurred, resulting in net chromosomal shrinkage. Neither do conserved regions correspond to transcribed functional genes. The most strongly conserved corresponds to a ‘genetic desert’ containing no coding sequences for proteins, consistent with the regulatory role of other human ultra-conserved regions (Bejerano et. al. R53).

Gene regulation is also significantly different between the species, with 20% of the genes showing significant differences in their pattern of activity. 15% of ‘CpG-islands’, associated with gene regulation, also differ between the species (Ebersberger R180). Two genes, the human versions of which contain large sections that are missing in the chimp, NCAM2 and GRIK1, are both known to be involved in neural function. The effects of such changes can be seen predominantly in the regulation of brain genes particularly those to do with further cycles of cell division during development. Starting with a set of about 12,000 genes, Cáceres et. al. (R97) found 91 that differed significantly in human and chimp brains. In 83 of these cases, the human brain had higher gene activity. In contrast, where genetic activity differed in heart and liver, human genes had decreased activity just as often as they had increased activity. However even subtle changes in a single key gene can have major effects. Ridley (R580 36) notes that ASPM (p 103), a large 10,434 ‘letter’ gene contains 28 functional exon regions, of which numbers 16 to 25 contain isoleucine-glutamine repeats which seem to determine how many cell generations occur in brain development in the vesicles about two weeks after conception. Humans have 74, mice 61 and fruit flies 24, in proportion to the number of neurons in the adult brain of each. Significant divergences have also been discovered in microglial cell sialic acid receptor genes (R334).

A detailed map of human evolution is emerging from comparison between the results of the human and chimp genome projects (R117). The discoveries so far are summarized below:

The single nucleotide divergence between chimp and human is only 1.23% (35 million base pairs) of which 1.06% corresponds to fixed fixed divergence between the species once 14-20% of intra-species polymorphisms are taken into account. The correspondingly higher divergence of the Y of 1.9% and lower of the X of 0.94% indicates the male mutation rate is 3-6 times the female rate. This mutational discrepancy between the sexes supports the necessity of female reproductive choice in all hominids, including humans.

CpG (cytosine-guanine) bases are prone to deamination to TpG and constitute the dominant form of chemical damage, causing 25.2% of mutations but only occurring in 2.1% of bases. Mutation rate variations between sexes are not CpG correlated because chemical damage is time related as opposed to replication errors from the 5-6 fold higher number of cell divisions in spermatogenesis.

Mutation rates also vary with location with 15% more near the ends of chromosomes, with higher local recombination rate, high gene density and high GC content. This effects the shorter chromosomes more significantly. Dark bands which are gene poor have a 10% higher mutation rate. Telomere regions have a higher rate rate in hominids than in murids, suggesting less selective pressure.

Insertions and deletions are rarer individually than point mutations but are larger, so 1.5% of the euchromatic differences are species specific, a larger difference than point mutations. Overall indel divergence is about ~45 Mb in each species or about 3% of the genome dwarfing the single nucleotide divergence. Most are very small, but the total contribution is 73% from larger >80bp indels. Over a third of these come from repetitive micro-satellite and satellite sequences, a quarter are caused by transposable elements, with a residue coming from deletions in the other species. 8.3 Mb of these in humans contain 34 exon regions indicative of new genes.

The history of transposable elements (p 332) differs significantly between the species. Endogenous retroviruses have died out in humans except for HERV-K with 73 human insertions (of which 66 have only the long terminal repeat remaining, indicating old insertions) This occurs also in chimps 45 insertions (44 LTR only) but chimps have other active ERVs. PIERV1 has over 200 copies over half of which are full length indicating active insertion. SINEs in particular Alu has been 3 times more active in humans (7000/2300 lineage specific insertions) mostly due to two new subfamilies (Ya5 Ya8), but baboons are 1.6 times higher still. Old Alu elements lie in GC rich gene-rich regions but newer ones are in AT rich gene-poor regions where LINEs also accumulate, consistent with L1-based retro-transcription. There is similar L1 activity in both species (~2000 insertions), as well as 200 human and 300 chimps processed LINE-related retrogenes (pseudogenes). SVA an Alu repeat with a CpG island and potential transcription factor binding sites occurs (~1000) in both species. 3 human genes show SVA insertions resulting in species differential transcriptions. There are also 612 human and 914 chimps Alu-Alu deletions, 26 and 48 L1 deletions and 8, and 22 LTR deletions, none involving exons of human genes in chimp. An Alu mobile element derived gene has been found in humans which encodes a neural small cytoplasmic RNA BC200. Conserved features of the active BC200a gene suggests that its RNA product has been “exapted” into a function of the primate brain, since the human-chimp divergence and provides a selective advantage to the human species (Martignetti and Brosius 1993 PNAS 90 11563-7).

Humans have about 13 times as many RNA edits as non-primate species, including inosine insertions associated with Alu elements, as well as intron deletions (Holmes R325) and newly inserted exons (Ast R26), which may differentiate humans from other apes through alternative splicing of genes expressed in the brain (p 102).
There are also larger scale inversions and fusions. Chimp chromosomes 12,13 now called 2A,2B fused to make human chromosome 2. There have also been pericentric inversions.

Orthologous proteins are very similar between the species, with 29% identical. Recombination is limited by a low cross-over rate with 1kb only having only ~1 crossover every 100,000 generations, or 2 million years.

Estimates of the effects of natural selection, neutral evolution and other factors can be gleaned by examining KA the amino acid substituting mutations, KS the synonymous mutations and KI the non-coding mutations. KA is 37% higher in the most distal 10 Mb than in proximal regions so careful averaging across the genome is needed. Both KA/KS and KA/KI are around 0.23 <= 1 indicating significant purifying selection. This value is 35% greater than for murids (rodents) indicating either greater positive adaptation or fewer evolutionary constraints. There is also weak purifying selection on silent sites in exons compared with introns. In terms of gene evolution a KA/KS of 0.23 indicates 77% of amino acid substitutions are sufficiently deleterious to be eliminated by natural selection. 4.5% of human-chimp orthologues (585/13,454) have KA/KL>1 indicating strong selection, however because of the low divergence between the species, about half could occur by chance variation among genes. The high KA/KS for these genes also shows that 25% of amino acid substitutions contribute to the current human genetic load. The KA/KS for human polymorphisms of 0.20-0.23 is very similar to that for human chimpanzee divergence, indicating little positive selection across the genome driving evolutionary divergence, because positive selection would cause many selective sweeps and reduce polymorphisms, indicating fewer evolutionary constraints in the hominid lines than in murids. X has KA/KL = 0.32 skewed high and low with higher selection on testis-related genes. The median is similar to autosomes indicating a skewed subset with very high evolutionary selection. Many low values indicate greater purifying selection consistent with being genes expressed in the hemizygous single X state in males, and high values could also result from positive selection from adaptive hemizygosity of the X in males, particularly if a substantial proportion of these genes are recessive.

Genes involving disease resistance, reproduction and reproduction (semen protamines and seminogelins), and nocioception (awareness of pain and toxic substances) stand out as rapidly evolving. Gene evolution is faster on rearranged chromosomes 1, 2, 5, 9, 12, 15, 16, 17, 18. Rapidly evolving gene clusters are associated with immunity, host defense, chemosensations and inflammation. Hominid lines show increased divergence of genes associated with ion transport, neurotransmission, sound perception and reproduction by comparison with murids. Large gene families such as those involved in immunity and olfaction are harder to test but are also subject to accelerated divergence.

Six regions of low diversity have been noted, consistent with linked genes hitchhiking on strong selective sweeps in recent human history. In addition one region containing several high diversity divergence scores contains genes noted for selective mutations, FoxP2 (involved in speech See Suite of chatterbox genes discovered Nature, DOI: 10.1038/nature08549), as well as CFTR (connected with asthma resistance). Other selective sweeps have also been discovered in recent human evolution putatively associated with brain size determining genes microcephalin and ASPM (p.105).

500,000 year old hand axes believed to date from Homo erectus found at Jajlula, Israel.

Looking at regulators and genes which have been lost in the human lineage one prominent one removes a forebrain subventricular zone enhancer near the tumour suppressor gene growth arrest and DNA-damage inducible, gamma (GADD45G)11,12, a loss correlated with expansion of specific brain regions in humans. (McLean CY et. al. 2011 Human-specific loss of regulatory DNA and the evolution of human-specific traits. Nature 471/7337, 216-9).

Many brain genes are more strongly conserved than other genes, although brain evolution may be affected by new alternative splicing arrangements in a small subset of genes, and strong selective sweeps made by new highly selective genes. Gene conversion with a pseudogene for example in the human line has altered sialic acid expression in brain tissue so that only human microglia express sialic acid.

One of the prominent genes essential to the majority of mammals which has been deleted in humans is the androgen regulator for penile spines. Penile spines which are accompanied by basal nerve fibres may have many functions including increasing male sexual sensitivity, reducing the length of female estrus, removing competitors sperm and many others. The authors point out that the loss correlates with the evolution of pair bonding in humans and that chimps and bonobos which do have neuro-sensitive spines have a very short copulation time like 5 to 7 seconds. Hardly enough to keep a woman happy (McLean C et al (2011) Human-specific loss of regulatory DNA and the evolution of human-specific traits Nature 71/7337 216-9.)

Until now, anthropologists have thought that Homo erectus evolved between 1.78 million and 1.65 million years ago. However at the Dmanisi site in the Caucasus Mountains of Georgia archaeologists found stone artefacts - mostly flakes that were dropped as hominins knapped rocks to create tools for butchering animals - lying in sediments almost 1.85 million years old (Human ancestors in Eurasia earlier than thought Nature Jun 11). The immediate precursor of Neanderthals and humans is termed Homo heidelbergensis, emerging some 600,000 years ago.

At some point from around the time we began to become bipedal to when the increasing human head size began to cause delivery problems, requiring births of helpless babies, needing more support to survive, this promiscuous ape pattern evolved towards one which gave more emphasis to longer-term semi-monogamous bonds between partners. Adovasio et. al. (R792 76) suggest the need for the larger head to twist in the pelvis may have required the attendance of 'midwives' and hence the birth of cultural interactions. There are many slightly different renditions of this story, some emphasizing shared child-rearing by female kin and friends rather than male partners. Others vary from emphasizing female reproductive choice to the repressive impact of male coalitions on female reproductive covertex.
Evolutionary conditions now began to favor a stronger pair bond between partners, which would aid offspring survival, at least for the first few years until an infant could join a peer group and fend for itself. Into this picture, we find the development of a form of serial monogamy, extremely rare in mammals, only about 3% of which are overtly monogamous, but much more common in birds where it takes two and a next to incubate and feed the young. The estrus became permanently suppressed, instead of the overt ape form found in chimps, and the female became perpetually sexually receptive, promoting strong psycho-sexual partnership bond formation, developing as well erotic tokens of fecundity in curvaceous fatty, sensitive breasts, only a small minority of whose tissue is involved in lactation, with buttocks and an hour-glass torso indicating ripe fertility.

Some writers, such as Sarah Hrdy (R330), question how much fathers have ever been involved in parenting, citing modern, 'primitive' and ape societies, and others consider that male coalitions may have had a significant influence towards female reproductive coverness rather than female choice, or partners alone. These are all features of a complex evolutionary dynamic whose centre is and has to be the reproductive relationship in a context of a ramifying linguistic grape vine, much of whose gossip, beyond sexual displays and emotional networking, has to have revolved around issues of fidelity and intimations of deceit.

We have noted (p.33), that mutual parenting needs are not a good predictor of monogamy in mammals, but rather the spatial distribution females to form exclusive domains, forcing males to guard a single female (Komers and Brotherton R386). A consistent and more complex interpretation might thus be that women evolved to have private sex within closely cooperative human social groups in which, like tamarins and marmosets, the females kept other females out of their own private sexual sphere, (Miller R475 185, Hrdy R330 180) by expecting fidelity of commitment from male partners, thus creating small exclusive sexual ranges, keeping track of the consistency of their lovers through gossip with other women during gathering forays, at the same time embracing the prowess of good hunters. The relative difficulty for males of crossing between partners without friction would then bias the natural male tendency towards polygyny towards overt monogamy with secretive affairs unless a male could openly resource sufficient to protect and support two partners. Human pregnancy is about as much of a maternal crisis as a twin birth would be for a tamarin. Maternal ambivalence would thus seem to be inevitable, and like other mammals to fall both on a male partner and on other kin in the kind of cooperative breeding arrangement Hrdy has associated with allo-mothering.

500,000 year old spear heads believed to date from Homo heidelbergensis found at Kathu Pan in South Africa (First stone-tipped spear thrown earlier than thought New Scientist).

The crucial for such evolution, rather than the small-brained Australopithicenes, with a cranial volume of some 450 cc similar to other apes, appears to be the major push made by Homo erectus and his alter-ego Homo ergaster who is consigned by some to an African rather than a dispersed Asian locale (Dennell and Roebroeks R157), although other research suggests he was the first Homo species coming out of Africa, went from a 750cc brain to 1250cc close to our own average size of around 1400cc. This expansion occurring between 1.6 million and 500,000 years ago achieved even in 75,000 generations, has to have been driven by a high degree of selection unlike any selection we see today in the relatively static brain size of modern humans. It is somewhere in this process, we can expect the human head size and retarded development to have played an increasingly significant role. There is little evidence of changes of tool-making during this time, with the handaxe playing an almost unchanging role, as continuing stereotype , but by 790,000 years ago, there is already evidence of control of fire, associated with flints and wood of six species including olive, wild barley and wild grape (Goren-Inbar et. al. R250).

There is some evidence that colonization of cooler climates may have been consistent with the use of skins or other forms of clothing. Analysis of erectus skulls and the discovery of a hyoid bone involved in speech vocalization is also consistent with an increasing use of language in erectus (Broadfield et. al. R79). On the other hand 1.6 million year old Nariokotome Homo ergaster skeleton, which does have some evidence of Broca's area (Taylor R688 41) has been claimed to have too narrow a spinal cord at the neck to have enabled the chest control for speech and some later examples have a high ape-like larynx that might be incompatible with speech (Ridley R580 219). Evidence for development of auditory areas associated with language goes back much further. Early work by Tobias (R693) and others suggest that the beginning of brain asymmetry in early Australopithecus exists. There are current studies on chimpanzees that suggest that there are certain very specific lateralized brain functions having to do with language which are present in chimpanzee brains. In particular is the 'planum temporale' which is a specialized area in the auditory association cortex which receives sounds, and attaches meaning to them. In most of the chimpanzee brains tested, this area was larger on the left side hemisphere than in the right one, which is also the human pattern (Begley R52). This evidence is also supported by Kanzi, a bonobo who has been in a language learning environment for nearly 20 years and has a very good level of comprehension of spoken English. He was tested on 660 novel English sentences and responded to the correctly on 72% of the trials, which was an equivalent response rate to that of a two year old human child tested on the same problems. (Savage-Rumbaugh et al. R613). Tobias (R693) had suggested that Homo habilis might have a Broca's area and Falk (R200) feels that by specialized measuring techniques she has confirmed its presence. A team of researchers has also established that Homo heidelbergensis thought to lead to Neanderthal had a hearing profile consistent with attention to speech rather than the high and low alert frequencies of chimps (DOI: 10.1073/pnas.0403595101).

The shape of the Neanderthal larynx and tongue was not positioned in the same way as ours for language (Conne et. al.) and the skull shapes are significantly different (Harvati et. al.).

On the other hand the Neanderthal throat is believed to have been less suited to verbal vocalization. Recent research, both from mitochondrial DNA (Krings et. al. R394), and from careful skull measurements (Harvati et. al. R296), suggests Neanderthal diverged from the line of Homo some 465,000 years ago and are a distinct species. Ridley (R580 214) has also drawn attention to the FoxP2 transcription factor gene on chromosome 7 whose mutations can give rise to severe selective language impairment and appears to be associated with fine motor coordination of the larynx. Mutations in this gene are rare. They have only been two functional mutations detected, one in the ancestors of mice and one in those of orangutans. But
there has been a double mutation in this gene and the paucity of ‘silent’ neutral mutations which don’t change the protein suggests it is a very recent change, later than 200,000 years ago, which has swept through the population by conferring a major selective advantage (Callaway E 2009 Suite of chatterbox genes discovered New Scientist 11 Nov).

However there is evidence for Neanderthal bone flutes (Gray et. al. R262) similar to those found all the way to Dolni Vestonice (p. 173).

The most ancient flutes of Neanderthal and H. sapiens

There are hints that these differences in Neanderthal are linked to social differences in sex roles. Lewis Binford speculates that the pattern of bones and tools in the French cave of Combe-Grenal reveals two separate but contemporaneous kinds of living area, one suggesting a life lived very locally, the other showing the comings and goings of more mobile folk. Binford calls the first type "the nest", and believes its occupants were females and their dependent children, foraging in the immediate vicinity. The second kind – smaller, more peripheral to the cave itself, he calls "scraper sites," suggesting these sites were produced by males. There is a connection between the two types, but a small one. Binford sees some provisioning of the young on the part of the males, but only in a haphazard sort of way. This dual pattern occurs through the 75,000 Mousterian years in Combe-Grenal, unlike the way modern men and women live together and divide the labor of food procurement and preparation between them. The Neanderthal sexes may thus have lived more apart with independent food preparation, different land-use patterns, different uses of technology, suggesting sexually mature males and females were not bound together by the long-term, reasonably stable sexual and economic relationships that exist between the sexes in all known human communities today (Shreeve R641 331). Dental evidence also suggests Neanderthals had a more rapid growing, becoming fully mature at 15, consistent with a higher mortality rate (Rozzi and de Castro R596) in contrast to delayed human development, although this is contested (R198). However at Shandar there is evidence of burial and caring for the disabled (Taylor R683 108).

According to initial genetic analysis, Neanderthals diverged from homo sapiens ~500,000 years ago. There has been interbreeding, and some transfer of genes e.g. from human males to Neanderthal females, although candidate human genes conferring natural advantage do have a profile consistent with transfer from Neanderthals (Green et. al. R663, Science 314, 1068-71).

More recent comprehensive investigation of the Neanderthal genome (Green, R. E. et al. (2010) Science 328, 710-722., Nature | doi:10.1038/news.2010.225) suggests that there was a period of interbreeding between Neanderthals and humans in the Near East around the time of the first migration out of Africa, rather than more recently in Europe, as the putative sequences are shared by non-African French, Han and Papuan, but not by the African Yoruba or San. It is estimated that among the former, 1-4% of the genome derives from Neanderthal sequences, although there is little evidence for these corresponding to the specific genes suggested by Lahn's team. Other transfers could have occurred but are not apparent in the research.

Computer simulation of genetic flow suggest that Neanderthals were about 40% less fit than their human counterparts, due to small population diversity and a social pattern of inbreeding and that given a migrant human population of 10 times the Neanderthal population, and the lower fitness of Neanderthal genes, the proportion of Neanderthal genes in humans feel from an initial 10% consistent with fairly indiscriminate interbreeding to the selective few percent we find today (Harris K & Nielsen. R 2016. The Genetic Cost of Neanderthal Introgression Genetics, 203/2, pp. 881-891 doi:10.1534/genetics.116.186890).

Assumptions that Neanderthal's exclusive meat diet contributed to their extinction has also come unstuck with the discovery of vegetable seeds in Neanderthal teeth, although previous discoveries of Neanderthal cannibalism ref 2 suggested they also ate one another, becoming the basis for another extinction scenario based on a kuru-like brain prion disease.

- Breeding with Neanderthals helped humans go global Jun 11
- DNA reveals Neanderthal extinction clues Feb 12 Study shows a collapse of Neanderthal genetic diversity 50,000 years ago before Homo sapiens arrived in Europe.

We propose the driving force for human brain growth was the complexification of the entire world of Homo brought about by the involution of semantic language into consciousness (and thus society) as an outgrowth of gesture and emotional vocalization and that it has been driven principally by social complexity, expressed in mate selection and social standing. Mirror neurons have been cited in this regard (p. 379). In this description, the evolution of language is a crisis of social interaction generated by genetic systems through the dynamic capacity to encapsulate language as ‘memes’ rather than hard-wired genetic determinism.

In terms of reproduction, language has a pervasive role from birth to reproduction. Adovasio et. al. (R793 103-113) advance the notion of 'motherese' the language between mother and child, in the process of females inventing language, but it is clear that to complete the reproductive cycle, language needs to be as much about influencing reproductive choice, in terms both of information shared between females while gathering and the winning of sexual favours in courtship, as in Geoffrey Miller's scenario. This would involve both females and males in language evolution even though the roles of each would be different and complementary.

The "Out of Africa" hypothesis may be consistent with a degree of regional development involving some sexual interbreeding with Neanderthals and Homo erectus. Specific genes such as PDHA1 consist of two families with the last common ancestor 1.8 million years ago, and microcephalin variants appearing 40,000 years ago (p 105) also have differences suggesting an original divergence 1 million years ago suggesting 'introgression' from Neanderthals (Jones R347). An even more ancient divergence in the pseudogene RRM2P4 in East Asian people suggests interbreeding with Homo Erectus. Some evidence from skeletons is also consistent with this picture. However more recent sequencing of the Neanderthal nuclear genome suggests little or no interbreeding with Homo sapiens and has cast doubt on the existence of the microcephalin variant in Neanderthals, as well as a gene associated with increased fertility in Icelanders also attributed to transfer from Neanderthals. However, research in 2010 into microsatellite variation in the human genome suggests that there have been two interbreeding events with other hominid species, one about 60,000 years ago in the eastern Mediterranean after the emergence of Homo sapiens from Africa, and the other about 45,000 years ago in eastern Asia (Nature doi:10.1038/nature08976).

The "Hobbit" persisted until 12,000 years ago on Flores. The situation has more recently been complicated by two finds. Firstly we have the 'hobbit' human remains found on Flores, named Homo floresiensis, who lived from 70,000 to around 12,000 years ago. These are variously claimed to be a separate human species, which may be a remnant of Homo erectus stock adapted for small size (R82, R490). Bones of another species Homo naledi have been discovered in a deep cave in South Africa having characteristics similar to early Homo erectus, currently dated to around 250,000 years ago (https://www.newsscientist.com/article/2128834-homo-naledi-is-only-250000-years-old-heres-why-that-matters/). This complements evidence for interbreeding with another hominin species, in ancient African populations of Biaka Pygmies and San Bushmen.

More recently we have the discovery of remains of Denisovians, Ref 2, a further species branching off from the Neanderthals. Genetic analysis of the remains indicates a significant interbreeding specifically with Melanesian people of some 6% (Reich D, et. al. 2010 Genetic history of an archaic hominin group from Denisova Cave in Siberia Nature doi:10.1038/nature09710, Meyer et al. (2012) A High-Coverage Genome Sequence from an Archaic Denisovan Individual 30 Aug Science express DOI:10.1126/science.1224344).

In the standard "Our of Africa" view of human evolution, H. erectus first evolved in Africa more than 2 million years ago. Then, around 600,000 years ago, it gave rise to a new species: Homo heidelbergensis, the oldest remains of which have been found in Ethiopia. About 400,000 years ago, some members of H. heidelbergensis left Africa and split into two branches: one ventured into the Middle East and Europe, where it evolved into Neanderthals; the other went east, where members became...
Denisovans - discovered in Siberia in 2010. The remaining population of H. heidelbergensis in Africa eventually evolved into our own species, H. sapiens, about 200,000 years ago. Then these early humans expanded their range to Eurasia 60,000 years ago, where they replaced local hominins with a small amount of interbreeding.

But the evidence from Chinese fossils remains at variance with those from Africa. The original Peking Man is an example of Homo erectus. A group of fossil specimens was discovered in 1923-27 at Zhoukoudian near Beijing. Recent dating suggests they are in the range of 680,000-780,000 years old. But more recent Chinese fossils show that, between roughly 900,000 and 125,000 years ago, east Asia was teeming with hominins endowed with features that would place them somewhere between H. erectus and H. sapiens. One nearly complete skull unearthed at Dali in Shaanxi province and dated to 250,000 years ago, has a bigger braincase, a shorter face and a lower cheekbone than most H. heidelbergensis specimens, suggesting that the species was more advanced. Such transitional forms persisted for hundreds of thousands of years in China, until species appeared with such modern traits that some researchers have classified them as H. sapiens. One of the most recent of these is represented by two teeth and a lower jawbone, dating to 80,000 - 120,000 years ago, unearthed in 2007 in Zhirendong, a cave in Guangxi province, the jaw has a classic modern-human appearance, but retains some archaic features. But studies of Chinese populations show that 97.4% of their genetic make-up is from ancestral modern humans from Africa, with the rest coming from extinct forms such as Neanderthals and Denisovans. One suggestion is that these more modern fossils were Denisovans. Similar ideas have led to an alternative explanation that heidelbergensis or its source population diversified outside Africa before one group returned to Africa and in turn led to modern Homo sapiens (Qiu J 2016 How China is rewriting the book on human origins Nature 535 22-25 doi:10.1038/535218a).

Orthodox ideas of language evolution emphasize how natural selection shaped our ancestors to improve their talent for complex communication. Noam Chomsky (R118) famously pointed out that infants learn language quickly and reliably from sparse and chaotic input. For him and many linguists, this 'poverty of the stimulus', is evidence that much of our language ability is innate, directly encoded in our genome, and takes the form of a neurologically hard-wired universal grammar. Steven Pinker (R543) argues that the ability to communicate effectively would have given early humans a 'fitness advantage'. Natural selection favoured genetic mutations that improved our language faculty, so they spread through the hominid gene pool. The legacy is that we all have brains adapted for speech. However the development of the human brain, unlike that of song birds, doesn't simply consist of an enlarged language centre but an entire enlarged and complexified cerebral cortex, indicating evolution has been in the direction of adapting to a universal increase in complexity of the social environment.

Left: Evidence for violence in a 430,000 year old skull from a deep vertical shaft in the 'pit of bones' Sima de los Huesos in Spain. DNA evidence suggests the skull is Neanderthal and shows both the earliest known evidence for homicidal violence in Homo and possibly the earliest evidence for funerary behavior. Right: It has been suggested that Neanderthals became extinct partly because they adapted to the long European winter nights by evolving larger eyes (left) which meant their brain evolution centered on increased sensory processing, rather than the prefrontal cognitive expansion and social networking of Homo sapiens, leading to critical social disadvantage.

More recent investigations show that interbreeding with other hominins was critical to the globalization of Homo sapiens. Human leukocyte antigens (HLAs), a family of about 200 genes that essential to our immune system also contains some of
the most variable human genes: hundreds of versions - or alleles - exist of each gene in the population, allowing our bodies to react to a huge number of disease-causing agents and adapt to new ones. One allele, HLA-C*0702, is common in modern Europeans and Asians but never seen in Africans; Peter Parham has found it in the Neandertal genome, suggesting it made its way into H. sapiens of non-African descent through interbreeding. HLA-A*11 had a similar story: it is mostly found in Asians and never in Africans, and Parham found it in the Denisovan genome, again suggesting its source was interbreeding outside of Africa. This tallies with interbreeding giving H. sapiens pivotal resistance to non-African diseases. While only 6 per cent of the non-African modern human genome comes from other hominins, the share of HLAs acquired during interbreeding is much higher. Half of European HLA-A alleles come from other hominins, says Parham, and that figure rises to 72 per cent for people in China, and over 90 per cent for those in Papua New Guinea (Marshall M. 2011 Breeding with Neandertals helped humans go global New Scientist 16 Jun, Neandertal sex boosted immunity in modern humans BBC 26 Aug 2011).

The contribution to immunity from Neandertals has now become strongly evident, with highly significant differences between immune response to pathogens in both macrophages and monocytes in separate studies highlighting differences between African and non-African populations, which involve genes with Neandertal homology, implying a Neandertal-derived shift in the immune response to cope with new kinds of pathogens in new areas the migrants found themselves in. The greater intensity of immune response in African populations may also explain the three-fold higher rates of auto-immune disease in African women (Reardon S. 2016 Neandertal DNA affects ethnic differences in immune response Nature doi:10.1038/nature.2016.20854).

In a 2014 study by David Reich and coworkers, genes for keratin filaments that lend toughness to skin, hair and nails, were enriched with Neandertal DNA. This may have helped provide the newcomers with thicker insulation against cold conditions, the scientists suggest. But other genes are implicated in human illnesses, such as type 2 diabetes, long-term depression, lupus, biliary cirrhosis - an autoimmune disease of the liver - and Crohn's disease. Other regions of the human genome, including the X-chromosome, are devoid of Neandertal sequences, suggesting they were selected against as deleterious. A genome region that lacked Neandertal genes includes FOXP2, thought to play an important role in human speech (Sankararaman et al 2014 The genomic landscape of Neandertal ancestry in present-day humans Nature doi:10.1038/nature12961, Vernot B and Akey J 2014 Resurrecting Surviving Neandertal Lineages from Modern Human Genomes Science doi:10.1126/science.1245938).

Functionally important regions are deficient in Neandertal ancestry (Sankararaman et al 2014).

More recently selection for specific Toll-like receptors significant in disease resistance and acclimatization to high altitudes in Tibetans have both been tied to Neandertal alleles among a wide survey of relative contributions to disease related genes (Callaway E 2015 Neandertals had outsize effect on human biology Nature doi:10.1038/523512a). The cold adaption of Inuit has likewise been traced to a variant of a geneTBX15/WARS2 from a relative of the Denisovans (Fumagalli M. et al. 2015 Greenlandic Inuit show genetic signatures of diet and climate adaptation Science 349 (6254) 1343 DOI: 10.1126/science.aab2319). In a 2016 study traits linked to hypercoagulation, depression and tobacco addiction correlated with Neandertal alleles. Although these may be disadvantageous in older modern populations they must have either conferred advantages during reproductive age or general advantages for the population of the time. Coagulation may have protected against injury but makes people more prone to stroke in modern populations (Simonti et al. 2016 The phenotypic legacy of admixture between modern humans and Neandertals DOI: 10.1126/science.aad2149). A second 2016 study by Akey and coworkers confirms that hybridization with Neandertals and Denisovans provided an important reservoir of advantageous mutations for modern humans that enabled adaptation to emergent selective pressures as they dispersed out of Africa. Our results show that immune and pigmentation traits were frequent substrates of adaptive introgression and that in many cases adaptive archaic haplotypes also contribute to the disease susceptibility in contemporary individuals. Many positively selected archaic haplotypes act as expression quantitative trait loci, which modulate the quantitative expression of particular genes, suggesting that modulation of transcript abundance was a common mechanism facilitating adaptive introgression (Gittelman R et al. 2016 Archaic hominin admixture facilitated adaptation to Out-of-Africa environments Current Biology doi:10.1016/j.cub.2016.10.041).

Two studies examining immune response to infection highlight such differences. Nédélec et al. (doi:10.1016/j.cell.2016.09.025) measured how gene expression in macrophages changed in response to the infection. About 30% of the approximately 12,000 genes that they tested were expressed differently between the two groups, even before infection and many of the genes whose activity changed the most during the immune reaction had sequences that were very similar between Europeans and Neandertals, but not Africans (Quach et al. doi:10.1016/j.cell.2016.09.024) grew monocytes in a dish and infected them with bacteria and viruses. Once again, the two groups showed differences in the activity of numerous genes, and Neandertal-like gene variants in the European group played a major role in altering their immune response. The differences were especially stark in the way that those of African descent and the other half of European descent responded to viral infection. For some diseases, such as tuberculosis, a lower immune response tends to help with survival, and modern humans in Europe adopted the Neandertal traits that helped with this. Overactive immune systems could help to explain why African American women, for instance, are up to three times more prone to the autoimmune disease lupus than white American.
The oligoadenylate synthetase (OAS) locus, which consists of three genes - OAS1, OAS2, and OAS3 - that encode enzymes involved in the innate immune response against viruses, and are among the core genes that are important to stop viral replication. A further comparison of OAS sequences among human populations revealed that this OAS Neanderthal allele is found in about 60 percent of individuals in Africa. However, outside of Africa, it is only found in individuals that harbor the Neanderthal haplotype. It is likely that Neanderthals were better adapted to the pathogens present in non-African environments than anatomically modern humans that had newly moved into these regions and it appears that this allele was lost during the out-of-Africa migration and that the Neanderthal haplotype resurrected this allele after the bottleneck following the human migration out of Africa (Sams A et al. 2016 Adaptively introgressed Neandertal haplotype at the OAS locus functionally impacts innate immune responses in humans Genome Biology 17 246).

McCoy, Wakefield and Akey (doi:10.1016/j.cell.2017.01.038) note that there is significant downregulation of Neanderthal genes in both the brain and testes, indicating that these genes are mildly deleterious: "Recent theoretical work predicts that Neanderthals suffered a high load of weakly deleterious mutations accumulated during extended population bottlenecks. Assuming additive fitness effects, this mutational burden was estimated to have reduced Neanderthal fitness by at least 40% compared to modern humans. Under this model, deleterious haplotypes introgressed into larger modern human populations would have been subject to strong selection during the first ~20 generations after hybridization — a prediction with growing empirical support from genetic data. Nevertheless, many weakly deleterious variants are predicted to persist in present-day human populations, with a cumulative impact comparable to that of the Out-of-Africa bottleneck. Contributing to this result, we observed a striking bias toward downregulation of Neanderthal alleles in the brain and testes. Brain regions had significantly lower expression of Neanderthal alleles than non-brain tissues, particularly in the neuron-rich cerebellum and basal ganglia regions. This level of downregulation is exceptional, as equalized samples of non-introgressed SNPs matched for sample sizes of individuals and tissues showed no such bias. Further consistent with these data, brain regions including the cerebellum were enriched for significantly down-regulated compared to significantly upregulated Neanderthal SNPs. Significant downregulation of introgressed alleles in the brain is particularly remarkable given the previous observation that brain-expressed genes show less allele-specific expression (ASE) overall, a finding that was attributed to reduced levels of genetic diversity in this gene set. One brain-specific gene that exemplifies this pattern of down-regulation is NTRK2, which encodes a neurotrophic tyrosine receptor kinase that regulates neuron survival and differentiation as well as synapse formation."

Neanderthal versions of genes in the testes, including some needed for sperm function, were also less active than human varieties. That finding is consistent with earlier studies that suggested male human-Neandertal hybrids may have been infertile. But Neandertal genes don't always lose. In particular, the Neandertal version of an immunity gene called TLR1 is more active than the human version. Lopsided gene activity may help explain why carrying Neandertal versions of some genes has been linked to human diseases, such as lupus and depression.

A study of the Neanderthal Y chromosome, which is probably extinct in the human population, despite interbreeding, has shown that several key male histocompatability genes on the Y are mutated in a way which could have led to a maternal immune response and miscarriages, forming a barrier to interfertility (Mendez F et al. 2016 The Divergence of Neandertal and Modern Human Y Chromosomes The American Journal of Human Genetics 98 728-734). Moreover there are signs of hybrid infertility, suggesting only about 1 in 50 inter-matings resulted in fertile offspring, as regions in the X-chromosome, and on other chromosomes linked to testis genes, and mitochondrial DNA are all devoid of Neanderthal genes, a pattern common to interspecies infertility.Evidence from a study of European Ice Age genomes shows the proportion of Neanderthal DNA has been declining due to natural selection Fu et al. (2016 The genetic history of Ice Age Europe Nature doi:10.1038/nature17993.). As a result, evolution wiped away the Neanderthal DNA that negatively affected procreation. It is thus from these rare events that introgression into the human line has occurred, resulting in selective sweeps of a small subset of Neandertal genes into the entire human population.

Some doubt had been cast on the Neanderthal interbreeding idea, attributing the effects instead to shared sequences arising from isolated African populations of the two species separating some 300-350,000 years ago, with the last exchanged genetic material some 47-65,000 years ago. However these results are contested by the original researchers from Paabo's team. They say recent analyses firm up the evidence for interbreeding. Their evidence also suggests non-Africans have shared genes in common with Neandertals for only a few tens of thousands of years, so these genes cannot predate the origin of Neandertals (Ball J Neanderthal breeding idea doubted BBC 13 Aug 2012, Marshall M. Human and Neanderthal interbreeding questioned New Sci 13 Aug 2012).
In 2014 more accurate datings of the demise of Neanderthals in Europe suggests they were already in serious decline 50,000 years ago probably as a result of a climate cooling phase and that by the time sapiens arrived they were already only a small fragile remnant population in scattered isolated bands (Brahic C. 2014 Neanderthal demise traced in unprecedented detail New Scientist 20 Aug, Nature, doi.org/bxh255). The use of wolf-dogs by Homo sapiens has also been suggested to be a factor (Shipman P 2015 How our wolf-dogs hounded out the Neanderthals New Scientist 16 Mar). By 39,000 years ago they had largely vanished. This doesn't imply they were actively killed off by Homo sapiens but that their territory and resources were compromised by a new invasive species. Neither is it clear that they were manifestly intellectually inferior to modern humans, as artifacts from both species show similar innovations (Barras C 2014 Neanderthals may have been our intellectual equals New Scientist 30 Apr).

There is also suggestive evidence for up to 2% interbreeding with another hominin species, in ancient African populations of Biaka Pygmies and San Bushmen (Human ancestors interbred with related species (Nature doi:10.1038/news.2011.518, Hammer, M. F. et al. Genetic evidence for archaic admixture in Africa Proc. Natl Acad. Sci. USA http://dx.doi.org/10.1073/pnas.1109300108) although this is based only on statistical divergences in some loci, and lacks a sister species reference sequence, it suggests interbreeding around 35,000 years ago with a population that originally diverged from the Homo sapiens line some 700,000 years before. A further introgression of one, or more unknown hominins possibly erectus has been found in the genomes of Andaman Islanders (Mondal M et al. (2016) Genomic analysis of Andamanese provides insights into ancient human migration into Asia and adaptation Nature Genetics doi:10.1038/ng.3621). The female Neanderthal sequenced in the above study also had extensive inbreeding, with up to an eighth of the genome devoid of allele variation implying breeding between half siblings, possibly as a consequence of small isolated populations.

Left: Earlier interbreeding also occurred 100,000 years ago in which human genes and those of another mystery hominin were transferred to Eastern Neanderthals and Denisovans respectively (Callaway E 2016 Evidence mounts for interbreeding bonanza in ancient human species Nature doi:10.1038/nature.2016.19394). Centre and right: The same events giving percentages and populations sizes (Kuhlwilm M et al. 2016 Ancient gene flow from early modern humans into Eastern Neanderthals Nature doi:10.1038/nature16544).
This led to notable incidence of deformities. Those he studied have a range of deformities, many of which are rare in modern humans (PLoS ONE, doi.org/p6r). Our genomes likewise still carry traces of past small population bottlenecks. A 2010 study concluded that our ancestors 1.2 million years ago had a population of just 18,500 individuals, spread over a vast area (PNAS, doi.org/dv75x8).

A 110,000-year-old Denisovan tooth, 60,000 years older than the previously analyzed Denisovan remains, suggest that this group of people was able to survive the harsh Siberian climate for millennia. Comparisons between them established that Denisovans were nearly as genetically diverse as modern Europeans, and much more so than Neandertals. The new tooth also contains DNA unlike that of Neandertals or modern humans, suggesting that Denisovans interbred with an even more mysterious branch of the human family tree, either unknown to science, or known only from fossils without preserved DNA. A, B Denisovan evolutionary tree. C, relative genetic diversity of Denisovans compared with Neanderthals and Humans (Sawyer et al. 2015 PNAS doi/10.1073/pnas.1519905112).

In October 2014 Nature reported the analysis of a leg bone of a ~45,000-year-old modern human male from Siberia, which carries a similar amount of Neandertal ancestry as present-day Eurasians (2.3% against 1.6-2.1%), however, the genomic segments of Neandertal ancestry are substantially longer than those observed in present-day individuals, indicating that Neandertal gene flow into the ancestors of this individual occurred 7,000-13,000 years before he lived. There are however no Denisovian insertions detected. The discovery also sets a lower mutation rate for humans over the intervening period of 0.43x10^-9 per site per year than previous estimates but similar to current population de novo estimates of ~0.5x10^-9, with somewhat higher values of 0.76x10^-9 for Y genes and 2.53x10^-8 for mitochondrial genes. The lower overall mutation rate suggests an older origin for the divergence of the human line from apes to 10 million years ago rather than the 5-6 million previous genetic research has suggested (Fu et al. 2014 doi:10.1038/nature13810).

A theory of language as an evolutionary ‘parasites’ reaching towards internal efficiency has recently been advanced. Darwin, the founder of the evolutionary approach speculated that language was potentially an invention (R149 60): "Man not only uses inarticulate cries, gestures and expressions, but has invented articulate language, if indeed the word invented can be applied to a process completed by innumerable steps half consciously made". Morten Christiansen (Christiansen and Kirby R121) questions the need to invoke a Chomskian generative grammar. Instead, he argues, language has adapted to utilize more general cognitive processing capacities that were already part of our ancestors’ brains before language came along. Among these, he focuses on ‘sequential learning’ - the ability to encode and represent the order of the discrete elements in a sequence. This ability is not unique to humans: mountain gorillas, for example, use it in the complicated preparation of certain spiky plant foods, where a sequence of tasks is required to remove the edible part. Language, he says, is a ‘non-obligate mutualistic endosymbiont’ - a kind of evolutionary structure like a ‘symbolic virus’. Kirby suggests our brains are not so specifically designed for language and that we appear to be biologically adapted to language because language which evolves much faster than biology has culturally adapted to us, gaining semantic power and representational efficiency as it evolves.

Various lines of evidence support such optimization of representational and cognitive efficiency in existing languages. For example dependency length minimization, in which words which depend on one another come closer in a sentence than random (Futrell et al. 2015 doi:10.1073/pnas.1502134112 ), makes it easier to recognize meanings in both spoken and written sentences, although the efficiency of existing languages varies widely. Widely used languages such as English have evolved to simplify changes of tense, person, gender and number to avoid complex conjugation and declension of verbs and nouns. There is also evidence that the root of languages might be partly iconic rather than the arbitrary relationships between sound and meaning of traditional linguistic theories, so that words indicating slowness, descent or negative emotions have a falling pattern of intonation while those with the opposite have a rising one, like down as opposed to up (Matacic C 2015 doi: 0.1126/science.aad1612). “Splash” provides a good example of a word whose spoken sound mimics its natural sound.
Rings of stalactites piled in Bruniquel Cave Aveyron, Valley, France, deduced to be early Neanderthal activity dated to some 176,500 years ago by minerological analysis.

Languages as different as Danish and Hindi have evolved in less than 5000 years from a common Proto-Indo-European ancestor. Yet it took up to 200,000 years for modern humans to evolve from archaic Homo sapiens. The latest estimates of the oldest skulls discovered, from the Omo river by Richard Leakey are 196,000 years (McDougall et. al. R445).

Pinker (R545) notes steps of this type in the experiments of Martin Nowak’s group (R507, R508) in establishing both sequential symbols such as vowels and consonants to form a word and positional syntax in which words describing single events give way to active characterization of a type of event. Both are adaptive responses to informational crisis as a large number of symbols each associated with a single context or event involves too many similar symbols to adequately discriminate one from another. The emergence of such structures could in turn have enabled the semantic enfolding of the rational mind. Reading written language is clearly such an adaption of visual pattern recognition and other skills.
creations – the outline of a hand, an array of lines, and a painted cave formation – from three caves in Spain all date to more than 64,800 years ago, at least 20,000 years before modern humans reached Europe (doi: 10.1126/science.aap7778). Insect 1: Shells from a fourth Spanish cave, pigment-stained and pierced as if for use as body ornaments, are even older, dating to 115,000 years ago implying a Neanderthal origin (Hoffmann D et al. 2018 Science Advances 4/2 eaa5255 doi:10.1126/sciadv.eaa5255). Insect 2: A 35,000-year-old flint flake found at a Middle Paleolithic site in Crimea, Ukraine, may have been engraved symbolically by a Neanderthal (Mačík A et al. 2018 PLoS ONE 13/5 e0195049 doi:10.1371/journal.pone.0195049).

Ape communication is a fluid mix of gesture, body, hand and facial movements, and vocalizations, all of which play a role in expressing meaning in emotional terms. Yawning is catching in chimps suggesting self-awareness (DOI 10/1098/rsbl.2004.0224). Karen McComb (R455) tested an idea of Robin Dunbar's that language arises from mutual or reciprocal grooming as ape societies become larger and more complex. In a study of 42 primate species she found that call repertoire and time spent grooming increases with group size.

Corballis (R133) suggests language arose from a selective convergence of these diverse attributes to give rise to semantic language, possibly also accompanied by a convergence of other faculties such as mental perspectives of others, consistent with an early common origin of click sounds (p 106). Gestures like the shrug are also ancient responses, while smiles, and snarls with all their dimensions from appeasement to tooth threatening exposure go all the way back through our primate relatives. Laughter is an example of a central chaotic and explosive emotional response to contradiction, or surprise, which is suggestive of an ancient origin, earlier than language as we know it, in sharing emotional reactions, which also appears to have a basis in sexual courtship and family bonding:

"Women laugh most in the presence of men they find attractive.
Men are the leading laugh getters, women are the leading laughers"

Robert Provine University of Maryland (R381)

The advent of semantic exchange would place a huge new evolutionary burden on all areas of the cortex by exploding time, space and society into an historical process in which more and more contexts, individuals and situations came to be named and hence distinguishable from one another. Such a language involution would then place a burden of selection on larger brains which could handle the new and diverse complexities of a world imbued with historical and semantic meaning required to slow fetal development and a new awareness of social and sexual relationships and their implications. We can see the germ of this complexity in ape societies, such as grazing gelada baboons where there are a host of cries indicating all manner of interactions, from courtship, through male competition, to emotional 'social contracts' of mutuality, reciprocation, aggression and reconciliation, as well as group warnings about predators. Among these, sexual courtship and competition are both very strong and also very subtle fleeting yet highly focused influences, as a glance at a female macaque inciting an extra-alpha 'safari' coupling behind the alpha males' backs indicates. This supports a general role for Machiavellian social interactions, with a core emphasis on reproduction and sexual selection driving the burgeoning complexity of semantic language, consistent with both Geoffrey Miller's sexual selection ideas and honesty and deceit in wider social contracts. Consistent with this view is the fact that the sneakiest monkeys have the largest brains (DOI: 10.1098/rspb.2004.2780)). Dunbar (R178) suggests that, as neocortical size increases, more subtle social and political strategies, such as tactical deception come into play. As a result, lower-ranking individuals are able to find loopholes in the social dominance hierarchy. Their special cognitive capacity makes them able to improve their reproductive success, in spite of lower rank - in line with the Machiavellian Intelligence hypothesis (Whiten and Byrne R742, R743). Boehm (R68 182) comments that the political invention of egalitarian society during this process enabled such individuals to forgo or invoke strategies of social deception, suggesting that lower ranking coalitions bullied or forced their way, as male coalitions of chimps can do, to form large, stable and purposeful coalitions which are at the root of our social egalitarianism, politics and morality.

Erectus is conceived as a gatherer-hunter species, so one can envisage a leading edge of such evolution applying to coalitions of gathering females consistent with sexual differences in human language acquisition in humans today. This in turn could have driven increased opportunities for female reproductive choice and the growth of a capacity to define long-term relationships and forms of serial monogamy within an existing social grouping not found in ape societies, where monogamy occurs only outside immediate social groupings, which are either harems, or promiscuous troops. We can envisage a continuing trend of sexual selection, increasing long-term partnership, female cooperation in gathering and social cohesion, the avoidance of male-driven infanticide and strong sexual selection for males with a good social capacity for fathering, entertainment, protective prowess and partnership.

Concealed Estrus, Menstruation and the Sex Strike

Menstruation is common in simians (Old World monkeys, New World monkeys, and apes), but completely lacking in lemurs and pottos but is possibly weakly present in tarsiers. Most monkeys living in Africa and Asia, such as rhesus macaques, menstruate and great apes do it too. Menstrual bleeding is easily detectable in chimpanzees and gibbons. Beyond primates, it is known only in bats, the elephant shrew, and the spiny mouse, while other species reabsorb their uterine linings. A few mammals besides humans have concealed ovulation and do not experience obvious, visible signs of fertility. In humans, while women can learn to recognize their own level of fertility, whether men can detect fertility in women is debated. Recent studies have given conflicting results, consistent with concealed estrus making it harder for men to know when a woman may be getting pregnant, so he has to stick around.
Orangutans also lack visible signs of impending ovulation, and the extended estrus period of the bonobo (reproductive-age females are in heat for 75% of their menstrual cycle) may have a similar effect to the lack of a "heat" in human females. A 2016 study (Douglas et al. 2016 BMC Evolutionary Biology doi:10.1186/s12862-016-0691-3) found that the duration of females' maximum swelling phase - MSP - was highly variable, ranging from 1 to 31 days. Timing of ovulation varied considerably in relation to the onset of the MSP, resulting in a very low day-specific probability of ovulation and fecundity across female cycles. Ovulation occurred during the MSP in only 52.9% of the analysed swelling cycles, and females showed regular sexual swelling patterns in swelling cycles where ovulation did not occur. These findings reveal that sexual swellings of bonobos are less reliable indicators of ovulation compared to other species of primates. Menstrual cycles in apes are frequently different from the 29.53 day lunar cycle; the average cycle length in orangutans is the close to that of humans, 28 days, while the cycle for chimpanzees is 35 days.

Darwin also thought that hairlessness was caused by sexual selection applied to women, which had happened early on in human evolution (R683 35):"No one supposes that the nakedness of the skin is any direct advantage to man; his body cannot have been divested of hair through natural selection". In 'The Decent of Man and Selection in Relation to Sex', he concludes that women lost their hair, because men found hairlessness attractive, not because it was burdensome; women's loss of hair led to a concomitant but less marked loss in men.

An affectionate father of an infant daughter gently rocked in a baby sling, Taylor cites another single cause theory that the baby sling was the single most crucial step in the evolution towards larger brains (R683 44). The argument is that to get through the pelvis, given the constraints which now make human childbirth difficult and require the rotation of the head during delivery required a slowing of brain development until after birth (human give birth at 29% of adult brain size rather than the 47-8% of chimps) and hence a less developed newborn. The sweeping claim is that the baby sling was the turning point which made possible, not only the 'development of the human brain but human sexual culture and the very idea of gender - the extension of human categories into the realm of objects and ideas … sex ceased to be necessarily short and sharp and become an act of potentially ecstatic contemplation'. While the baby sling is a major invention of women, central to both the gathering way of life and the capacity to demand feed and hence keep a balance between the number and quality of offspring (p 107) this is another single external factor theory, when it is the inventiveness of sexual selection at play in generating innovations, from the sling through the wheel, to fine music, and the arts of love, rather than the artefacts driving evolution, although they may irreversibly change the social milieu.

Hrdy (R330 264-6) ponders how humans could have evolved at all given our current forces of patriarchal domination so endemic in ape societies as well. "How could females so clearly at risk of reproductive exploitation be selected to produce such a large-brained, slow maturing offspring?" Based on her studies of langurs and other cooperatively breeding primates she proposes that "the earliest representatives of the genus Homo were cooperative breeders" suggesting that a variety of 'allo-mothers' including grandmothers, daughters, siblings, relatives, female friends and incidentally parental partners may all have been involved. This has the virtue of allowing for a flexible interplay of reproductive behavior incorporating both matrilineal and partner-based dynamics. However chimp females our nearest relative are very protective of their young and don't even hand them over to older siblings (Hrdy R330 502). Furthermore in addition to the manifest incidence of pair-bonding across all human societies, mate guarding is an almost universal feature of male mammals and so, even though men may not spend anywhere near as long in infant care as mothers, they are likely to have applied enough selective pressures throughout human emergence for partnership to have played a significant reproductive role. Since mate guarding is a better
predictor of monogamy than paternal parental effort, monogamy would be expected to evolve based mutual competition between females for sexual territory. Human females do express preferences for monogamy and resist to a fair degree being co-wives, but moderate polygyny and affairs are common, consistent with a complex and varying social pattern of sexually antagonistic coevolution, poised in a state of paradox between the sexes.

What then of the relationship between our concealed ovulation and monogamy? While 10 out of 11 monogamous species have concealed ovulation, the reverse is not true. Monogamy occurs in only 10 out of 32 primates with concealed ovulation, the majority consisting of promiscuous and harem-forming species. Paradoxically the logic works in reverse for overt ovulation. While most boldly-advertising species are promiscuous (multi-male), 20 out of 34 promiscuous primates have concealed ovulation. Harem-forming species fall right across the spectrum. These confirm that concealed ovulation is a fundamentally successful strategy which can thrive in all mating systems, because it abets female choice, and that overt ovulation tends to be a specialized adaption. Many switches of mating type are believed to have occurred when tree analysis is taken into account. Overall it appears that social monogamy has evolved 7 times in different branches of the primates including humans, gibbons and 5 groups of monkeys, and harems 8 times (Diamond R166 103).

All these societies have frank characteristics of the "sexually-antagonistic coevolution" noted by William Rice (p 16). Male infanticide in all these social systems is in evolutionary conflict with female choice. Concealed ovulation creates a paradox between overt polygyny and the covert polyandry of many 'possible fathers' (Hrdy R331). In promiscuous chimps society by some accounts we have some half the offspring being sired discreetly 'on safari' despite overt ovulation, so the paternity uncertainty is both an overt one shared between genetically related males from the same troop and a covert one of secret unions of more uncertain parenthood. Human societies go further than simple infanticide and stone women for adultery, showing this sexual antagonism to be central to religious imperatives.

Desmond Morris (R486) and others (see Hrdy R329 141) assumed that concealed ovulation and continuous sexual receptivity, rather than the cyclical or seasonal reproductive patterns characteristic of other primates emerged on the basis of 'copulation as a female service' (Symons R678) on a 'man the hunter' basis to give men competing for hunting intelligence more stable rights to maintain cooperative interaction in the hunt and enticements for pair-bonding. Taylor also debunks the 'man the hunter' view, as sexist, despite noting that Linda Hurcombe has pointed out that calling the division of labour between gathering and hunting sexist ignores the facts of life … that a mother holding a young child cannot be a steady hunter and foot hunter (R682 26).

Certainly overt ovulation runs counter to pair-bonding, as noted by Lancaster (R398). However Hrdy (R329 135-144) notes a poor correlation between pair-bonds and high levels of sexual activity in primates (except marmosets). Gibbons, the only monogamous ape for example make love only twice a day during an estrus which lasts only a few months every 2 to 3 years with no sexual activity in between. Moreover constant sexual activity is not a good evolutionary basis to select for paternal behavior and could compete with reproductive imperatives. The occurrence of both 'assertive solicitations of males by non-ovulating females among primates which are not pair-bonded and female 'orgasm' in other primates also scotches ideas of its role being unique to humans, for example in making it 'easier for the female to be satisfied by one male'. Non-reproductive female-initiated sexual activity is likely to be selected for to impute paternity and avoid male infanticide in many species. At another extreme Nancy Burley (R34) suggested that concealed ovulation serves to prevent the human female opting out of evolution because of the pain and stresses of childbirth. However this denies women have any sense of their own ovulation which they often do, and ignores women's capacity to resist sex altogether as a means to the same end.

Alexander and Noonan (R7) argue that concealed ovulation, and the breast as a permanent signal of receptivity, enabled a female to hold on to a mate by reducing paternal certainty at the same time as inviting sexual receptivity, making it difficult for a male to know when she is on heat and thus having to stick around. Receptivity is then both an invitation and 'sex as a weapon' to enforce male resourcing compliance. Jared Diamond (R166) calls this the 'daddy-at-home theory'. Diamond argues that a woman had to conceal her ovulation; otherwise her husband would only stay with her when she was exhibiting signs that she was fertile. The rest of the time, he would be out trying to find other women, who were exhibiting signs that they were sexually ready. His absence would be detrimental to his children, and by concealing her ovulation, a woman convinced a man to stay by her side and make love to her throughout the month, so that he could be sure he was fathering the children she bore. However Shlain (R638) notes that several flaws and inconsistencies, weaken the argument that promotes sex as the glue holding human relationships together. If sex served the purpose of ensuring the durability of the human parenting commitment, then parents should become more ardent in their lovemaking following the birth of a baby. Instead, the opposite occurs. Both parents routinely report a sharp fall in their respective libidos. Barbara Smuts adds the ironical twist of females tolerating male mates to protect against coercion by other males, thus forcing males to accept these bonds even when they involved lower-ranking males (Pusey R561). Wrangham (R765) has even speculated that pair bonds may relate to food guarding, with the establishment of cooking.

According to the ape family tree (p 68), and the relative success of concealed ovulation across many mating habits, concealed ovulation evolved not to keep dad at home in an already monogamous family unit, but to promote the central reproductive issue for females in ape societies - reproductive choice - immediately equitable with paternity uncertainty of 'polyandrous motherhood' or 'possible fathers' (Hrdy R331). In some primate species such as Barbary macaques, which like chimps are promiscuous multi-male troops and where the attention of several males seems essential for offspring survival, paternity uncertainty may actually aid total paternal investment (Hrdy R329 157). A similar situation prevails in human societies which believe in 'partible paternity' (p 166) the idea that many inseminations are required to form an embryo (Hrdy R330 246). Birkhead (R63 204) notes that extra-pair couplings in socially monogamous birds, aid fertility, reducing the number of eggs which fail to hatch through histo-incompatibility. Human parents with the same HLA leukocyte haplotype also have miscarriage of very early embryos. Prairie dogs also improve their fertility during their afternoon of estrus by copulating with more than one partner.

In the human context sexual privacy along with concealed ovulation acts to optimize covert and particularly female infidelity. According to Geoffrey Miller (2000 The Mating Mind Random House), such 'reproductive inscrutability' may have catalyzed language, art, science and cultural complexity. Human gossip and judgement of personality tend to focus on detecting deceit
from honesty in love and betrayal. The village grape vine round camp fires at night are a prime source of gossip and sexual intrigue. Good art and astute skill in hunting are in turn genuine indicators of fitness giving the entire process of cultural evolution a valid drive in terms of sexual selection. But female 'infidelity' also invites female competition. Several studies in birds confirm the fact that competition between females is a substantial factor inhibiting polygyny, which could, in its absence, be as successful at rearing young as the monogamous state. Ridley (R577) notes that in humans, just like sparrows, "adultery is common. It is commonest between high-ranking males and females of all ranks. To prevent it males try to guard their wives, are extremely violent towards their wives' lovers and copulate with their wives frequently, not just while they are fertile."

Richard Prum in The Evolution of Beauty (2017 Doubleday) amplifies on this point: "I think a very powerful case can be made for the role of female mate choice in the evolution of the human species. Solving the evolutionary challenge of male sexual violence, coercion, and infanticide through an aesthetic remodeling of maleness would certainly have given females much greater sexual autonomy. But male deweaponization could also have been the key innovation responsible for the subsequent evolution of human social, cognitive, and cultural complexity. Less aggressive, more cooperative males living in ongoing relationships with females would have created an environment of greater social stability for their developing offspring, which in turn would have made possible the longer development times and greater investment in each offspring that were required for the evolution of all the qualities we prize as evidence of our humanness-intelligence, social cognition, language, cooperation, culture, material culture, and ultimately technology. This new view of human evolution requires much work to test, but the stakes couldn't be higher."

Bobbi Low (R427 67) in her own research also confirms that, in human cultures, one of the strongest indicators of polygyny is parasite stress. High pathogen stress accounts for 28 percent of the variation alone and with rainfall seasonality, irrigation and hunting adds to a total of 46 percent of the observed variation in polygyny. High parasite loads favour more careful investment in exogamy, involving on the males' parts wife capturing and seeking wife diversity by choosing partners at a genetic and/or physical distance and promoting genetic diversity in the offspring. Sororal polygyny is avoided. On the woman's side it is better to be the second wife of a healthy man than the sole wife of a parasite-ridden man.

Chris Knight (R383) is scathing of the evolutionary weakness of monogamy because of its sterility and lack of adaptive and social novelty in ape and other animal societies. He notes: "Among non-human primates, monogamy produces not advanced forms of sociability but a very elementary, simple and sparse social life, with little variety or political complexity to select for novel forms of self-awareness or intelligence. Compared with other primates, those which are monogamous appear to eat lower quality diets, have inferior ability to perceive social relationships, and have minimal levels of role differentiation. Moreover monogamous primates are known to be behaviorally more conservative and ecologically more restricted than their non-monogamous counterparts. ... Among non-human primates, in fact, a monogamous mating system appears to have been the least long-term adaptive value and it has been argued that this may apply to humans too." Kinsey (R377) elaborates "The lack of social networks is the major disadvantage of monogamy per se. Promiscuity does not normally occur in any human society but polygyny and polyandry taken together are much more frequent than monogamy. They encompass a greater extension of social networks than monogamy they have greater long-term adaptability and consequently they are more common. Probably the majority of cultures in the world practice some form of extended family in which the living group contains more than a single pair and their children." In considering human emergence, Carel van Schaik and Robin Dunbar (R164 62) have suggested a radically different basis for pair-bonding as a form of mate guarding to prevent infanticide. Gibbons are socially monogamous, partly because the females distribute themselves too widely for a male to form a harem or a fission-fusion society to form. Consistent with female territory rather than paternal care being a predictor of monogamy, the male does little in infant care although he is remarkable tolerant of juveniles. Their conclusion is that he guards his mate to prevent another male committing infanticide.

Helen Fisher in "An Anatomy of Love" (R209), advances a more flexible version of the monogamy-child care theory, which is not located so specifically early in time as Lovejoy's monogamy theory and is consistent with a later emergence with Homo erectus. She sees in the development of human sexual receptivity and reproductive inscrutability a human origin in which pair bonding had become strong enough that the frank promiscuity of our closest ape cousins had given way to a form of 'serial monogamy' important for successfully rearing increasingly dependent more slowly maturing human infants, lasting for around the four years required for the first offspring to become independent, weaned and able to join a peer play group. If a couple were incompatible or did not have further children, these bonds would frequently dissolve. Unlike people like Desmond Morris (R486) who see female receptivity directed as a monogamous service to males, she notes that monogamy does not imply fidelity and that, on the evolutionary evidence, women pursued a variety of covert affairs as an integral part of their reproductive strategy. This makes much more sense. As Ridley (R577) notes: "The use of veils, chaperones, purdah, female circumcision and chastity belts all bear witness to a widespread male fear of being cuckolded and a widespread suspicion that wives, as well as their potential lovers, are the ones to distrust (why else circumcise them?)" Given an established paradigm of concealed ovulation, monogamy could thus emerge on a 'daddy-at-home' basis, as a late comer, from greater needs for the 'father' to share resourcing, because of the delayed maturation of the human offspring.

Socio-sexual interaction has been proposed to be the prime generator of social diversity because it is the reproductive feedback process through which all other generators of culture such as toolmaking and language are utilized. Sexual paradoxi thus drives the resulting evolution of the human brain all the way to the Homo level because sexual paradox perpetuates all the way up the tree of increasing social and intellectual diversity (Miller 2000 The Mating Mind Random House). Robin Dunbar (R179) has demonstrated a consistent correlation between social group size and neocortex to brain ratio, across wide groups of primates consistent with brain evolution being primarily related to social complexity. Socio-sexual complexity is also reflected in the dolphin brain's equivalent complexity to the human organ.

Geoffrey Miller also notes (Ridley R577): "The neocortex is largely a courtship device to attract and retain sexual mates: its specific evolutionary function is to stimulate and entertain other people, and to assess the stimulation attempts of others. ... Just as the peahen is satisfied with nothing less than a visually-brilliant display of peacock plumage, I postulate that hominid males and females became satisfied with nothing less than psychologically brilliant, fascinating, articulate, entertaining companions" - the cultural equivalent of runaway sexual selection - no one can afford to select for anything else and survive.

We can surmise that in the evolution to Homo, females with a less pronounced cycle became more easily able to secure a 'monogamous' partner 'on safari' without attracting the attentions of the dominant alpha male. Covert ovulation gave the females more control over their choice of sexual partners, and provided steadier mates, because it required consistent sexual attention by a male to have any real chance of fertilization. This also favoured sub-dominant attentive males, who gained much greater chances for survival of their offspring. Menstrual synchrony (*R354*), would also make it hard for an alpha male to corral all the simultaneously fertile females in a group. We have seen concealed ovulation operates successfully in many mating patterns, so we can't attribute its occurrence in humans to monogamy. Hrdy (*R329* 158) has this to say of the transition: "A highly assertive female sexuality marked by a potential to shift from cyclical to situation-dependent receptivity constituted the physiological heritage that prehomimid females brought to this evolutionary experiment."

The human menstrual period is coupled to the lunar cycle in a way which is different from those of our close relatives. Chimps have a cycle of 36 days and bonobos a doubled cycle of 60 days (de Waal *R161*). The Barbary macaque's menstrual cycle is 31 and the Japanese macaque's is 28 days in duration (Shlain *R638* 177). Human cycles average very closely to the 29.53 days of the lunar cycle. About 28% of reproductively mature women show a 29.5 ± 1 day cycle length (Cutler et. al. *R142*). Vollman et al. (*R716-R718*) as well as Treloar et al. (*R696, R697*), have shown that women whose cycles approach the 29.5 day span have the highest likelihood of fertile cycles, while women whose cycles become longer or shorter have a proportionately diminishing incidence of fertile cycles.

Female receptivity for sex, manifested by swollen genitals, occupies a much larger proportion of the estrus cycle of bonobos and humans than of chimpanzees. The receptivity of bonobos continues through lactation. (In chimpanzees, it disappears.) This circumstance allows sex to play a large part in the social relations of bonobos. (Dahl, de Waal R161, King). Chimps have periods longer than the lunar-related human cycle (*R651*), although the bonobo half-cycle is very close.

This differs from the 28 day cycle ascribed to the human female and with it the 28 day menses composed of 4 weeks of seven days, 13 of which comprise a 364 day year'. However it is known from deep cave studies that the human circadian rhythm is about 25 hours, not 24, and yet the action of the melatonin cycle keeps it primed to the sun, so many of these primate cycles, including a slightly shorter or longer human cycle could still be held in lunar synchronization by a melatonin-induced non-linear pacemaker effect from the lunar nightly illumination cycle, provided there is exposure to natural moonlight fluctuations, as has been the case until recent times for humans. Coordinated phase relationships between reproductive rhythms and lunar rhythms are documented in the old-world monkey genus Cercopithecus, which includes vervets (Reiter *R572*).

There are a number of studies that both confirm and dispute the correlation of the moon's cycle and a woman's. The majority of them, however, confirm a statistically significant relationship. The largest, conducted by Walter and Abraham Menaker (*R468*), collected data on over 250,000 menstrual cycles in over 2,700 women. Their findings revealed that the average length was 29.5 days. Virtually all the studies have been conducted after the invention of artificial light, a fact that could influence each study's outcome. Sung Ping Law (*R400*) studied women in rural China, a group minimally affected by artificial light. Her published data strongly suggest that the link between the moon and menses was statistically significant. While Law finds menstruation occurring around the ideas of the new moon, Cutler et. al. (*R142*) working with US university students in a more urban situation claim that menstruation in the lighter part of the month close to the full moon. Criss and Marcum (*R138*) document that births vary systematically over lunar cycles with a peak fertility at 3rd quarter.

The lunar cycle and sex strike: Menstruation is associated with the dark moon, and the lightening moon gives good evening hunting. Sexual withdrawal is followed by the hunt, capped by the full moon, meat feasting and sexual favours.

Attention has also been drawn to the notion that gatherer-hunter societies may have exchanged sex for meat and that men may have hunted to gain sexual favours, supported by some older accounts of Southern Bushmen. We have noted that chimpanzees have recently been found to also offer sex for meat suggesting an ancient evolutionary origin.

Chris Knight (*R383*) has proposed that a critical development in human evolution running right through to the cultural phase has been an association between a sex-for-meat exchange between women and men, the moon and menstrual synchrony. In a frankly socialist interpretation of human origins, he suggests that menstrual synchrony, coupled to the lunar cycle enabled the females to exert a form of 'sex strike' in which the males were forced by the women to go 'hunting' in return for sexual favours. Given the human variation in cycle length and the mild and ambiguous coupling with the lunar cycle, the idea of a monolithically consistent sex strike strategy remains speculative, however it may have played a formative role in cultural motifs and had a major influence over the relationship between hunting, sharing and sexual favours in a social ebb and flow from celebration in the moonlight to the stark nights before the new moon. While menstrual synchrony does depend on a relatively non-competitive relationship between the females (unlike savannah baboons), Taylor's idea of it being a survival adaption to enable stressed acyclic women to prime themselves on more fecund womens' cycles (*R683 103*) is an evolutionarily unstable strategy. Neither does Desmond Morris's critique (*R488* 159) of sex strike that many of the women would be non-menstruating due to pregnancy and prolonged lactation compromise the validity of the reproductive argument.

Consistent with the idea of a sex strike is the nineteenth century anecdote from Smith's notebook (*R551* 322):
The theory of female cosmetic coalitions (FCC) is a new and controversial attempt to explain the evolutionary emergence of art, ritual and symbolic culture in Homo sapiens. It is proposed by evolutionary anthropologists Chris Knight and Camilla Power (Power, C. 2009. Sexual selection models for the emergence of symbolic communication: why they should be reversed. In R. Botha and C. Knight (eds), The Cradle of Language. Oxford: Oxford University Press, pp. 257-280, http://radicalanthropologygroup.org/sites/default/files/pdf/pubPower_JCS.pdf) together with archaeologist Ian Watts (doi:10.1086/666484). a. Females competing for good genes should avoid ovulatory synchrony. Moving from one female to the next, a single dominant male under these conditions can exercise a monopoly. Key: Circle = female. Pointer = ovulation. Triangle = male. b. Females in need of male time and energy should synchronize their cycles, preventing any single male from monopolising access. Figure c. Males abandon females once ovulation has passed. d. Females counter this problem by concealing ovulation and extending receptivity. e. Menstruation now attracts disproportionate male attention. f. Coalition members respond to this threat by controlling male access to the (imminently) fertile female. Figure g. To prevent males from picking and choosing between them, members of the coalition join forces and 'paint up'. h. "Wrong sex, wrong species, wrong time."

It is also consistent with Catherine Key's (R359) prisoners' dilemma analysis of human sexual relations (p 34), as reproductive investments shifted to the differential between smaller male and larger female reproductive effort with increasing head size, and slowed growth and development, and the ensuing need for females to cooperate to ensure adequate investment from the males through sexual control. Here males become non-reciprocal altruists partly in the hope of securing later matings. One of the strengths of the sex-strike sexual faking theory is that it addresses the question of why symbolic culture evolved, rather than simply how it did so, according to Robin Dunbar (Douglas R171).

Key notes that the presence of estrus females is the best predictor of hunting behaviour in male chimp, just as bonobo males give food for sex and subordinate baboons (Papio anubis) court favoured females in a harem in expectation of future matings. Key's Prisoner Dilemma simulations displayed complex system behavior with many strategies needed to be followed by players to survive the reproductive round. Females cooperated with females more than males and under reduced male reproductive effort. However when their reproductive effort was higher females could adopt a strategy of alternate deflection tolerating only non-reciprocal altruist males who offered consistent cooperation. Key notes also that women defect when playing the prisoners' dilemma more frequently than men.

Menstruation can be thought of as a 'no' signal replacing the 'yes' signal of overt estrus, but still implies fecundity overall. Camilla Power (R551) extends Knight's ideas directly into the use of ochre (p 94) as a symbolic substitute extending menstrual 'cheating' into the explosion of the cultural phase through the symbolization of the reproductive strategy.

The significance of menstruation and the moon are coupled in !Kung San (p 113), Hadza (p 131), and Sandawe rites (p 118). In the San eland dance during menarche, the girl plays the part of a bull, sending out a 'wrong sex, wrong species' signal. Meanwhile, the women of the camp dance around her as if mating with the bull, taunting the local men with their complete lack of interest in them. Power says: "The message to the males is absolutely clear - you go off, you hunt some eland, and then we'll see. It's a sex strike in all but name." The Hadza have a similar ritual called 'epereme', linked to symbolic menstruation and the new moon, associated with a mythical heroine who hunts down male zebra and wears their penises. The Sandawe have a corresponding fertility rite by the light of the full moon in which the women expose their buttocks invitingly to the men in the moonlight.

Leonard Shlain (R638) has extended the significance of menstruation in cultural emergence to development of awareness of 'deep time' over months and the idea of gaining control of one's destiny through women discovering the coupling of their reproductive cycle to the moon and its relationship with birth nine lunar cycles later - a gaining of reproductive power over men which was only later usurped by male control over female fertility and the natural productivity of the planet. However responsiveness to seasonal cycles in the brain is evidenced in the migrations of many species. Nevertheless intriguingly close links among the words for moon, menses, and time are present in every language. The English menses,- month, moon and measurement have their roots in the Latin words mens 'mind' and mensis 'menses' and the Greek word menos 'menses'. So, too, do 'mental'. 'meter', 'metric', 'mentor', 'diameter', 'commensurate', 'immensity', 'parameter', 'perimeter' and 'dimension'. Shlain associates this transition with difficulties in childbirth associated with an increase in head size and a transfer from overt ovulation to concealed ovulation with advertised menstruation as a timekeeper. As a laparoscopic gynecologist, he is aware of the increasingly heavy demand on women to replace the iron lost by menstruation (at least in some women) and speculates...
that this became a burden of this evolutionary adaption which placed women hostage to a degree to the need for a meat component of their diet supplied by the men.

Women's string-figure depicting "menstrual blood of three women", illustrating the Yolngu people's tribal mythology of menstrual synchrony Arnhem Land R383. "We Yolngu are a jealous people and have been since the days we lived in the bush in clans. We are jealous of our wife or husband, for fear she or he is looking at another. If a husband has several wives he is all the more jealous, and the wives are jealous of each other ... make no mistake, the big J is part of our nature".

There continues to be controversy over the status of both menstrual synchrony and lunar coupling. Martha McClintock's original research methods R453. have been questioned and other researchers have failed to replicate her findings. But both effects could be more predominant in cultures living with the sun and moon and coexisting in tribal bands. Differing evolutionary arguments have been made. One argument is that reproductive synchrony is a relatively common mechanism in animal populations through which co-cycling females can increase the number of males included in the local breeding system. Conversely, if there are too many females cycling together, they would be competing for the highest quality males; forcing female-female competition for high quality mates and thereby lowering fitness disfavoring synchrony. Differences of Neanderthal reproductive strategies from those of modern Homo sapiens have recently been analysed in these terms. Modern human female ancestors, less seasonally constrained, pursued a strategy of cosmeticization of menstrual signals. This Female Cosmetic Coalitions model accounts for the African Middle Stone Age record of pigment use. Among Neanderthals, strategies alternated. Severe seasonality during glacial cycles tied Neanderthal males into pair-bonds, suppressing cosmetic signaling. Only during interglacials when seasonality relaxed would Neanderthal females require blood-red cosmetics (Power C, Sommer V, Watts I 2013 The Seasonality Thermostat: Female Reproductive Synchrony and Male Behavior in Monkeys, Neanderthals, and Modern Humans PaleoAnthropology doi:10.4207/PA.2013.ART79).

Sapientia: Adolescent Adam and the Unbearable Beauty of Eve

The emergence of modern Homo sapiens, is accompanied by a slight decrease in brain size from an average of about 1500cc to 1400. Although this is well within the range of human variation between 1100 and 2000cc, it does suggest that some form of compactification has taken place. One view of this is that the development of culture and language has actually made it cognitively easier for the brain to assimilate the world around us. Another suggested by Matt Ridley (R580 34) is that a reduction of aggression may be accompanied by a neotonic (tending towards embryonic form) reduction of the limbic brain areas associated with aggression, which appear to be among the latest to mature. A similar argument has been made about the evolution of the bonobo by comparison with chimps. More extreme such reductions in brain size have been seen in breeding domesticated animals from the wild.

The oldest human fossils ever found outside Africa suggest that Homo sapiens might have spread to the Arabian Peninsula around 180,000 years ago - much earlier than previously thought. The upper jaw and teeth, found in an Israeli cave, pre-date other human fossils from the same region by at least 50,000 years. But scientists say that it is unclear whether the fossils represent a brief incursion or a more-lasting expansion of the species (Hershkovitz, I. et al. 2018 Science doi:10.1126/science.aap8369).

An in depth study into human origins (Schlebusch et al http://biorxiv.org/content/early/2017/06/05/145409, doi: 10.1126/science.1227721, doi:10.1126/science.aao6266) estimates, using ancient and modern genome data, including the benchmark genome of a boy from Southern Africa 2000 years ago, found that Homo sapiens originated as a genetically distinct species between 350,000 and 260,000 years ago. African populations branch in two directions and then further subdivide around 200,000 years ago. Non-African populations, appeared shortly after 100,000 years ago. A genetic split between the Khoisan and other Africans occurred roughly 260,000 years ago, shortly after humankind's origins and around the time of the Florisbad individual. Khoisan people then diverged into two genetically distinct populations around 200,000 years ago, the researchers calculate.

keleteral remains including skulls and tools from the Jebel Irhoud massif in Morocco, some 100 kilometers west of Marrakech first discovered in 1961 and dating of new finds in 2017 have pushed back the origins of Homo sapiens to 315,000 years ago (Nature 2017 546, 289-292, 293-296). The recent finds of Homo naledi noted above and of H. floriensis add complexity to this
picture. However it is also possible the Jebel Irhoud individuals lie closer to fossils from Spain dating to more than 800,000 years ago that belong to H. antecessor, an archaic population with facial morphology that resembles modern humans in many ways, so Jebel Irhoud might be either a hominins evolving into modern humans, or retaining facial morphology from an H. antecessor - like population that may have been the last common ancestor of Neandertals and later African archaic humans. Nevertheless, as noted below San Bushmen mitochondrial origins do go back 150,000 years when a division in San populations across the Kalahari occurred until around 70,000 years ago.

Human evolution stands at an extreme of animal evolution (Morris R487). Mammals are the most sexually polarized of animal classes because of the development of both uterine gestation and lactation. Human pregnancy is at a mammalian extreme. The difficulty of human pregnancy and delivery and the physiological affect on the female are unsurpassed. Although the human egg is tiny, the investments made by men and women in reproduction are very far from equivalent. The female has to make a genuine open and 'travail' investment, which continues long after birth in lactation and intimate child-rearing, while the male can simply impregnate and depart for greener pastures. While most women are selective about their partners, most men are prepared if given the opportunity to 'copulate with anyone bearing ovaries'.

The sexual evolution of the female human has become unique in many diverse ways. Female humans have evolved physically to become perpetually attractive to males, through continual receptiveness, able to make love 'in continuum', over prolonged periods, resulting in an intense sustained form of social bonding unparalleled in other socially monogamous species. These evolutionary characteristics involve the whole female body in such a way as to advertise ripe fecundity - fat-engorged breasts, hour-glass torso, larger buttocks. Despite Hrdy's demurring at Buss's 'patriarchal' emphasis on feminine beauty in sexual selection (R96), this uncontrollable beauty of the feminine form, which has obsessed artists, scholars, lovers and fearful religious patriarchs alike is an aspect of human sexual evolution which, like the female's choosy preference for 'declared' monogamy to a resourceful partner, rings true throughout our evolutionary and cultural emergence.

This is complemented by a sensuality capped by a profound female orgasm which is tuned for reproductive selection of highly desired partners, whether long-term, or a secret love tryst. Ovulation is cryptic mid way between menstrual periods, making it difficult for any male to be sure whether or not he has succeeded in the fertility quest without sticking around. The sexual act is pursued largely in privacy which makes it as hard as possible for others to trace the intimate details of who was present and what went on. Sexual relationship is intense and long-lasting and has the capacity to become an abundant and fulfilling life transaction which has a major role in establishing, a primary child-rearing resource in long-term partnerships with a male, as well as the thrill of the chase in a strange affair.

There is also a great variety of sexual development among individual women. By comparison with the peacock's tail as a powerful indicator of alpha male genetic prowess and little else, human females appear to have evolved sexual diversity as a signal to accomplished and desirable males that they are uniquely different, alien, alluring, exotic and erotic in the extreme, thus responding to the innate philandering polygyny of the male and the high variance in male resources, by evolving sexual variety as an irresistible enticement.

Human pregnancy is at an extreme of living species, leaving the female vulnerable and travail in her final months, with birth a major compromise to fit the human head through the birth canal, and lactation and child rearing expanded into a fully fledged cultural discovery process which takes more care and effort than any other species. This is complemented by a human male who can excel as 'dad' but which also betray as a 'cad', who may oppress as a 'despot', or come to the rescue as a temporary hero. This perpetuates a situation's sexual paradox in which neither gender has ultimate control of their own reproductive destiny.

Into this mix enters an evolutionary race between the clitoris and the penis, the clitoris becoming ever more demanding and the penis more satisfying - the principal instruments of emotional lust, love and togetherness, a glue cementing the human family, from which all our notions of passion, romantic and compassionate love emerge. The human penis is the thickest, and most hydraulic of ape penises, by comparison with the thin pencils of muscle and bone sported by other apes. Jared Diamond laconically complained of the great failure of modern science to come up with an adequate theory of penis length, suggesting it might relate to aggression displays with other males (Blum R66 31). This is matched by the time and energy involved. Humans make love for periods of ten minutes to half an hour or so. Gorillas barely manage one minute. With bonobos its over in fifteen seconds and excitable chimps barely make seven seconds. The entire species is founded on premature ejaculation.

The answer to the enigma of the penis according to Geoffrey Miller (2000 The Mating Mind Random House lies in its mysterious sister-spouse the clitoris. The apparently vestigial, but astonishingly powerful clitoris, despite its small size, has twice as many sensitive nerve endings as the penis. The clitoris and its hidden complement, the G-spot, now came into play in an evolutionary 'amatory race' with the penis, aptly described by Geoffrey Miller: "The penis evolved to deliver more and more stimulation, while the clitoris evolved to demand more and more." Both of these, according to Miller, were driven by female reproductive choice, the clitoris, which is not prominently displayed to male view and hence choice, unlike the estus, swollen buttocks and reflex pheromones of apes, as a discriminator of sexual love, and the penis as an indicator to, and satisfier of, women's mate choices. In fact female orgasm dwarfs that of the male in its capacity for extremes of ecstasy, body-wracked convulsions and multiple, or even continual orgasm, undiminished by the 'downfall' and refractory 'impotence' following male ejaculation. It is also, unlike the physical necessity of male orgasm for insemination, an ephemeral discriminator, of male ardour, never dependable but coquettish and precarious, depending on the mood of the moment, which does not serve the routine life of monogamous pair bonding so much as it acts as a sense organ of novelty and excitement - an evolutionary discriminator which separates the man who can really give the lady "all she desires" from the boys who shoot once and think they are king of the road. A central part of male sexual denial in the desire to sexually dominate is a vain attempt to deny the full flood of female ecstasy and its implications.

Richard Prum in "The Evolution of Pleasure" (Doubleday 2017) has made an eloquent case for the diversity of evolutionary processes from the courtship plumage and elaborate songs and reproductive routine of birds, through to human sexual anatomy and sexual pleasure being an aesthetic product of mutual mate selection. He suggests the clitoris and female orgasm is neither an evolutionary "spandrel" or relic simply derived from the developmental homology of female and male
sexual development, nor is it a directly adaptive process of natural selection as suggested by the "upsuck hypothesis", both of which have manifest flaws, but is rather a product of females finding sex pleasurable and in turn seeking sexual liaisons which promote behavior which reinforces sexual pleasure from their partners, thereby driving evolutionary enhancement of sexual pleasure in both sexes. This perspective transcends the arms race between the penis and clitoris cited by Geoffrey Miller, which also conveys a broadly positive view of sexual selection promoting mutually beneficial relationships between the human sexes.

Shlain (R638) describes 3 theories of female orgasm which sexologists and anthropologists have whimsically given the names Pole Ax, Upsuck, and Cuddles. Pole Ax is the idea that laying a women out with a powerful orgasm will cause her to lie down and keep the sperm in place ensuring fertilization in a bipedal upright species with a downward pointing vagina. Baker and Bellis (R38) have suggested that female orgasm, particularly the stronger variety which may accompany a passionate affair, may provide and ‘upsuck’ which selectively improves the chances of conception with the partner of choice. This in association with the tendency of women to be more prone to sexual activity during ovulation, with both their existing partners and others, could provide another partial explanation for its role in reproductive terms, which so far remains unproven. The third theory Cuddles, postulates that Mother Nature bestowed on 'Gyna sapiens' a multisynaptic orgasm to help a couple more thoroughly bond with each other through mutual great sex. However this is again a little naive in terms of their differing strategies and ignores the fact that natural selection has not seen fit to take this route in other socially monogamous species.

Mary Sherfey (R637) in "The Evolution of Female Sexuality" noted that "to all intents and purposes, the human female is sexually insatiable in the presence of the highest degree of sexual satiation". Despite being based on the now believed to be false notion of a primal matriarchy and having no clear evolutionarily rationale, Sherfey's view coincides with that of pre-Victorian Europe where female sexual precociousness was recognized in an "exuberant and inexhaustible appetite for all variety of sexual pleasure", (just as it is feared in the Old Testament and Amazonian societies). Kim Phillips in "Medieval Maidens" (R539) has noted that in old Europe mutual orgasm was deemed necessary for conception.

Infrared imaging: Female sexual arousal is accompanied by blood flow to the labia and clitoris just as it is to the penis. This is central to the nature of human courtship and bonding between the sexes (p.381) but does it also function to confuse or even diminish paternity certainty?

An interesting twist to this comes in the form of research in to genes we have lost that may characterize human emergence. In a fascinating paper in Nature looking for genes, or regulatory sequences, which have been deleted in humans that may make us different from other animals, the authors report that one of the prominent genes essential to the majority of mammals which has been deleted in humans is the androgen regulator for penile spines. Penile spines, even though they are smaller and flatter in chimps than those in cats and other mammals, nevertheless are accompanied by basal nerve fibres which across mammals may have many functions including increasing male sexual sensitivity, reducing the length of female estrus, removing competitors sperm and many others. In the paper and its follow up comments the authors point out that the loss correlates with the evolution of pair bonding in humans (McLean CY et. al. 2011 Human-specific loss of regulatory DNA and the evolution of human-specific traits. Nature 471/7337, 216-9). The bumps or papules that can appear on the glans of some human men are not neuro-sensitive spines, and have a different origin and basis.

Chimps and bonobos with neuro-sensitive spines have a very short copulation time of 5 to 7 seconds, hardly enough to keep a woman happy with her hubby. They also have a pronounced estrus unlike the concealed estrus in humans, which serves to minimize male knowledge of when to ‘make love' thus favoring social sexuality on a stable basis with a partner. So it looks like we have lost our penile spines so that we can make love in a way which gives women a convincing climax and gives both men and women a deep sense of bonding. Humans have also lost the baculum or penis bone which occurs in many mammals including chimps and bonobos, and have a consistently larger erect penis and smaller testes, consistent with...
human pair bonding through regular social sexuality satisfying to females as opposed to promiscuous sex at estrus, or to relieve groups tensions as in bonobos. Correspondingly human females have evolved permanently fatty breasts as part of their sexual enticement of male attraction and retained the capacity for ecstatic orgasm, whose role has become central to reproductive choice, rather than fertilization itself as in male physiology.

All in all the evolution of several aspects of the human male sex characteristics are consistent with the males having to give a genuine indicator of sexual fitness satisfying to choosy females making astute strategic decisions about who to copulate and form relationship with. Hence one might also conclude that this selection of male characteristics has been driven by women's preference for males who can really go the mile to make them feel fulfilled and bonded with, suggesting that female choice has driven human sexuality throughout our emergence.

By contrast, the Victorian era ushered in the notion that "the majority of women (happily for them) are not much troubled by sexual feelings of any kind" - a form of psychic female circumcision partly in concordance with the Darwinian awareness of greater reproductive variation and sexual competition in males. In response to Sherfey, Donald Symons (R678) comments "It is difficult to see how expending time and energy pursuing the will-o'-the-wisp of sexual satisfaction, endlessly and fruitlessly attempting to make a bottomless cup run over could conceivably contribute to a female's reproductive success" noting it would both interfere with food gathering and child care and even subvert female choice. This case is based on females having little variation in reproductive success and that copulating with many males cannot improve their reproductive success.

This has led to the notion that both female orgasm and the clitoris are 'spandrels' like the appendix and male nipples as Stephen Jay Gould speculated - evolutionary relics, or results of underlying sexual homology. Some support for the idea comes from twin studies in which there is a 32-45% genetic factor involved in the wide variation in orgasmic ability of women from 14% who always succeed, through 32% who only do some quater of the time to 14% who cannot reach orgasm either by sex or masturbation (Spector et. al. R655). ElizabethLloyd (R421) takes this case further, that like stump-tailed macaques and bonobos, female orgasm is more for female-female social bonding than reproductive advantage - a spandrel for pleasure, riding on the coat-tails of male evolution, extending this to questionable claims based on FGM (p.285). However the 'choosiness' of the clitoris, in coitus does not imply no reproductive advantage but high discrimination in reproductive choice.

Sarah Hrdy's (R329 - R331) view, offers an ironic twist, with formidable undertones. She proposes that females evolved an interest in promiscuous sex so that many males would 'presume' that they could have 'fathered' a female's child. Multiple male care for, or at least lack of harm to, her offspring would result, thus enhancing her fitness and offspring survival. Hrdy and others have also seen the human female's loss of physical signs of ovulation in this light: Concealed ovulation was naturally selected since it helped to decrease paternity certainty. Hrdy, despite extolling a life of monogamy herself, argues that paternal uncertainty was an advantage for evolving homind women, but that, as human society developed, males devised ways to increase paternity certainty (through exclusion of women, chastity belts, and so on), women lost their autonomy, otherwise at a high level among primate females, as a result of male success in increasing paternity certainty.

One should note that although human ovulation is concealed, males still find a woman more attractive during ovulation and can tell that the vaginal mucosae, rich with fern-like polymers to aid sperm transit are unusually slippery and attractive. Kuukasjärvi et. al. (R396) note that female body odours are more attractive to men during mid-cycle.

Her experience with primates (R339 160-180) has led her to realize that there are a variety of reasons why females may elicit sex with more than one male, both in the relative frenzy of estrus and outside it. These actions are both an expression of graduated female sexual choice, focusing on prime genetic partners towards the peak of estrus, from a wider range she entices beforehand and they serve her reproductive efficacy in claiming many 'fathers' thus helping to give her offspring the relative protection of the males in her vicinity and reducing risks of injury or infanticide - specifically by reducing paternity certainty! Notably human step fathers are 65 times more likely to kill infants (p.49). Noting the behavior of macaques and experiments on the stimulation of female rhesus monkeys, she has even gone so far as to suggest that the unique features we experience in female orgasm serve this promiscuous end, continuing after a male has completed his all-to-transient act of insemination and thus inviting the implied attention of more ardent suitors:

"What we know about primates suggests that prehominid females embarking upon the human enterprise were possessed of an aggressive readiness to engage in both reproductive and non-reproductive liaisons with multiple, but selected, males. What happened next is, and probably will always remain, shrouded in mystery. We can only document the attitudes prevalent in human cultures during historical times. There can be no doubt from such evidence that the expectation of female 'promiscuity' has had a profound effect on human cultural institutions."

This explanation is frightening, with dark undertones, explaining in one step why female sexuality is repressed caturezed and incised by a fearful patriarchy, perceiving that it reduces paternity certainty. Eighteen years later Hrdy (R330 222-3) plays devil's advocate to her own radical position, in the light of our excoriating patriarchal history.

"Female libido and sexual assertiveness are dangerous predispositions in such contexts, more likely to get a woman beaten disfigured or killed than to increase her reproductive success ... Knowing how risky extra-pair sex can often be for females in my own species has led me to wonder if female orgasms may be a once adaptive retention, now no longer selected for, like the grasp of a just-born baby for maternal fur that no longer exists, a reflex gradually fading out of the human repertoire".

Jared Diamond (R166) compares Alexander and Noonan's "daddy-at-home" theory with Sarah Hrdy's "many fathers" theory. Hrdy contrasts langurs, which have concealed ovulation with chimps which have overt ovulation, noting that overt ovulation is a rare (only 27 out of 175 primate species) evolutionary response to full-developed promiscuity, in which females mate with as many males in the troop as possible to avoid any of them having a reason to commit infanticide. Effectively this advertises to all "come and get me" for a gang bang while dealing with the matter effectively and quickly. By contrast, langurs have a single male in a harem and the females have concealed ovulation, again as a hedge against infanticide, because this makes it possible for the females to mate with a stray male outside the extended family without either her 'husband' or the 'gigolo' knowing whether she has gotten pregnant, or by whom. In more sinister terms it helps protect the female from infanticide
when stray gangs of males take over the harem and displace the protecting male. Sperling (R656) has claimed that, although Hrdy's vision of primate polyamory may be more acceptable to feminists, it is still based on unwarranted assumptions interpreting primate behaviors as end points, in evolutionary adaptations which are also more complex, varied, and context-dependent than sociobiological theory suggests. However this looks more of a case of denial of the disquieting roots of human culture which religious conservatives and gender feminists alike would seek to avoid, lest they throw their preconceived defences into disarray. Evolutionary ecologists maintain that social behavior, including that in humans, is influenced in subtle but fundamental ways by natural selection, fitness and sexual selection without the hard-line genetic determinism of earlier sociobiologists.

None of this complex picture of polyamory amidst social monogamy in humans implies that fidelity reigned, even if emerging Homo was predominantly patrilocal like other apes and pair-bonding was a strong feature associated with the needs of slowly-developing infants. Human males have medium sized testicles and killer sperm consistent with moderate sperm competition, but less than those of the larger ejaculates of promiscuous chimps. As a proportion of body size human testicles are five times the size of gorillas and one third the size of chimpanzees (Ridley R580 21). In the Cosmopolitan survey of 1980 half of married women under 35 had been unfaithful and 70% of those over. Likewise for men sewing wild oats is accepted as natural. Human males are about 10% larger than females consistent with moderate polygynous competition, but not the large harems of gorillas. Men are more aroused by images of males competing for a female than readily available females and produce better sperm after watching such images (Biology Letters doi:10.1098/rsbl.2005.0324).

Sexual privacy in humans is a complex process which seems to be driven by both male and female strategies. In primates where there is strong male competition such as orangutans and gorillas, alpha males copulate openly, but subordinate males are so discrete that no one realized they did at all until genetic paternity testing came along. Female dominated bonobos by contrast have sex openly, while chimps have an overt estrus in which the dominant male clan have sex openly, but females may also go on discrete safari with select males.

Humans have a complex sexual history. Women have won some control from men by evolving concealed ovulation and continual sexual receptivity to confuse paternity (Ethology and Sociobiology, vol 14, p 381) which gives the females an incentive to also seek privacy for sex to give more freedom of choice without consequences such as infanticide. Humans have also evolved to engage in pair-bonded parenting, with the emotional bond of love entering into the sexual equation and the stakes becoming even higher for discovery of infidelity. For human males sex becomes a precious commodity and to avoid jealousy and envy for one's own male mates it is easier to be discrete in the same way people conceal food in a time of famine.

Clandestine copulation thus becomes an intriguing male-female trade-off in which relationships are strengthened but infidelity becomes easier enabling us to be socially monogamous but not sexually monogamous in a context where frequent social sexuality is the emotional glue of familial relationships (Human nature: Being clandestine New Scientist 23 April 2012 Bob Holmes and Kate Douglas).

Into this arena falls the highly contentious question of whether human male acts of sexual coercion also have a biological basis, or are a cultural expression of male power and patriarchal dominance (p 47). While some authors such as Thornhill and Palmer (R690) argue for a sociobiological basis, others in reaction (Travis R695) see the question of rape as at the very least a multi-disciplinary issue. This is clear from our studies of slavery and concubinage (p 195), where forms of effective male coercion have become institutional, however one can also argue that these are obvious expressions of sexual sociobiology. Moreover rape is rare in our primate cousins with one notable exception. In one study almost half the copulations in an orangutan troop happened after fierce female resistance had been overcome by the males ( Sparks R654 153). Immature male orangs, which have a distinct phenotype (p 33), use sexual coercion as their main mating strategy. Baboon males also engage in aggressive sex which appears reluctant on the part of the female (R654 156). Jolly (R346 80) comments that real rape is very rare in primates besides ourselves and orangutans but that it is natural in humans, although whether it is inevitable or right is a separate question.

Human females have a more heavy reproductive commitment than almost any other species, with massive pregnancy, difficult childbirth, and a period of vulnerability after lactating, with a small infant on the hip. To spread their massive out-front investment it is essential for virtually every species for the female to be able to exert genuine female reproductive choice. When reproduction depends also to some degree on the partnership and resourcing of a male, this involves a dissonance between the resources of the partner and the best genes available. Both humans and colonial monogamous birds solve this dilemma by investing about 80% in their overt partner's genes and up to 20% in those from covert af.

Human nature: being clandestine New Scientist 23 April 2012 Bob Holmes and Kate Douglas.

Barash and Lipton (R41 154) note the irony of how universal jealousy is in males, even more so in those whose beliefs are towards promiscuity: Wilhelm Reich the imprisoned founder of 'orgone' sexual energy therapy insisted in his work and writings that monogamy was an unhealthy state for human beings, undermining their sexual health and stunting their emotional lives. Yet his wife reports that Reich was often insanely jealous:

"Always, in times of stress, one of Reich's very human failings came to the fore, and that was his violent jealousy. He would always emphatically deny that he was jealous, but there is no getting away from the fact that he would accuse me of
infidelity with any man who came to his mind as a possible rival, whether colleague, friend, local shopkeeper, or casual acquaintance."

Polygyny is practised in the 85% of human societies which permit it pretty much to the extent which differing male resources allow. Distribution of wealth occurs in a roughly inverse cubic law, so one in eight men has the resources of twice the average male and can support two wives. Although there is often jealousy and dissension in polygynous partnerships, some women decide that it is better to be a second wife of a well-appointed male than dependent on a poor, or a genetically, physically, or intellectually disadvantaged man with few, or no resources. Although the fertility of a polygynous wife may be on average lower than a monogamous one, the principal wife is likely to gain a higher fertility (Hrdy R329 133). By contrast overt polyandry is almost unknown, occurring only in 0.5% of societies, and then only to retain family land ownership. In addition, genetic testing confirms 4-30% of ostensible children of a given father in human societies (p 93), and 10-20% in monogamous colonial birds are the offspring of a secret affair, confirming that monogamy is 'social', as biologists state. There is a peak in human divorces around the time a single child would become able to fend for itself in a social grouping when they can run and talk (Fisher R209). Humans are thus serially monogamous for a time phased to carry out our basic reproductive function, in this way producing a majority of our offspring.

Many writers gloss the question of monogamy and its alternatives with their own orientation. Male researchers tend to stress the 'seeking wild oats in young buxom fertile women' scenario while female writers veer towards a plea for monogamy, or serial monogamy, on a resourcing basis. Geoffrey Miller (R475) espouses the role of a resourceful lovabe male who extols mutual mate selection while espousing sexual selection and its inevitable reproductive choice (and hence infidelity), as central to our cultural flowering. In being so affectionate to monogamy he looks ever more like a leeking grouse strutting ever-so-astutely on the human stage of sexual charisma. From her side Helen Fisher conveniently champions a short four-to-five year serial monogamy and separates monogamy from fidelity, thus bringing into swing all sorts of strange affairs characteristic of unfettered female choice, keeping the field wide open for female reproductive 'inscrutability'.

Sarah Hrdy (R330) quite rightly homes in on the parental aspects of reproductive process as equally essential to reproductive efficacy, as is sexual choice, in espousing the need to emphasize infant survival and its flip-side - infanticide in social relationships. She also advances a role for allo-parenting - the extended family help of daughters, grandmothers etc. with child support, rather than a dependence on 'monogamous' male partnership in human evolution. It is important to take this into account as it occurs in various forms among mammals and primates and is a human cultural motif which is prevalent or even predominant in some cultures. It extends to the historical epoch in beena marriages of biblical times typified by Jacob's sojourn with Laban. It also reflects the very significantly lower paternal investment made by men in many cultures, although many of the founding cultures we know of from Africa do have affectionate fathers (p 109), (p 124).

Hrdy's evidence for obligate allo-parenting (R330 90), where its role is critical to infant survival comes only from "many species of birds, and about 10 percent of mammals, including a tiny fraction of primates (humans and a few species of monkeys and prosimians that bear multiple young)". However she notes (R329 97) that in many primate species, including squirrel monkeys, howlers, vervets and colubines, mothers readily give up their newborns to the attention of others. A newborn langur may spend half their first day with other females. On the other hand baboons and rhesus monkeys refuse to give up their infants for some weeks. This sharing offers advantages of unencumbered foraging and additional protection and even, in an emergency, adoption. It also gives young females, who have not given birth, a chance to learn infant care. However it also involves negatives. In macaques and baboons where there are several competing matrilines, high ranking females may take infants of low-ranking females and injure them or refuse to give them back, causing them to starve (R330 52). Young females may not be fully competent and drop their charges. The recurrent observations of abuse suggest not all females who borrow infants are doing so merely to care for them. Most allo-mothers are also exploiting their charges in some way, using them as pawns in social interactions or as props to practice maternal skills (Hrdy R339 98, Low R427 187).

Allo-mothering does not occur in apes, and so cannot fairly be advanced as an evolutionary strategy in the transition from apes to Homo, except as a human innovation. Chimp females do not release their offspring to the care of others even older siblings (Hrdy R330 161, 502), and have a 5 to 8 year gap between pregnancies (Jolly R346 362) (5 to 6 years for bonobos) so do not have the repeated reproductive pressures of many cooperative parenting species such as tamarins who have multiple births. Chimp mothers only resume estrus after lactation stops at three to four years, although this is not true for bonobos (de Waal R164). While chimp mothers often wander alone with infants, a strategy of defence against infanticide, bonobo mothers with coalitions which make infanticide an unknown rejoin their group immediately after having given birth and copulate within months. The closest we come to such activities in apes may be male games with infants in bonobos (Endomo, R194). Like reciprocal altruism, allo-parenting is not just an issue of mutualism but of trusting interdependence. On the other hand there is good evidence in human society for a relatively high degree of mutual help with child care among families, particularly in matrilocal and or matrilineal societies, but also in patriarchal societies where there is adequate access and contact between maternal kin, and where there is respect for the bond between a first time mother and her maternal grandmother as in the Ikung.

One explanation for human menopause is that a slowly maturing, long-lived species may gain an evolutionary advantage from a 'biological clock' which causes a female who has reached the age where her children have offspring to enter menopause and to invest in the welfare of her children's offspring rather than her own - the grandmothering hypothesis. Chimps, unlike Humans (p 348) remain fertile until too old to bear pregnancy. Kristen Hawkes (R302, Blurtion Jones, Hawkes, et. al. R67) has put forward evidence from groups such as the Ikung and Hadzda. A study (Lahdenpera et. al. R397) of 2,800 18th and 19th century women has confirmed that they had two extra grandchildren for each decade they lived after 50, confirming a selective advantage for grandparenting resulting from the help and experience received. Orcas share this menopausal biology, with females living to 90 yrs and taking a lead role in group salmon hunting, unlike males which live on average to about 40 and whose survival is adversely affected by the death of their matriarch (Current Biology, DOI: 10.1016/j.cub.2015.01.037).

However there is no such advantage for grandfathers. The same type of historical research in Finland has shown that fathers with only one wife provided no benefit to their grandchildren. Neither did men who sired more than one family. Only widowed
men could remarry, and if they had children with their new wife, they fathered more kids, on average, than men who married once. But ultimately remarried men don't end up with any more grandchildren. The presence of a grandfather tended rather to be associated with decreased survival of grandchildren - possibly because the children of the first mother lose out on food and resources that go to the second mother's kids. The researchers then compared the lifespan of men from polygamous countries with those from monogamous nations taking careful account of collateral factors and found that fathering more children with more wives leads to increased male longevity - suggesting that polygyny is at the root of male longevity, rather than it being simply a free-ride effect of the genes for female longevity (Callaway E 2008 Polygamy is the key to a long life New Scientist 19 Aug).

Trends is the proportion of individuals living to an age consistent with grandparenting (Caspani Rachel 2011 The Evolution of Grandparents Sci. Am. Aug)

It has been debated whether the rise of grandparenting has a genetic or cultural origin bearing in mind that cultural factors can also give rise to genetic changes through selective sweeps under the unique selective regimes cultures create. Archeological evidence based on tooth wear, secondary dentine and tomography indicate the proportion of individuals living to grandparenting age for their populations expanded only recently in evolution and might have a cultural basis. However menopause, which is not shared by chimps suggests an older origin, particularly bearing in mind that the mitochondrial evolutionary tree of the Bushmen goes back some 140,000 years, rather than the 40,000 years associated with cultural emergence in Europe.

Judith Rich Harris (R293) also stresses the importance of horizontal peer groups in human development as opposed to the manifest vertical importance human societies pay to kinship and family parenting. Although these horizontal and vertical influences are largely complementary in any society, as we have noted in the prisoners dilemma, peer groups form an extension of the allo-parenting concept, as children mature. Human families and extended families are well positioned to gain help from existing daughters, as well as siblings, uncles and aunts. Humans also engage in more complex reciprocal and mutual relationships than any other species and social networking, even in the face of patriarchal dominance appears to be a central aspect of how human females maintain a state of relative autonomy, even under repressive conditions. Given the relatively low level of paternal investment in infant care in most patriarchal societies, such factors are certainly no less important.

Ironically, Hrdy gained this perspective in a climate of anxiety about her own absences and the allo-parenting of her own offspring (which she fittingly (62) calls "the day care factor") by a paid care-giver, while she was engaged in field studies, and her husband was occupied in a medical practice, placing her in a privileged position, not dissimilar to a tamarin mother. The allo-mothering issue is thus close to home and by no means entirely objective, although it is a dilemma of maternal ambivalence shared by many women in attempting to resolve the Hamiltonian prisoners' dilemma of the mother-child relationship:

"One angle to the story had to do with women who combined motherhood with demanding careers, a reasonable line of inquiry since my daughter had just been born ... No doubt Trivers spoke straight from the heart when he told the reporter 'My own view is that Sarah ought to devote more time and study and thought to raising a healthy daughter That way misery won't keep travelling down the generations'. Needless to say these off the cuff remarks, which cut straight to the heart of feminist wariness of evolutionists were prominently published. Here was not just a reference to inter-generational transmission of bad mothering ... this was a reference to the ghosts in my nursery. Was I offended? After all my daughter's father was an infectious disease specialist working long hours and Professor Trivers, also a father was just as consumed by his work as I was in mine. Clearly in addition to the assumption about what infants need, there was an assumption being made about precisely who should meet those needs. Progenitors of one sex only had to realign their priorities to prevent 'misery' passing down the generations. At the time though, the unfairness of this logic was far less riveting than my own nagging anxiety lest 'Trivers was right'... vocation or reproduction. Twenty years later I still return to this topic with trepidation (Hrdy R330 490).

Anne Campbell (R103 250), perhaps as a result of dealing with female competition and girl gangs, give a more prosaic gloss: Polygyny is a system that has been and is practised in many societies but it is one that most women have resisted (it generates strong conflicts of interest between co-wives) and while men may have envied polygynists, democracy has meant that their envy has ultimately overthrown the system. It is not democracy, but Christian anti-sexual morality that has outlawed polygynous marriage in the Western world. Monogamy seems to have won for now.

Campbell's work has upset some evolutionary psychologists and those who believe that the world would be at peace if women were in charge. "Good male partners can be very thin on the ground [in US inner city gang areas] - male mortality is high, many men end up in jail, and the ones who are successful will often leave the neighbourhood," she says. Here the most desirable men are often gang members who have money and status. "They can provide for their girl, but since they're spoilt for choice, they can also afford to treat the girls quite abusively," says Campbell. "Yet, because of the intense competition for male partners, girls tend not to band together to teach those guys a lesson, but take it out on each other - especially on the new girls." She takes a more detached view. "Even though biology may help us understand where some of our more unpleasant tendencies come from, it never prescribes how things ought to be," she says. "On the contrary, I think understanding why people may feel or act this way may help us to deal with it" (Vernimmen T 2015 Gentle sex? Females just as feisty as males over reproduction New Scientist 25 Jun).
She goes on to cite the experiment by Holland and Rice (p.16) which forced monogamy on normally promiscuous house flies. This demonstrated that their usual arms race of semi-toxic male semen and female immunity resistance waned, leaving the females defenseless to the toxicity of natural males and the males unable to compete. It also showed that the monogamously sequestered flies had more successful offspring under these artificial conditions. This is placing monogamy in double jeopardy - it is not an evolutionarily stable strategy in house flies and enforcing it is causing the loss of adaptive characteristics. Should we all seek stricter morals to increase the human population at risk of losing our own adaptability and creative ingenuity?

Bobbi Low's (R427) study in "Why Sex Matters" considers human marriage patterns best fit a form of serial monogamy, but classifies humans as 'slightly polygamous', based on the manifest differences in variance of reproductive potential between men and women, noting (55): "Most societies with a one-spouse-at-a-time rules would be called polygynous in a biological definition." Deborah Blum (R68 110) admits Low's evidence: "In the United States though, she suggests we maintain a kind of informal polygamy. The overall pattern in America is that more divorced men than divorced women remarry and when they do remarry, more of the divorced men begin new families ... it turns out that we in the United States look more like polygamists in general, than serial monogamists". However she then envisions hopefully (109-125) that we are 'travelling toward monogamy' - going so far as to identify monogamy with 'equal parenting partnership': "If we want to define ourselves as a monogamous species, then we need to accept all the biological implications" - namely equal parenting family values in which both partners 'bring resources, love and affection to all aspects of marriage' - this said from a position of a career marriage in journalism where a 'traditional' set of sex roles is sine qua non 'inappropriate'.

Sexual double-think in Western society. Left the typical pattern of serial monogamy: adventure, betrayal and divorce is really a cover for male polygynous desires, covertly expressed in the lone polygamous courting alpha male underwear among a 'harem' of bras and panties (right).

Barash and Lipton (R41, 153) in "The Myth of Monogamy" sum up this complex situation:

"Having looked, although briefly, at the diversity of human mate-ships, what can we conclude? For one thing, it seems undeniable that human beings have evolved as mildly polygynous creatures whose "natural" mating system probably involved one man mated, when possible, to more than one woman. It is also clear than in societies that institutionalized some form of polygyny, monogamy was nonetheless frequent, although, for men at least, this typically patterns of monogamy, ranging from frequent extramarital sexuality, conditioned and sometimes even encouraged by the social code, to occasional affairs, frowned upon but not taken very seriously, to rigid monogamy, jealously and violently enforced ... although even here it seems likely that the rules of absolute sexual fidelity are often violated, in secret. Certainly there is no evidence, either from biology, primatology, or anthropology, that monogamy is somehow 'natural' or 'normal' for human beings. There is, by contrast, abundant evidence that people have long been prone to have multiple sexual partners. In a sense, however, even if human beings were more rigidly controlled by their biology, it would be absurd to claim that monogamy is unnatural or abnormal, especially since it was doubtless the way most people lived, most of the time ... even while men strived for polygyny and women (as well as men) engaged in EPCS (extra pair couplings). This is clearest for men, if only because polygyny has often been institutionalized-and, thus, proudly displayed by the male 'winners' - whereas EPCS among Homo sapiens, as among most living things, have been much more covert, because of the costs of disclosure. Nonetheless, male philandering would never have become part of our biological heritage if women did not permit some men, at least on occasion, to succeed in their quest for EPC. Which is to say that, whether officially polygynous or monogamous, women-perhaps no less than men-have long sought extramarital lovers. What makes human beings unusual among other mammals is not our penchant for polygyny but the fact that most people practice at least some form of monogamy."

Barbara Smuts' (R651) ideas of the evolutionary origins of patriarchy, or male dominance begin with the same assumptions, that nonhuman and human primates seek to maximize their fitness and that males and females have different reproductive strategies. In short, males go for 'mate quantity' whereas females pursue 'mate quality'. Smuts is quite explicit about not seeing human behavior as 'genetically programmed' and argues that "natural selection has favored in humans the potential to develop and express any one of a wide range of reproductive strategies, depending on environmental conditions". Smuts focuses her attention on male aggression against females and female resistance to this aggression - that males are aggressive against females in order to mate with them, to pursue 'mate quantity'; but females, following their own reproductive interests, can and do resist. At the same time, there is variation in the extent to which females can successfully resist male aggression. Consideration of the numerous factors that may be involved concerns females' ability to resist male aggression by forming alliances with other females against males. Among the many primate species in which females bond together, this strategy works quite well. Among others, such as the common chimpanzees, females disperse at maturity to join new groups where they do not have female relatives to protect them. Among the bonobos, females disperse out but are also able to form alliances with unrelated females in the new groups. Thus, among common chimpanzees we see relatively high levels of male aggression against females, whereas among bonobos male aggression is successfully resisted and males do not sexually coerce females. Applying the same logic to human evolution, she proposes that the prevalence of patriarchal residence in human societies means that women are often deprived of the support of female kin and allies, leaving them more vulnerable to male aggression "In pursuing their material and reproductive interests, women often engage in behaviors that promote male resource control and male control over female sexuality. Thus women, as well as men, contribute to the perpetuation of patriarchy". Here Smuts suggests that in some circumstances women can facilitate their own reproductive success not so much by allying with other females as by allying with mates who command more resources and by complying with customs that increase paternity certainty, promoting patriarchy. Smuts is correct in that cultural developments appear to have developed strategies of reproduction which have acted to enforce male domination to the detriment of sexual paradox. Human
society is integrally complex and responds both to evolutionarily acquired traits and cultural interaction in choosing complex forms of social adaption (Stone R667).

Steatopygous fat buttocks are shared by some !Kung genotypes (Low R427, Hrdy R330) and the paleolithic 'Venus' figurines such as Lespugue (right). Among the !Kung (then called Hottentot), Darwin's informant reported, a truly sexy woman was one who was unable to rise from level ground because of the weight of fat on her buttocks (Low R427 81). Unlike apes, human babies are usually born with a healthy store of fat. Mothers also accumulate reserves of fat on the breasts and buttocks to provide for, and indicate fecundity (Hrdy R330 126).

Gatherer-hunter societies with ancient roots, as well as most current societies show a spectrum of relationship patterns in which monogamy predominates, adultery is frequent and in addition to sewing wild oats, outside the Christian sphere, up to 15% of men who have the resources to support two families are in polygynous marriages. Serial monogamy accentuates this polygynous tendency. The possible sperm retention of female orgasm, occurring simultaneously or subsequent to male ejaculation and the fact that women having affairs frequently mate close to ovulation and have a predominance of powerful retentive orgasms all attest to an evolutionary basis for 'infidelity'. Even if an 'unfaithful' woman has sex more often with her husband, she is still more likely to conceive by her lover. On the male side, sperm competition supports the same conclusion. Men also make larger ejaculates when they are away from their wives during the day, again indicating sperm competition. The evidence of genetic testing suggests up to 30% of offspring of ostensible fathers (with a possible average figure around 4%) are sired covertly by another man confirms female reproductive 'inscrutability' is likewise operating at a steady level (Bellis et. al. R56).

Concealed ovulation empowers the potential mother, both in long-term relationship, by keeping the daddy around, and the strange affair, by enabling covert infidelity and encouraging other men to consider themselves possible fathers, as long as this doesn't result in public accusations of 'loose promiscuity'. It thus entices toward monogamy, while promoting female reproductive choice. Given menopause and the much higher female fertility in the years after menarche, the higher mortality rate of young males and the male desire for fertile partners, rather than the resourcing and protection women seek, older men tend to seek young nubile partners they believe can produce the offspring they themselves are unable to. It is thus easy to see how female beauty becomes a biological indicator of fitness, with all the evolutionary manifestations of fecundity, in breasts, buttocks, hour-glass waist-hip ratio and the accessory features, including bodily symmetry which epitomize female beauty and which a variety of evidence shows is a genuine indicator of genetic fitness and a key indicator of reproductive potential.

Female concern for physical beauty as a reproductive asset is attested to throughout archeological history from the ochre and beads in Blombos cave (p 94), ancient venus figures and jewelry at Dolni Vestonice to the mirrors and jewelry at Catal Hüyük. While male Paleolithic art focuses on the prowess of the hunt, female representations are of fecund anatomy as in the lunar Venus of Lauselle (p 174). Notably the venus of Willendorf has been associated with the 'string revolution' of Elizabeth Barber (Adovasio et. al. R792 177-183) as she appears to be wearing a textile 'cap' rather than a head of hair. Needles were inveted by 37,000 BC (ibid 212) and weaving appears at Dolni Vestonice (ibid 181).

The significance in Homo sapiens of the unique features of female sexual evolution is enshrined in many of our founding archetypal myths, including the Fall from Eden in Genesis, where it is Eve's natural beauty which is tragically linked to her earthy temptation:

Eve was said to be so beautiful that no one could look upon her.
For her the sun and clouds would arc into a rainbow
the flowers would bloom where she walked
and the birds burst into spring song (Kabbala).

The relatively smaller reproductive investment of the human male in each offspring than the female favors polygyny, various of forms of which are common from hunter-gatherer bands through the Jews of Old Testament times to many modern cultures, including the Islamic world. A male will tend to seek to fertilize several females to broaden his reproductive potential, simply because he lacks the power for autonomous reproduction and must invest in mating strategy and less-direct child support. An astute female may in turn seek covert adultery to be fertilized by a highly-regarded, manifestly fit or histocompatibly exotic male who is not her immediate 'domestic husband' to seek the 'best of both worlds' - genetic and resource-bearing. Women prefer men with complementary histocompatibility (giving off an exotic pheromones) when ovulating, but revert to preferring familial antigens when on the pill (mimicking data on mice during pregnancy). The newly recognized VNO organ of smell appears to be specific in sensing for such physical nuances. The pattern is in this sense 'cooperative' between the genders as a reproductive strategy shared by humans and monogamous birds, in the prisoners' dilemma of sexual paradox, except when it is repressed, e.g. by draconian male suppression of female infidelity. Such 'moderate infidelity' is indicated by the existence of 'kamikaze' blocking sperm in humans, the intermediate physiology of human testes between the promiscuous chimp and polygynous but non-promiscuous gorilla, the sperm-retentive nature of female orgasm and the concealed estrus itself, which is clearly a form of 'evolutionary female empowerment' consistent with it evolving in a context in which female sexual choice has been an ongoing reality, putting the female in Matt Ridley's words 'one step ahead of the male'. It is also consistent with the privacy of sexual relations, which make it difficult to detect covert infidelity.
In hunter-gatherer societies, the male opportunist streak would have been far more easily satisfied by adultery than by polygamy. In most gatherer-hunter societies it is uncommon to find a man with more than one wife and very rare to find a man with more than two, but wherever adultery has been looked for, it is common. By analogy with monogamous, colonial birds, therefore, one would expect to find human beings practising either mate guarding, or frequent copulation. Richard Wrangham has speculated that human beings practise mate guarding in absentia. Men keep an eye on their wives by proxy. If the husband is away hunting all day in the forest, he can ask his mother, or his neighbour, whether his wife got up to anything during the day. In the African Pygmies Wrangham studied, gossip was rife and a husband's best chance of deterring his wife's affairs was to let her know that he kept abreast of the gossip. Wrangham goes on to observe that this is impossible without language. So he speculates that the sexual division of labour, the institution of child-rearing marriages and the invention of language - three of the most fundamental human characteristics that we share with no other ape - all depended on each other (Ridley R577 220).

On a counterpoised tack, Chris Knight (R383) and Camilla Power (R551), (p.77) have suggested that the lunar and menstrual cycles became locked into the strategic relationship between the sexes in terms of a meat for sex exchange in a real, or imputed 'sex strike' by the women, associated with inducing the men into resourceful hunting and with maintaining female reproductive choice over the men around 500,000 years ago, when brain size started expanding rapidly in the form of a phase of sexual withdrawal. This is in line with Catherine Key's Prisoners' Dilemma analysis (p.34) of the shifting reproductive investments towards greater female commitment, given both increased risks and difficulty of delivery and longer child-rearing with a slowed neotonous infant growth pattern as part of an adaption to the larger brain size within the constraints of cervical delivery. Camilla Power (R551 310) proposes that women extended any patterns of lunar menstrual synchronization by faking the signs. She suggests that menstruating women would have become a threat to other females by attracting much-needed male attention, particularly when menstruating women were rarer as a result of pregnancy and anovulatory demand breast feeding (p.107). So women who were nursing and pregnant took control of the situation by feigning menstruation. What began as impromptu borrowing of one another's blood or using animal blood became ritualized culturally in the use of red ochre. She points out that the word 'cosmetics' comes from Greek, cosmos, or order. "In traditional cultures cosmetics are not mere frippery. They define who belongs to which group, who can touch who, and who can mate with who. The regularized use of cosmetics as a sexual signal could even have been the thing that marked off modern humans." So perhaps lipstick is not just the key to culture, but also to the origin of our species. Ian Watts' study of 74 sites in southern Africa dating from more than 20,000 years ago, including Blombos, reveals an explosion in the use of red ochre and other red pigments between about 100,000 and 120,000 years ago (Douglas R171). Findings in Zambia and the re-dating of Border Cave in South Africa (Villa et al. 2012 doi:10.1073/pnas.1202629109 ) may push the date of the earliest use back to 170,000 years ago. Some have yet to be convinced about the symbolic purpose of ochre and say the use is rather to do with preserving animal hides. Chris Henshilwood suggests the shells were jewelry or for accounting and associated with peoples such as the San. Independently from the suggested link between ochre, menstruation and sexual control, the early appearance of cultural forms in cosmetic and jewelry suggests females had a formative role in the emergence of culture. Timothy Taylor (R683) questions why ancient cosmetics should apply to women rather than men, since men like peacocks are the more competitive sex, but a simple argument based only on male reproductive competition ignores the manifest complexity of human sexual selection by both sexes.

Briffault (R76 v3 572) sees the relationship between woman as danger, menstruation, and the moon as universal to our cultural origins:

"The maleficient, or more properly speaking, the dangerous and dreaded character which is ascribed to women extends ... to that celestial body which is everywhere intimately associated with women, namely the Moon. The tabu with which the menstruating woman is invested attaches to the cause of menstruation also." (583) The Moon is the regulator and according to primitive ideas the cause of the periodical functions of women. Menstruation is caused by the Moon; it is a lunar function, and is commonly spoken of as the 'moon'. It is frequently regarded as being the result of actual sexual intercourse between the Moon and women. ... The Maori expressly affirm that 'the moon is the husband of all women', and that their mortal husband is only as it were a subsidiary co-husband. The 'heitiki' which represents a foetus ... was said to have been given to the women by the Moon. The situation is similar with Soma the Moon God. In Persia the moon is keeper of the seed of the bull as the Moon and its crescent shape is associated with the bull's horns. Sin the Moon God is also a bull who sought to renew the seed of royalty eternally. The Moon is in this role primally male preceding its association with the Moon Goddess (592).

The social pattern of overt monogamy and covert adultery is common to all socially-monogamous animals which gather together in close communities and have a degree of resource dependence on a male to assist in child rearing. Adultery is thus a biologically important contributor to the genetic diversity and genetic fitness of humanity. (Fisher R209, Ridley R577, Watson
The two sexual hormones are also intimately interwoven (p 347). Women also have circulating testosterone and have been found to become resilient to stress when given small traces of testosterone analogues and to respond to pornographic enticement with a testosterone burst of 80% over background, compared with a similar male burst of 100%. Complementing this, males require estrogen to be fertile (p 349). Progesterone is likewise present in both sexes and has a pronounced daily fluctuation in men peaking in the evening when love-making is common (Science面前Americal Jan 94 103). Men also respond to female ovulation, with increased testosterone levels, although it is largely concealed, and the men may not consciously recognize they are doing this. It may even be that they are responding to the women's tendency to engage sex more often and passionately around ovulation. There are also indications that women prefer men with marginally more female characteristics, suggesting a Dionysian direction of human evolution, consistent with the more evolved (neotonic or child-like) female physique. The ironic exception is in mid-ovulation, when they prefer the strong features of a fit high testosterone male.

The monthly mood swings experienced by many women may serve an evolutionary purpose, researchers say, by helping to get them pregnant. The brains of 15 women were scanned at different stages of menstruation as they played a game with hypothetical prizes of money at the end. During the follicular phase, both the orbitofrontal cortex and the amygdala showed higher activity both when the women were anticipating a reward and when the reward was delivered. The orbitofrontal cortex is associated with decision making, reward and emotion processing, and the amygdala mediates emotional reactions (p 364). This means the women were probably experiencing greater feelings of reward during the first half of their menstrual cycles than during the second half (Menstrual mood swings may have a use after all New Scientist 29 Jan 07).

Written texts of all ages have the same drift when it comes to the midriff - they consistently describe women's thin waists as attractive. The conclusion comes from an analysis of British, Indian and Chinese texts dating as far back as the first century AD. According to the researchers, the finding supports the idea that we are hardwired to prefer slender waists, which are linked to good health and fertility (The hourglass figure is truly timeless New Scientist 10 Jan 07).

Large-breasted, narrow-waisted women have the highest reproductive potential, according to a new study, suggesting western men's penchant for women with an hourglass shape may have some biological justification. Women with a relatively low waist-to-hip ratio and large breasts had about 30 per cent higher levels of the female reproductive hormone estradiol than women with other combinations of body shapes. If there are 30 per cent higher levels, it means they are roughly three times more likely to get pregnant (Barbie-shaped women more fertile 5 May 04).

Women take greater care over their appearance when they are at peak levels of fertility. A study working with a group of 30 women aged 18 to 37, took two full-body photographs of each woman, one close to ovulation when the woman was highly fertile, and one at a point of low fertility in the menstrual cycle. Volunteers were then invited to decide which of the two photos showed the woman trying to look more attractive. They chose the woman in her "high fertility" photo some 59.5 per cent of the time, more often than would be expected by chance (Hormones and Behavior, vol 51, p 40).

They say opposites attract and a couple's differences may be key to lasting happiness, according to a new genetic study of people in relationships. The study revealed that as MHC (p 355) genetic similarities increased, it was the women who were the most dramatically affected. They were less sexually responsive to their partners, more likely to have affairs, and more attracted to other males, particularly during fertile days of their menstrual cycles, Garver-Apgar says. In relationships where MHC genetic differences were significant, these potentially relationship-splitting behaviours were either absent or greatly reduced. The fraction of MHC genes shared directly correlated to the woman's number of adulterous partners ? if the man and woman had 50% of the MHC genes in common, the women had a 50% chance of cheating with another man, on average. Men did not seem to be affected by genetics at all (Don't pair up with matching genes New Scientist 5 Jan 07).


As noted, Smuts (R651) has suggested that females may have by evolutionary reliance on male resources, inadvertently promoted patriarchal control of the female. In patriarchally dominant societies women who give birth to more male offspring may have a better chance of reproducing their genes through high-born sons who have greater reproductive opportunities. Sex ratios in highly fed animals can reach 1.4 males to each female. Sexual bias in animals may be partly a result of a process of selective abortion, even sometimes of whole high-female litters. However, it turned out to be more the mothers rank in the social group which influenced the sex of their offspring. Valerie Grant discovered that mothers who subsequently had daughters rated 1.35 on a psychological dominance scale, but those who later had sons rated 2.26 - a highly significant difference, possibly mediated by testosterone levels. In studies of some feudal societies Laura Betzig and Sarah Hrdy have noted bias towards more males among elite class groups, while the peasantry have a compensating slight bias towards more daughters. This is reflected in patterns of marrying up in the Indian dowry (p 288). The requirement for a 50:50 ratio of sons and daughters stemming from the collectively equal reproductive potential of each sex as a whole will lead to such compensation. Since the male inherits his rank, the female has a chance to marry up, but because she moves, she cannot carry her rank and family connections, with implications about the dowry in its varying forms (Ridley R577). There are also differential effects on a mothers life-span, with sons reducing life-span by 34
weeks, possibly because of testosterone immune reduction and the impact of a larger baby, and daughters extending it by 23 weeks. This is consistent with boys being favoured when mothers have better resources (Science 296, 1085).

The discovery of carvings on a snake-shaped rock along with 70,000-year-old spearheads nearby has dramatically pushed back the earliest evidence for ritual behavior, or what could be called religion. The finding comes from a cave in the Tsepong Hills of Botswana, a mecca of sorts for the local San people, who call it the Mountain of the Gods. The 6m rock bears a striking resemblance to a snake, including a mouthlike gash at the end. Hundreds of small notches covered the rock. Entrants to the cave apparently made these markings to enhance the snake illusion by creating the impression of scales and movement. Snakes feature prominently in the traditions and the mythology of the San, sometimes called the Bushmen (Scientific American 1 Dec 2006).

A 2004 study by the US National Bureau of Economic Research, based on data from 86,436 births established that 51.5% of babies born to couples living together at the time of conception were boys, compared to 49.9% among parents who were not. Studying brothers and sisters, the study found that couples who were living together before conception were 14% more likely to have a male child than when they were not. There are reports dating back to the 19th Century of a lower percentage of boys being born to women who were not married. Studies in modern Kenya have found a similar trait among polygynously married women. Male embryos are less robust than their female counterparts, and so require a greater degree of nurturing through pregnancy if they are to survive to full term. It may be that a woman who is in a stable relationship may be in a better position to provide this care. Karen Norberg (R504) notes “There are several possible mechanisms that could explain the effect. Factors operating at conception could include the mother’s or father’s hormone status, or the timing or frequency of intercourse; factors operating later in pregnancy could result in sex biases in risk of miscarriage.” The natural bias of the sex ratio of about 106 boys to 100 girls may compensate for sex-linked diseases such as muscular dystrophy, which affect males through their single X-chromosome.

Sarah Johns (R341) asked 609 first-time mothers, who had already given birth, to guess when they thought they would die. By subtracting the mother’s age, she then calculated the number of years each woman thought she had left to live. As the number of perceived years left rose, so too did the chance that they had had a son. Every extra year on the clock increased the odds of producing a male by 1%. The finding backs up a 30-year-old hypothesis that suggests women can bias the sex of their unborn babies, to enhance the chances of their genes being passed on to future generations. Boys need more looking after than girls, the theory says. So when food is scarce and resources are low, females preferentially give birth to girls because they are more likely to live through the hard times. But boys are able to produce more offspring, so when resources are plentiful, mothers should be more likely to give birth to boys, to maximize the number of potential grandchildren. The research accords with other human and animal studies. Mhairi Gibson showed that rural Ethiopian women with low levels of nutrition are more likely to give birth to girls. As we have noted, this is consistent with the Trivers-Willard hypothesis of women biasing the sex of their offspring biologically to suit their reproductive prospects (p 30). However there is no evidence that genes can cause some mothers to conceive embryos exclusively of one sex or the other. Researchers at the ART Reproductive center Beverly Hills found that couples seeking pre-implantation genetic diagnosis (p 401) to correct a run of one sex, produced embryos equally of both sexes (Independent).

If we consider the likely effects of the out of Africa hypothesis, we would expect that founding African populations not subject to active expansion and migration would have greater genetic diversity and that the genetic makeup of other world populations would come from a subset of the African diversity, consisting of those subgroups who migrated. This picture is corroborated by the evidence for one or more bottlenecks that reduced the genetic diversity of the surviving human population to 3000-10,000 breeding pairs around 70,000 years ago, which has been associated with the supervolcanic Toba eruption in Sumatra.
Language and tool-making are becoming less-likely candidates for distinguishing human evolution from the great apes. However maintaining a resourceful social and reproductive position in the face of covert sexual deceit requires astute judgement, sensitive ‘intelligence’, poetic eloquence, skilled craft, astute affection and all the diverse resourcefulness that language and tool-making can bring. All the trappings of culture and intellect come down ultimately to one genetic reality - reproduction - and acceptance, or affirmative choice, by the opposite sex.

Continuing reproductive asymmetry in human society is supported by the near uniformity of the human Y-chromosome in Africa. This is significant in the context of the putative origins of human diversity in Africa as evidenced by the African root of the ‘mitochondrial Eve’ - the earliest common female ancestor of modern humanity (p.103). The male need to seek as many sexual partners as possible also explains why male mammals don’t lactate and feed their young (Diamond R169). This process is enhanced by full internal fertilization and particularly uterine live birth, which breaks sexual symmetry completely at the outset. Male child-rearing occurs primarily in externally fertilizing species such as fish and amphibians, and in warm blooded nesting birds where two partners are required to ensure survival of the offspring, however it is essential for men to father their children in a world which is both culturally complex requiring all the astuteness both parents can muster to succeed and where maternal ambivalence is a necessary part of female choice given that we are a species in which the female has a higher risk and more massive investment than almost any other.

Reproductive bottleneck in Y-chromosome diversity began about 10,000 years ago and continued for several millennia (Karmin M et al. 2015. A recent bottleneck of Y chromosome diversity coincides with a global change in culture (doi:10.1101/gr.186684.114).

In 2015, research into the comparative population diversity of maternal mitochondrial DNA and the male Y-chromosome led to an astounding contrast. Around 10,000 years ago, corresponding to the birth of agriculture, the diversity of the Y-chromosome underwent a collapse across vast areas on the human-colonized planet. There is no evidence this was a result of direct biological or genetic factors as there were no differences between differing Y-clades. The conclusion is that the effect was driven by cultural changes associated with agriculture in which powerful men were able to reproductively exploit large numbers of women and transmit their reproductive success on to their male heirs, squeezing the majority of males out of the reproductive race. Estimates of this phase of extreme reproductive polygyny suggest that for every reproducing male there were 17 reproductive females effectively making harems the predominant form of sexual relationship.

A member of the research team hypothesizes that somehow, only a few men accumulated lots of wealth and power, leaving nothing for others. These men could then pass their wealth on to their sons, perpetuating this pattern of elitist reproductive success. Then, as more thousands of years passed, the numbers of men reproducing, compared to women, rose again. In more recent history, as a global average, about four or five women reproduced for every one man, still a highly polygynous picture that leads into some of the great patriarchs of history from Ghengis Khan whose Y-chromosome continues to exist in 8% of men in 16 populations spanning Asia and some 0.5% of males worldwide (Zerjal, T et al. 2003 Am. J. Hum. Genet. 72, 717-21) and Udayama who was said to keep 16,000 virgins behind flaming walls (R577).

This comes as an ironical twist since it is assumed that agriculture was an invention of women coming out of their role as gatherers in gather-hunter societies and provides a new perspective on the societies of the planter queens where female deities appear to have been worshipped at the same time as this extreme form of male reproductive elitism. The other thing that is really stunning about this effect is that it has been repeated widely across disparate world cultures, from China through the Near East to Europe and even Precolombian America.

When three populations Khoisan from Africa, Mongolian Khalks and Papua New Guinea Highlanders were examined for the differences in age between the Y-chromosome Adam and the mitochondrial Eve, the ages of all three groups had a roughly 2:1 difference in age (SAN 73.6 kya vs 176.5 kya, MNG 43.6 kya vs 134.4 kya and PNG 45.5 kya vs 81.05 kya). These results are most consistent with a higher female effective population size skewed toward an excess of females by sex-biased demographic processes. They demonstrate that overall female reproductive populations sizes throughout the last 100,000 years of human evolution have been effectively polygynous by a factor of around 2:1.

Generally the Y-chromosome Adam is only about half as many generations back, because the much greater diversity of reproductive frequency among males quickly floods the population with a few successful genotypes. The mitochondrial Eve, the mitochondrial ancestor of all humans currently alive, has been traced to Africa some 140,000 years ago, with 80% of human diversity still present in African people. The Y-chromosome Adam has been found to be much younger. Roy Baumeister (Is There Anything Good About Men? Oxford Univ Pr.) notes: "Today's human population is descended from twice as many women as men. I think this difference is the single most under-appreciated fact about gender. To get that kind of difference, you had to have something like, throughout the entire history of the human race, maybe 80% of women but only 40% of men reproduced."

When three populations Khoisan from Africa, Mongolian Khalks and Papua New Guinea Highlanders were examined for the differences in age between the Y-chromosome Adam and the mitochondrial Eve, the ages of all three groups had a roughly 2:1 difference in age (SAN 73.6 kya vs 176.5 kya, MNG 43.6 kya vs 134.4 kya and PNG 45.5 kya vs 81.05 kya). These results are most consistent with a higher female effective population size skewed toward an excess of females by sex-biased demographic processes. They demonstrate that overall female reproductive populations sizes throughout the last 100,000 years of human evolution have been effectively polygynous by a factor of around 2:1. The human mating system has often been considered to be moderately polygynous, based on both surveys of world populations and characteristics of human reproductive physiology. The practice of polygyny, in both the traditional sense and via "effective polygyny" whereby males tend to father children with more females than females do with males - a common practice in many contemporary western cultures (Low B 2000 Why Sex matters: a Darwinian look at human behavior. Princeton Univ. Pr.), would tend to increase the variance in reproductive success among males, thereby lowering their relative to females. This can have extraordinary consequences if male mating success is inherited patrilineally, as demonstrated in the above research on the Y-chromosome bottleneck (Wilder J, Mobasher Z and Hammer M 2004 Genetic Evidence for Unequal Effective Population Sizes of Human Females and Males Mol. Biol. Evol. doi:10.1093/molbev/msh214).

The Out of Africa model, although strongly supported by genetic data, has been challenged by the regional development hypothesis which itself postulates sexual exchange as the formative influence on the co-evolution of human genotypes across vast regions of the planet. The Y-chromosome in Africa is of particularly low variation, although the putative Y-chromosome ancestor has also recently been linked to Africa (p 105). Part of the problem here is that the Y chromosome is suffering genetic minimization (p 343).

Human sexuality is a complex, fluid and culturally-responsive mix of overt and covert strategies - of professed monogamy and concealed or expressed infidelity. While women, no matter the degree of repression, endeavour to exercise reproductive choice, men with the resources do so, practise polygyny, either by loving em' and leaving em', having kept women, parlor maids or, outside Christian influence, overtly polygynous marriages. Long-term partnership, serial monogamy, polygyny, sewing wild oats and covert affairs are central continuing motifs of human reproductive strategies in the complex prisoners' dilemma game of advertised monogamy to secure long term resourcing and concealed or expressed reproductive opportunity on the part of both sexes. Rather than perceiving monogamy, and fidelity to be righteous in conflict with unholy polygamy, strange affairs, amid deceit, we need to respect the subtlety and maturity of human reproductive choice as at the heart of the creative complexifying power of sexual paradox. Looking back towards our cultural emergence, the lessons if any are that imposing moral rules by force has if anything undermined a natural state of creative paradox evident in our founding tribal societies, replacing it with an often violent male dominance.

**Human Nature, Gender Roles, Sexual Plasticity and Cultural Liberation**

Anthony Giddens (R239) has made the point that modern sex is characterized by the emergence of 'plastic sexuality' (R683 266) - the detachment of sexual life from any biological or reproductive imperative (p 396). We have already examined (p 39) whether there is such a thing as human nature in the debate between the proponents of sociobiology in its various forms and those who 'espouse' the ultimate supremacy of culture. This debate has pitted an early wave of male-oriented sociobiologists with a genetically deterministic overview, against cultural feminists and defenders of the 'post-modern' sociological idea that culture takes us unilaterally beyond the confines of nature. The pendulum has again shifted with a more resourceful and flexible view of our evolutionary heritage as a set of genetic potentialities which are able to respond to changing circumstances in a dynamic society, just as the genetic basis of our brain is able to generate an organ capable of responding to all the diversity and contradictions that culture and nature bring forth.

Sigmund Freud once claimed "anatomy is destiny" (R683 7). In writing "The Prehistory of Sex" (R683) Timothy Taylor's retort is that "culture is freedom" and he has set out to refute the sociobiological thesis specifically to affirm the liberating effect culture has on sexuality. However the main emphasis of his idea of cultural freedom is the tacit acceptance of the 'sexual
rainbow' of whatever social gender role a person cares to define for themselves in the pursuit of the pleasures of love - in particular the perceived liberations of homosexuality, transvesticism and sex-reversal.

This begs the question of the how the human species will continue to survive if we choose to define sexuality purely in social terms as 'gender roles' between consenting adults and neglect the integrating factor of reproduction and its manifestations in the complementary roles of woman and man, parenthood, family life and the extension of genealogy into relatedness generally, as a fabric of society, which carries us from generation to generation. It is this sense of ongoing relatedness that has given sex its meaning in all societies, and in turn given all human societies the ultimate resources in love and kinship which have sustained each as a living people with a sense of cultural identity and life direction.

The idea that culture is free ignores both the very coercive cultural restrictions many major world cultures have placed on sexuality and gender roles in defiance of nature to our detriment, and the blinding stereotypy of many forms of modern sexual variety, from hard-core porn to the kings and queens of drag, despite the healing effect of more liberal attitudes to sexual relationship and sensual pleasure, the exploration of exotic arts of love, from the Karma Sutra to the Scented Garden, and the capacity of us to see and feel the other gender in ourselves, rather than being starkly confined to iconic masculinity or femininity.

Young people will continue fall in love innately, as they have done since time immemorial, and will do so as biological beings, regardless of the enticements, or repressions, which cultures seek to impose. The power of falling in love and the intoxication of the love quest becomes ever more a light into which the moth will fly for life itself, even when faced with punishments as dire as death by stoning for adultery for any form of transgression. This is the emotional ground swell that sociobiology seeks to uncover so that we can better understand who and what we are as sexual beings. Our evolutionary heritage is our best defence and most trustworthy resource in the face of rapid social and cultural change. We are not cultural blank slates who can define ourselves and our sexual identities ad hoc without losing our relationship with nature and life itself.

We shall now investigate the cultural phase and show that in founding human societies, rather than clear motifs of sexual domination, a state of strategic paradox occurs, reflecting both the manifest complementarity between the sexes and the division of labour and it is this strategic paradox that has led to the explosion of social complexity we associate with the emergence of culture. The key to cultural emergence is a complex form of mutual sexual selection, in which the choices made by each sex upon the other are dynamically responsive to the social environment in which they are taking place, in a way which has facilitated all the stunning differences between us and the higher apes, from the sensual beauty of the female form to the mesmerizing enchantments of good music, art, myth, resourceful technical innovation and last, but not least, the sensual arts of love. Sex HAS become manifestly social, not just a reproductive process, and capable of a great deal of cultural diversity, but it is in the continued passage of the generations and the continuing dance of reproductive sexual choice between woman and man that all the characteristics of the 'sexual rainbow' find their genetic, social and cultural meaning and acceptance. The lesson, if any, from looking at our evolutionary heritage is that cultures will survive and succeed best when they resonate with the best in human nature and express it meaningfully in the span of life as a whole. We shall see in succeeding chapters that cultures have risen and fallen by either repressing sexuality and sexual diversity with dire punishments, or indulging every form of gratification the mind can hunger for without any limit to perversity. Seeking to discard human nature altogether in a cultural glasshouse is likewise a cul-de-sac.

On to Culture out of Africa